ECOLOGICAL RESTORATION LITERATURE COMPENDIUM FOR THE FERNALD ENVIRONMENTAL MANAGEMENT PROJECT

FERNALD ENVIRONMENTAL MANAGEMENT PROJECT
FERNALD, OHIO

MARCH 2001

U.S. DEPARTMENT OF ENERGY
FERNALD AREA OFFICE

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LIST OF ACRONYMS AND ABBREVIATIONS

DOE	U.S. Department of Energy
FEMP	Fernald Environmental Management Project
NRRP	Natural Resource Restoration Plan

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1.0 INTRODUCTION

The objective of this report is to provide a compendium of current research and associated literature sources in support of conducting ecological restoration at the Fernald Environmental Management Project (FEMP). This report was a collaborative effort between Fluor Fernald, Inc., and Texas Southern University. Several university libraries were utilized to perform database searches using key words such as restoration, wetland mitigation, and success monitoring. Book sources, journal articles and internet sites were reviewed for applicability to various ecological restoration components prior to inclusion in the bibliography. Due to copyright protection laws, only a portion of the references cited are provided as attachments. It is anticipated that the literature compendium will be available in searchable database form on the FEMP website.

2.0 IMPETUS FOR ECOLOGICAL RESTORATION

In 1986, the State of Ohio filed a $206 million claim against the Department of Energy (DOE) for natural resource damages caused by former uranium production operations. The Comprehensive Environmental Response, Compensation and Liability Act requires federal and state officials to act as trustees for natural resources on behalf of the public. The Natural Resource Trustees for the Fernald Site are composed of the U.S. Department of the Interior (represented by U.S. Fish and Wildlife Services), the State of Ohio (represented by the Ohio Environmental Protection Agency) and DOE.

A draft Natural Resource Restoration Plan (NRRP) was developed to resolve DOE liability for past and future natural resource injuries. The draft NRRP is expected to be finalized this calendar year. The draft NRRP provides conceptual restoration plans to address post-remediation conditions at the Fernald Site and is predicated on the technical definition of Ecological Restoration: *The process of intentionally altering a site to produce a defined, indigenous, historic ecosystem with the goal of emulating the structure, function, diversity and dynamics of the specified ecosystem.* This plan maximizes the benefits of natural features and accommodates the post-excavated topography of deep depressions and denuded topsoil.

3.0 HABITAT TYPES

The majority of ecological restoration will consist of a combination of upland forest, riparian forest, prairie, oak savanna and wetland/open water systems.

3.1 UPLAND FOREST

The FEMP is located in a transition zone between the Oak-Hickory and Beech-Maple sections of the Eastern Deciduous Forest. In wooded areas of the site, tree species are indicative of these forest types (the northeast and southwest corners of the Former Production Area), several evergreen species have also been densely planted. Upland forest areas to be enhanced and restored will contain native plant species typical of these ecosystems such as American beech, sugar maple, tulip poplar, white ash, northern red oak and shagbark hickory.

3.2 RIPARIAN FOREST

Riparian corridors exist along the floodplain areas of Paddys Run and the Storm Sewer Outfall Ditch. These areas will be expanded through the revegetation of native plant species conducive to periodic inundation. Typical native plant species consist of eastern cottonwood, swamp white oak, American sycamore and green ash.

3.3 PRAIRIE

The prairie is a relatively recent ecosystem in central North America, having developed following the last glacial epoch approximately 12,000 to 15,000 years ago. Prairies formed in Ohio after the retreat of the Wisconsin glacier approximately 15,000 years ago resulted in warmer and drier conditions. At least 300 prairies were once present across Ohio.

Prairies are characterized by an abundance of grasses that typically grow three or more feet tall, including Big and Little Bluestem, Indian Grass, Switch Grass, Prairie Cord Grass and Side-Oats Grama. The classic definition of prairie is an open community dominated by grasses and having less than one tree per acre.

Prairies establish well on nutrient-poor soils since rich soils favor weeds over prairie species. Native prairie species have an innate ability to do well in conditions of low nitrogen, having evolved in soils

with limited amounts of this important nutrient. For these reasons, prairie is ideal for planting in disturbed areas.

3.4 OAK SAVANNA

Oak savanna represents a transition between prairie and oak-hickory forest and is one the most endangered ecosystems in the nation as only remnants exist today. Oak savannas extended from western Kentucky and southern Indiana into southwestern and central Ohio. Oak savannas consist of prairie grasses with a scattering of bur oak and white oak.

3.5 WETLANDS/OPEN WATER

Prior to the rise of agriculture in the region, much of the FEMP may have consisted of wetlands. Several acres of poorly drained soils are located on FEMP property. Approximately 16 acres of mitigated wetlands are required under Section 404 of the Clean Water Act. For these reasons, wetland mitigation will be pursued in appropriate on-property areas. Some open water areas will also be established as a result of deep excavations.

4.0 OTHER CONSIDERATIONS

4.1 MIGRATION CORRIDORS

Migration corridors usually riparian in nature are desirable to migrating species because it provides food and cover in abundance. Traditional insights from habitat fragmentation studies defend the importance of large, continuous habitat patches but not small, isolated patches. These insights are based on landscapes in which vast expanses of contiguous habitat have been fragmented by human influence. Riparian patches are important as stopover sites to migrating species regardless of their size and degree of isolation or connectivity. The restoration of even small areas of riparian patches are important and desirable.

4.2 HERBIVORY TECHNIQUES

Mammalian overbrowsing by *Odocoileus virginianus* (white-tail deer) has devastating effects on the structure and function of vegetative communities. Deer are selective browsers and as such can eat some plants out of existence in overpopulated areas along with slowing the growth or reducing the height of other plants. In areas of high browse pressure, the herb layer, shrub layer and intermediate canopy become sparse, if not eliminated, replaced by carpets of ferns, which deer avoid eating. The dominance of ferns also impedes the growth of wildflowers and tree seedlings. Scientists have documented a lack of tree regeneration in forests subjected to deer densities in excess of 20 per square mile. These forests consisted of oak in the Northeast and hemlock/white cedar in the Great Lakes region.

Deer exert a strong influence on other animals by direct competition and alteration of habitat. As shrub and lower canopy layers disappear due to browsing, so do songbirds that nest in this habitat. In autumn, deer switch to a heavy acorn diet, directly competing with other mammals and birds. High deer densities also directly impact the deer population itself, exposing them to higher rates of disease and parasites, and to a greater risk of starvation in harsh winters when their degraded habitat cannot support them. Overpopulation also provides difficulty for the doe to seek solitude as birth approaches, to arrange suitable fawning territory, leading to fawn abandonment and increased infant mortality.

Wildlife managers realize there is no single ideal density for deer. The proper density varies with the habitat and what values are considered most important for that area. Many techniques have been used to inhibit browsing such as fencing, repellents, tree shelters, and hunting. Education is the most essential

aspect of obtaining a long-term solution. It is vital to educate the general public of the serious and permanent consequences of not reducing deer numbers.

4.3 BIOENGINEERING

Bioengineering is an area of technical specialization with merges engineering concepts with biological knowledge to design solutions to erosion and land stability problems. Coir (coconut fiber) based logs and fabric are used in conjunction with woody cuttings and herbaceous plant species to stabilize embankments. Coir matting provides soil moisture retention, allowing the seeds and vegetation to germinate and root. The matting also builds a soil matrix by accumulating sands and silts during storm events. The coir material naturally degrades while the root systems are established to stabilize the soil. Proper armoring of coir material is an effective device for soil erosion during low and high flow conditions.

4.4 MONITORING

The evaluation of each restoration project will emphasize empirical evidence based upon indicators of ecological synergy (positive change). Examples of empirical indicators could include plant growth, plant species, nesting and rearing species, water retention and resiliency (photo documentation of response and recovery to stochastity). This will be determined by the goals of each restoration project. Details of measurements, methods and assessment will be determined in the monitoring component of each restoration design plan. The monitoring approach will focus on mechanisms to correct problems which could lead to failure. At the outset of restoration, evaluation and correction of deficiencies in abiotic services such as substrate stability, soil suitability, and moisture availability are initiated to ensure ecosystem vitality. Ecological restoration is subjected to natural processes and as such has inherent imperfections which require compromise. Restored ecosystems, because of their dynamic processes, are always in a state of becoming, from the seral stages to advanced stages of development.

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5.4 ENVIRONMENTAL RESTORATION SITES ON THE INTERNET

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Society of Ecological Restoration	http://ser.org
WWW Virtual Library: Environment	http://earthsystems.org/tree.html
Environmental Journals	http://www.sciencekomm.at/journals/environ.html
Center for International Earth Science Information	http://www.ciesin.org/data.html

APPENDIX A

AVAILABLE REFERENCES

What is Good Ecological Restoration?

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Abstract: *The rapid rise of ecological restoration is forcing consideration of what good restoration entails. Defining an end point for restoration is as much an ethical matter as a technical one, but scientifically trained restorationists have largely ignored the former issue. I argue that good restoration requires an expanded view that includes historical, social, cultural, political, aesthetic, and moral aspects. This expanded definition is necessary at a practical level to guide practitioners in the pursuit of excellence and at a conceptual level to prevent restoration from being swamped by technological activities and projects that veer away from ecological fidelity. Ecological fidelity is based on three principles: structural/compositional replication, functional success, and durability. These principles produce effective restoration, which is a necessary but not a sufficient condition of good restoration. An examination of characteristic problems that emanate from technological practices—reverse adaptation, an attention to product at the expense of process, and the separation of actions from consequences—leads directly to an expanded, inclusive framework for restoration. The results of an inclusive restoration process set up conditions necessary for restoration to achieve both ecological fidelity and harmonious human relationships within ecosystems.*

¿Que es una Buena Restauración Ecológica?

Resumen: *El rápido desarrollo de la restauración ecológica lleva a considerar que implica una buena restauración. La definición de una meta para la restauración es un asunto tanto ético como técnico, pero los restauradores con formación científica han ignorado este último. En este trabajo argumento que una buena restauración requiere de una amplia visión que incluye aspectos históricos, sociales, culturales, políticos, estéticos y morales. Esta definición expandida es necesaria en un nivel práctico para guiar a profesionistas en la búsqueda de la excelencia y en un nivel conceptual para prevenir que la restauración se empantane por actividades y proyectos tecnológicos que se desvían de la fidelidad ecológica. La fidelidad ecológica se basa en tres principios: replicación estructural/composicional, éxito funcional y durabilidad. Estos principios producen restauración efectiva, que es una condición necesaria, más no suficiente, para una buena restauración. Un examen de los problemas característicos que emanan de las prácticas tecnológicas--adaptación en reversa, la atención al producto a expensas del proceso y la separación de acciones de las consecuencias--conduce directamente a un marco de referencia expandido para la restauración. Ello resulta en un conjunto inclusivo de condiciones necesarias para que la restauración logre tanto la fidelidad ecológica como relaciones humanas armónicas con los ecosistemas.*

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What we require, then, is neither disparagement nor celebration of place-sense but an account of those specific conditions under which it significantly furthers what Relph calls environmental humility, an awakened place-awareness that is also mindful of its limitations and respectful that place molds us as well as vice versa.

—*Lawrence Buell,* The Environmental Imagination

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Introduction

The rapid rise of ecological restoration practice is forcing consideration of what good restoration entails. Most evaluative work has focused on technical performance criteria (e.g., Briggs et al. 1994), such as structural replication and composition. Other factors that have been introduced relate to ecological functions of direct interest to people (e.g., wetland filtration) and efficiency considerations (e.g., least investment of materials for greatest return of restored site). These factors are often construed as technical matters, but they point to wider questions about community participation in restoration, the relationship between ecological and cultural restoration and the importance of aesthetics on restored sites. These concerns broaden the scope of restoration and turn What is good ecological restoration? into a moral as well as a technical question. I propose we broaden, in theory and in practice, the way we define our work as restorationists.

What is required is a definition of good restoration that simultaneously rests on clear and necessary performance criteria and on the knowledge that the worth of restoration is adjudicated in historical, social, political, cultural, aesthetic, and moral contexts (Higgs 1994) [redacted] This advocacy, however, emanates from a minority within the larger restoration community; most practicing restorationists, especially scientifically trained restoration ecologists, have little time, though little hostility, for discussions of an expanded context. Complicated moral and cultural questions are not given fair consideration if they receive "off-the-shelf" responses. I aim, in part, to bring all committed members—restoration ecologists, conservation biologists, restoration practitioners, volunteers, corporate and government sponsors, and environmental activists—into the conversation about the direction and significance of restoration. Failure to achieve clarity on moral and cultural considerations will hinder ecological restoration's potential to generate healthy relationships between the people and the land.

Good ecological restoration entails negotiating the best possible outcome for a specific site based on ecological knowledge and the diverse perspectives of interested stakeholders; to this end it is as much process as product oriented. The definition of good restoration will vary from site to site, but will always be rooted by ecological fidelity: the combination of structural replication, functional success, and durability. To consider only ecological fidelity, as is often the case currently, results in a product-oriented, technical definition of good restoration. Imbedded in a process-oriented view is an environmental humility that simultaneously demands rigor in searching out the best evidence on which to base our actions and an awareness that no matter how hard we try there is always something else to learn. In negotiating goals for a particular restoration, the assumptions that guide the practice are brought up for view and criticism. Good ecological restoration depends as much on technique as on arriving at sensible and defensible tentative answers to tough questions, such as, To what era should a site be restored? How much can be spent on achieving ecological fidelity? Is it better to have many adequate restorations, or a few good ones? Is restoration, in the sense of returning to some prior state, what we want, or are we better off with a model of regeneration? In adopting an expanded conception of restoration we are pressed to address these questions head on. Restoration practices that hold firm to ecological fidelity and embrace social and cultural goals are much more likely to prosper and endure. Conceiving and deliberating restoration, not just enacting it is eminently practical.

The formation of meaning about restorations thus emanates from our experience of the places we work and the interpretations of our culture that set the larger context. Aldo Leopold provides perhaps the clearest example. We remember his successful Sauk County, Wisconsin, restorations, the subject of his famous *Almanac*, and his vigorous championing of the University of Wisconsin–Madison Arboretum restorations, what most regard as some of the earliest intentional, ecologically based restoration in North America. His reputation is strongly supported through his lyric formulation of a land ethic that endures as the most significant and accessible testament to environmental ethics in North America.

This combination of experience and interpretation is what Buell (1995) calls "place awareness." He proposes that our environmental imaginations are shaped and constrained by this interplay. To attend only to experience foreclosures the contexts of our activity just as much as single-minded attention to interpretation ends up cheating the subject. This dialectic presents a clear view of how restoration is shaped in a wider context. For ecological restoration to manifest the qualities of environmental humility, we must become aware that our actions are guided as much by the various cultural environments that make technical achievements sensible as they are by the technical achievements alone. This former point is easily overlooked. Shepard (1995:22) suggests that

> In the past half century we have invented alternative worlds that give physical expression to the denial of disaster. Following the lead and iconography of *The National Geographic* magazine with its bluebird landscapes, and then the architecture of Disneyland happiness, a thousand Old Waterfronts, Frontier Towns, Victorian Streets, Nineteenth-Century Mining Communities, Ethnic Villages, and Wildlife Parks have appeared. One now travels not only in space while sitting still but "back" to a time that never was. As fast as the relics of the past, whether old-growth forests or downtown Santa Fe, are demolished they are reincarnated in idealized form.

What counts as natural is shifting ground in the wake of technological transformations. Borgmann (1995) traces this to a cultural shift in preference for the "hyperreal" over the real. In 20 years, perhaps less, good restoration will be judged according to different, predominant cultural attitudes. People are moving away from direct ecological experience to mediated ones: television, Nintendo, virtual realities. These indoor activities are shaped by a culture of consumption and techno-

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[illegible] the year 2015 [illegible] ing which [illegible] to our [illegible] the [illegible] of the ecosystem through [illegible] and imagination. This [illegible] in inversion of what conservation biologists, ecologists, and restorationists have been striving for. It is not a technological nature we are after; rather it is a nature, or natures, that is a counterpoise to technology.

To avoid this specter those concerned with restoration must address an expanded context in both practice and theory. I argue this in five stages. First, I review various definitions of restoration with regard to context. Second, I highlight the significance of restoration as a cultural movement by making a distinction between restoration and restorationism. Third, I present a traditional and general model of technical performance in restoration as an indication of good restoration is presently understood. This measure of technical performance forms a necessary, but insufficient, base for assessing restoration. Fourth, I add a wider context to the definition of good restoration, layer by tentative layer, until the outlines of a more complicated model can be formed. I conclude by proposing a process-oriented view of restoration practice as a way of arriving situationally at good restoration. This avoids the strong and counterproductive desire to apply to problems moral templates that will only worsen the situation.

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Defining Ecological Restoration

One would expect that a practice receiving so much attention and having so many adherents over the past decade would be clearly defined. Such is not the case. The Society for Ecological Restoration has wrestled with an official definition since the society's inception. Their original definition, adopted in 1990, was the longest lived and the most controversial: "Ecological restoration is the process of intentionally altering a site to establish a defined, indigenous, historic ecosystem. The goal of this process is to emulate the structure, function, diversity, and dynamics of the specified ecosystem" (Society for Ecological Restoration 1990). This definition, and similar ones proposed in its wake, indicate a lack of agreement on the most basic issues of what restoration is and what restorationists are attempting to accomplish. For example, some argue that historic standards should not be taken too literally, that a fixation on accuracy in this regard does not address why one time-slice is preferable to another. Others suggest historic standards are impractical in regions where ecological evidence of past conditions is mostly erased. The use of the word indigenous masks the extensive and long-running engagements that First Nations peoples have had with most of the ecosystems Euro-Americans tend to [illegible] once been pristine. European delegates to the society's conferences have puzzled over what indigenous meant on their own continent where the landscape has been transformed by peoples who trace their practices back more than a millennium.

The most recent official definition, put forth by the Society for Ecological Restoration (1995), is "Ecological restoration is the process of renewing and maintaining ecosystem health." The generality in this version is a manifestation of the underlying conceptual complications in arriving at an effective way of describing restoration. It is too general to be of much use in describing the basic elements of restoration practice. Some members of the society have commented rather cynically [illegible] debates over an appropriate definition are merely semantic squabbles and that no genuine contribution has been made to advance the practice of restoration. This view ignores the power of language in shaping belief. It also passes over crucial differences in the way restoration is perceived. An agreeable definition forms the base of the larger project of deciding what constitutes good restoration.

Of course, the Society for Ecological Restoration holds no monopoly on definitions. A brief review of alternate definitions illustrates the range of opinion, and more centrally for my argument, the breadth of the context surrounding restoration practice. One of the most widely cited definitions was issued in a report from the U.S. National Research Council (1992):

> . . . *restoration* is defined as the return of an ecosystem to a close approximation of its condition prior to disturbance. In restoration, ecological damage to the resource is repaired. Both the structure and the functions of the ecosystem are recreated. Merely recreating the form without the functions, or the functions in an artificial configuration bearing little resemblance to a natural resource, does not constitute restoration. The goal is to emulate a natural, functioning, self-regulating system that is integrated with the ecological landscape in which it occurs. Often, natural resource restoration requires one of the following processes: reconstruction of antecedent physical hydrologic and morphologic conditions; chemical cleanup or adjustment of the environment; and biological manipulation, including revegetation and the reintroduction of absent or currently nonviable native species (p. 18).

This definition is noteworthy for its detail and attention to the balance of functional repair and structural accuracy. However, it provides no indication of a wider cultural context for restoration practice. Bradshaw's (1980) earlier definition is similar: ". . . restoration is used as a blanket term to describe all those activities which seek to upgrade damaged land or to [illegible] and that has been destroyed and to bring it back into beneficial use, in a form in which the biological potential is restored." Definitions that fit this general theme of technical proficiency abound in the literature.

As far back as 1975 Cairns et al. distinguished between perception and scientific knowledge:

> The characteristics of restored ecosystems are bound by two general constraints, the publicly perceived restoration and the scientifically documented restoration. For example, recovery may be defined as restoration to usefulness as perceived by the "users" of the resource. This is significantly different than restoration to either the original structure or the original function (or both) as rigorously determined by scientific methodology (p. 522).

Here, the context set by public perception is plainly less important than that which is "rigorously determined by scientific methodology." How should perception and rigor be balanced? Cairns (1995), a long-time champion of restoration and chair of the National Research Council committee that produced the 1992 definition, answers this question more refinedly 20 years later with his proposal for "ecosocietal restoration:"

> Because of its interdisciplinary nature, ecological restoration must involve ecosocietal restoration. This is the process of reexamining human society's relationship with natural systems so that repair and destruction can be balanced and, perhaps, restoration practices ultimately exceed destructive practices. Human society's practices are the best indication of its ethos or set of guiding beliefs. Ecological restoration is a positive statement of cooperation with natural systems (p. 9).

The connection between restoration and humanity runs to the core of many debates over how to define restoration. Cairns' model of ecosocietal restoration forces a recognition that restoration practices manifest social values. However, the question of balance between perception and science remains tilted toward science:

> Not only have nonscientists in a wide variety of fields and places undertaken ecological restoration projects, but the field requires the input and cooperation of society to be successful. For example, if done on any significant scale, projects require approval of society or its representatives, significant funding, a long-term commitment to goals, and significant allocation of human, economic, and biological resources. Therefore, communication among disciplines and between scientists, engineers, and the general public and its decision makers is crucial. Also crucial is that all participants, including the general public, have adequate environmental literacy (Cairns 1995) (p. 9).

What Cairns advocates is a recognition of mutual interests on the part of restoration scientists/practitioners and the public. This is an important move, but it does not go so far as to suggest that social practices are an implicit part of restoration. Janzen's (1988) proposal for ecological and biocultural restoration in tropical ecosystems perpetuates a separation between the natural and the human; however, it acknowledges a more significant symbiosis than the economic sustainability of agroecosystems:

> Human culture evolved in mutualism and conflict with the natural world. The natural world is by far the most diverse and evocative intellectual stimulation known to humans. Tropical humans are experiencing nearly total loss of this integral part of their mental lives. It is as though they are losing their color vision and most of their hearing. Ten thousand acres of rice is one of the dullest habitats on earth (p. 244).

Rogers-Martinez (1992) pushes the integration of the human and natural one step further in his description of the Sinkyone Intertribal Park project in northern California. The region had been inhabited for millennia by aboriginal peoples who coevolved as part of the ecosystems. The results of Euro-American colonialism were devastating for both ecosystems and the human inhabitants. The challenge in restoring this region is ensuring ecological health and sustainable economic activities (e.g., low impact logging) and renewing cultural practices. If successful, the project will result in a reinhabitation of the landscape, including cultural and economic practices that run counter to the intuitions of many restorationists. The Sinkyone project offers a model for restoration at a larger scale, one that internalizes cultural, political, economic, aesthetic, historical, and ethical practices once thought of as external to and at odds with the main work of ecological restoration.

Jordan et al. (1987) offer this challenge to restorationists: "What sort of relationship with nature does restoration signify and encourage?" This apparently philosophical question compels restorationists to ascertain in clear terms an appropriate cultural context for restoration. I have described a range of definitions extending from the purely technical to "ecocultural." The current, official definition of the Society for Ecological Restoration has backed away from mention of cultural issues by couching the meaning of restoration in terms of the slippery phrase "ecosystem health" (which, of course, could include human presence and livelihood). What I propose is closer to the model advanced by Rogers-Martinez than any of the definitions that pay homage exclusively to ecological (i.e., nonhuman) fitness. A concept of good restoration must incorporate at the outset a wider context. Hence, such an account of restoration must push beyond recognition of a context (e.g., in the case of Cairns) to full acknowledgment of context. This expanded concept still allows a central place for scientific rigor.

There are those who, having read this account of definitions, must still wonder whether the debate over an appropriate definition of restoration has important consequences for what counts as restoration practice. One clear function of definitions is demarcating what is included and what is excluded. For example, would natural landscaping (e.g., the Robert Starbird Dorney Ecology Garden at the University of Waterloo), agroecological projects (e.g., the Land Institute's perennial polyculture projects), cultural-ecological restorations (e.g., the Applegate Partnership in Oregon), and thematic ecological constructions (e.g., the Biodome in Montreal) fit within the current Society for Ecological Restoration definition? A narrow definition risks marginalizing restoration as too expensive and exacting within broader ecological management practices. With a definition too wide, the practice of restoration becomes confused with a host of potentially disturbing initiatives (e.g., Disney's Wilderness Lodge).

focus, the challenge is to find an agreeable definition that maintains both ecological realities and an awareness of culturally contingent meanings (Hayles 1995).

Having made a strong pitch for the importance of definition, it is also easy to miss the larger cultural significance of ecological restoration by paying too much attention to what the definitions, official or otherwise, refer to. Definitions tend to force sharp boundaries around sites: either a specific project is or is not a restoration. It is easy to miss the more subtle patterns that define the quality and position of the boundaries. Ecological restoration has significance that runs far beyond the limited experiments and hesitant trials of the past few decades that most associate with prairie burnings, Aldo Leopold, wetland restoration, and community volunteer stream cleanups. These activities are important, but they inspire no more than polite smiles from hard-headed industrialists and global environmental negotiators concerned with massive bottom lines and stratospheric holes. To such people ecological restoration appears a fair and benign, Western middle class, pastoral practice, the kind of activity that harms no one and fills in the gaps among the really big problems. This attitude misreads the potency and cultural place of restoration in the contemporary era, as well as conflating size with abundance. There are, of course, a few restoration "mega-projects," such as the Kissimmee River. The Wildlands Project (Johns 1994, 1995) and the Buffalo Commons Initiative are promising, large-scale proposals. That such large projects are emerging is testimony to the force of restoration as a practice. However, to understand adequately the trajectory, importance, and worth of ecological restoration requires recognition of an expanded context.

Scope and Significance of Ecological Restoration

Perhaps the most transparent view of the larger cultural significance of restoration comes through the notion of redemption. Restoration offers a redemptive opportunity. We heal ourselves culturally, and perhaps spiritually, by healing nature. (To carry the biblical image further, in redemption there is also the possibility of absolution, which provides a strong incentive for action by those racked with guilt over environmental degradation.) Thus, restoration taps potent cultural values that may well accelerate both participation and commitment to its practice in the medium term (10 years).

Redemption, of course, is only one aspect driving the rapid rise of restoration practice. Closely connected is the "win-win" attitude that has swept public and corporate life. Traditional conservation and preservation techniques were, and are, perceived as denying certain groups (e.g., industrial loggers) their lifestyle in order to protect an ecosystem. With restoration degraded lands are returned to a former or ecologically diverse character or a new value is created (Light & Higgs 1996). This has not escaped the notice of environmental groups, government agencies, and corporations. Restoration is finding an especially comfortable home in corporate boardrooms; for example, an act of restoration in sites around corporate offices is perceived by all as a sound investment.

Not all cultural values are going to support a worthy idea of restoration. Redemption is for many, to be sure, an unusual and troubling way of justifying restoration. Religious images aside, redemption implies that human action can compensate for a prior human misdeed, a view that builds in complicated assumptions about the source of value in nature, the capacity to solve long-standing problems of human intervention with an effectively technical solution (restoration as "technofix"), and beliefs about the ascendancy of contemporary values and practices (i.e., the myth of progress). Similarly, Frederick Turner's thesis that restoration is of one piece with a larger cultural tradition of transvaluing shame into beauty (Turner 1992) has been criticized for universalizing heterodox phenomena (Meekison 1995). Perry (1994) has criticized the "corporatization" of restoration and questioned indirectly the legitimacy of win-win strategies: Who really stands to gain from restoration? We are caught also in a vortex of change about one of the most basic questions: What counts as proper representation of nature? Older images of bucolic country woodlots and mountain vistas are giving way to the cultural productions of roadside rest areas, MTV backgrounds, the "natural" text of video games, "imagineering" at Disney World, and a host of televised images of nature that bear faint resemblance to more deeply rooted cultural ideas about nature (Evernden 1992; Borgmann 1995). These are the kinds of transformations that literary theorists and philosophers speak of as postmodern. The world we are entering is only partly comprehensible in terms of antecedents.

Together this partial list of cultural values and ideas expands the conception of restoration from practice to "mode." The idea of a restorative mode is borrowed from Leo Marx's work on pastoralism, especially his recent speculations on its future. Marx's (1992:212) work is significant for restorationists in that he defines and describes a characteristic American mediation between culture and nature. Pastoralism is an ancient concept the essence of which "is a sophisticated vision of the simple life led by a shepherd (or surrogate) figure, one who mediates between the imperatives of nature and culture, between the dangers and deprivations of the undeveloped environment (wild nature) and the excessive constraints of civilization." By emphasizing its constitution as a mode instead of, say, a practice, is to underscore the mentality or general principle of pastoralism.

Restoration may be divided similarly between the manifold practices of restoration and restorationism. The latter is a mode referring to a characteristic way of thinking about the relationship between nature and culture and signals perhaps a devolution of these two traditionally opposite representations. Restorationism directs attention to the increasing habit of repairing damage or despoliation. It includes the cultural issues such as redemption and points directly to long-standing traditions of architectural and artifactual restoration. The debates over what counts as good restoration in nonecological domains are fascinating and illustrative for our purposes. They prefigure the kind of issues we might expect to come our way. For example, is it better in the case of the Old State House restoration in Boston to return it to 18th century provincial condition or to reflect the sequential changes made under different ideological and historical conditions (the answer, in 1991, was the latter)? With ecosystems, should we to return to some notion of originality or reflect a "storied" past? The technologies of representation have also become more sophisticated as in the case of Disney's Wilderness Lodge. In Florida Disney has managed the reproduction of an early 20th century national park lodge complete with redwoods and geyser, demonstrating the outer limits of what we might expect ecological restoration to represent (Cypher 1995). The apex of restorationism in one sense is found in the versatile and endlessly plastic technology of virtual reality in which the participant can select to restore whatever is desired in whatever setting.

Taken as a mode, then, restoration becomes a way of understanding "nature" that is connected to a diverse set of practices and institutions. The crucial question is, How is it that the restorative mode can be shaped to honor our relations with ecosystems? In other words, how can restoration as a practice be shaped and directed such that it manifests both high human virtue and ecological responsibility? These are, of course, enormous questions resistant to singular responses. However, the first and most important step to be taken is understanding what is meant by good ecological restoration. In the next section, I provide a straightforward and traditional characterization of effective or technical restoration. There are three main features of life in an advanced technological setting that confound the task of arriving at an appropriate definition. First, there is a tendency to invert means and ends to produce reverse adaptation. Second, there is an overemphasis on product at the expense of process. And, third, the distance between action and consequence grows beyond the easy range of responsible action. Together, these three challenges to the notion of effective restoration compel us to search for an expanded definition.

Effective and Efficient Restoration

How are most current restoration projects adjudicated? It is not difficult to arrive at the answer to this question especially if the various definitions cited above reflect accurately a general view of what restoration is. The goal of restoration is to reproduce by whatever means available a predetermined historic or indigenous ecosystem. This goal inscribes the concept of fidelity—that is, a quest to come as close as possible to restoring what once existed on a specific site. A completely faithful restoration, presumably, is one that exactly replicates the ecosystem. Hypothetically speaking, we could devise a test whereby ecologists were asked to view the so-called original ecosystem alongside the restored version. If no distinction could be made between them, this would be a perfect restoration. There are several difficulties with this asymptotic definition of restoration, not the least of which is the idea of nature as a fixed, determinable entity. What vests us with the authority to make claims about the kind of ecosystem to be restored, especially in cases where it is much easier to make the argument that the restored system is satisfying human interests at least as much as putative "ecosystem interests"?

Ecological fidelity is the avowed goal of restoration, and within it can be discerned three principles: structural/compositional replication, functional success, and durability. Structural/compositional replication most closely manifests the goal of fidelity. A restored ecosystem must strongly resemble the structure and composition of the so-called natural ecosystem. For example, a tallgrass prairie must have close to the expected diversity of floral and faunal species expected, not merely a few easily identifiable or charismatic species. Accordingly, the simple act of a controlled burn over a long-existing pasture, or the spread of seeds in tilled soil, is not likely to produce a faithful prairie in return. Weeding, selective plantings, judicious application of herbicides, and thinning are activities usually necessary to realize anything close to compositional and structural replication. Time is an important element as well. Replication may take as little as a few years in the case of certain kinds of wetlands and as much as many decades for forested ecosystems.

Functional success in inextricably tied to compositional and structural replication; neither one is possible over time without the other. The ecosystem must align ecologically with the system it is designed to reproduce. Biogeochemical processes must operate normally according to the expectations of the specific ecosystem (e.g., flushing rates, ion exchanges, decomposition). Functional success usually depends on management. A prairie cannot be properly sustained if fires are suppressed. Also, some ecosystems depend on human practices—for example, cultural landscapes that have long involved humans as part of the ecological functioning.

The durability of restored ecosystems is an issue of growing importance in the community of restorationists. Evidence is mounting that initial optimism about success rates of certain projects is undeserved. Following their installation a higher than expected number of

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[illegible] a significant period of time [illegible] being defined relative to the type of ecosystem. This creates difficulties for regulatory institutions beyond that which they are typically equipped to handle: striking a balance between longevity and expedience when setting performance criteria.

The extent to which any given restoration project achieves the goal of fidelity I call *effectiveness*. As restoration project, then, is successful in direct relation to how effective it has been in reaching the broad goal of fidelity relative to other similar restorations. Effectiveness is a convenient term because it permits comparison with another layer, or mode, of defining good restoration: *efficiency*. An efficient restoration is an effective restoration accomplished in the least amount of time with the least input of labor, resources, and materials. In identifying efficiency we shift away from strictly technical criteria in defining good restoration. Efficiency introduces a different value system. Instead of valuing the restoration against some predetermined view of what counts as nature, presumably an ecocentric perspective, an anthropocentric scheme is layered on top.

Efficiency matters for several reasons. In a competitive market of ecological restoration, which in some cases is beginning to form in the wake of American policies such as "no net loss," efficiency provides a performance edge for the restorationist. A doctrine of efficiency runs deep in American culture suggesting that in the competition between two activities heading for the same end, the more efficient one is more valuable. Beyond interproject competition, efficiency is defensible because it frees up more resources, materials, and personnel for restoration. Thus, if we want restoration to flourish, we ought to want efficient restoration.

Several distinctive problems arise with restorations measured only against effectiveness and efficiency, and such problems are characteristic of technological practices. The first problem is *reverse adaptation*, a condition that derives from an inversion of the traditional relationship between means and ends. Langdon Winner (1977:229) defines it as "the adjustment of human ends to match the character of the available means." Reverse adaptation is common in advanced technological settings where the sophistication of technique alluringly distracts the practitioner from normal goals. It is evident, for example, in the introduction of microcomputer word processors when writing habits changed in response to the easy movement of blocks of text. The traditional goal of clear writing is subordinated by many to the authority of precise word counts, graphical neatness, and grammar checkers. This is mild and relatively inconsequential. It is striking how much attention at restoration conferences and workshops is given to certain kinds of technological means at the [illegible] of clear thinking about the proper goals of restoration. In the absence of clear goals beyond effectiveness, reverse adaptation is a genuine problem for restoration. It produces restorations that match the characteristic patterns of the techniques rather than goals such as fidelity or environmental humility. This is not to diminish the importance of technical improvements in restoration, so long as these refinements are set in proper relation to goals.

The second problem, this one primarily aimed at the doctrine of efficiency, is the enlargement of product at the expense of process. Ecosystems are dynamic complicated living systems and notoriously difficult to predict and regulate effectively. The process of bringing an ecosystem back to health is often time-consuming. Our patience is sorely tried in a consumer society where final products of any kind matter more than the background conditions of production necessary to bring them about. If it were otherwise, we would be much more concerned abut sources of production, unfair labor practices, and environmental devastation of so-called third world countries. The commodity, whether in the form of Twinkies or a salt marsh, is what makes most sense to us in the late twentieth century. The commodification of ecosystems is likely with the advent of mitigation practices, ecological theme parks, and corporate restorations. This trend will focus attention on efficiency of production of restored ecosystems because our interests will lie with the conditions necessary to bring them about.

The third problem, the separation of action from consequence, is a crucial barometer of morality in a technological culture. In effect, the more complicated the infrastructure, the greater the distance between the act of consumption and production (Jonas 1984). Nowhere is this clearer than in the total "costing" techniques that have been devised over the past decade to account for social and environmental costs (formerly "externalities") of production. This separation of action and consequence may well become apparent as restoration practice becomes more professionalized. The professionalization of restoration, in the form of specialized techniques, growing consultancies, competitive strategies, bylaws, and certification, could displace significantly the community-based, largely volunteer projects that have been the inspiration and motive force in restoration over the past two decades (others are confident that professionals and amateurs will happily coexist). If effectiveness and efficiency are the main guides in determining the worth of restoration, then it matters little how restorations are brought about, as exemplified by "reverse adaptation" and the distinction between product and process, so long as they are brought about. The question of why restore becomes increasingly subject to the movements of institutions and technical judgments. In the absence of an expanded set of criteria for evaluating restoration, the continual separation of action from consequence in technological culture will act on restoration in such a way as to suppress local, heterogeneous, adaptive practices.

Expanding the Scope of Restoration

In searching for an appropriate way of defining good restoration, we should not toss away effectiveness and efficiency. In fact, effectiveness at the very least combines factors that are necessary for any restoration, good or otherwise: fidelity to structure, function, and durability. Efficiency is important inasmuch as these core factors are identified. However, the three technological problems—reverse adaptation, the confusion of product and process, and the separation of action and consequence—press us to consider other issues. Expanding the scope of restoration ecology means reaching out to these other factors.

A few, pointed conceptual questions move us quickly to an expanded realm:

- To what state should we restore (e.g., pre-European)?
- What or who is restoration for (anthropocentric or biocentric motives)?
- How important is participation in restoration practice?
- How much management is permitted on restored sites?
- How important are cultural practices (e.g., agriculture, burning) to restoration?
- Who wins and who doesn't in most restoration projects?
- How seriously should aesthetic considerations be taken in the design of a restoration project?
- Is a technically competent (i.e., effective) restoration accomplished through forced labor, or other coercive means, good restoration?

These questions challenge existing practice, forcing a reconsideration of the wider context of contemporary restoration. These are not epiphenomenal concerns, but vital to the successful development of restoration in the long term. No exhaustive list of categories is planned because categories are best taken cautiously. In the same way that not all ecologists support a separation of structure and function as categories, many social scientists and humanists reject, for example, a strict separation of social and cultural, or deny that one can be subsumed by the other. The issues described above can be arrayed conveniently under the categories of historical, cultural, social, political, aesthetic and moral, although it should be clear that each category will require much greater elaboration in future work.

Historical

There are two senses in which history is an important factor in assessing restoration. First, historical changes in understanding nature, [illegible] wilderness, and similar vocables point to a new understanding of the subject of restoration as something partly constructed by human values and attitudes. The idea of wilderness, for example, is described by Oelschlaeger (1991) as emanating directly from European colonization; there is no such thing as an essential wilderness. We know this now through an understanding of millennia of intensive and extensive human use of ecosystems. Callicott (1995) touched off a sharp debate when he presented a similar criticism of the idea of wilderness (Noss 1995; Foreman 1995). Second (and related to the question, To what condition should ecosystems be restored?), if wilderness begs reconsideration is it necessary to focus attention on the precolonial landscape? Or must we consider conditions before the arrival of humans, which in many parts of North America would date back to before the last glaciation? By testing assumptions about what counts as nature, a number of assumptions about the end point of restoration crumble.

Cultural

At the 1994 Society for Ecological Restoration conference a number of British restorationists complained effectively that a concept such as "indigenous" or "original" ecosystem is useless for a landscape that has been intensively used by humans for hundreds of years. Restoration for them means restoration of a cultural landscape. This is a matter that has become popular in Europe and also with First Nations peoples in North America. A significant focus in restoration, accordingly, ought to be bringing back into harmony the relations between sustainable human practices and ecological functions. This does not absolve us of responsibility for restoring ecosystems that are regarded as "pristine" or those reflecting little human activity, but, from an anthropological perspective, the pervasiveness of pretechnological human activity needs to be better understood. And, ecologists miss an important constituency if the role of humans in ecosystems is ignored (McDonnell & Pickett 1993).

Social

Reading through the journal *Restoration and Management Notes*, one is struck by the number of projects that involve volunteers. The labor required in many restoration projects has tended to promote community-based projects (e.g., Steve Packard's work in Chicago; Jordan 1993; Stevens 1995). One sensible reading of contemporary restoration is that it has been largely a grassroots movement. This is beginning to change. The scale of res-

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[illegible] projects is increasing (e.g., the Kissimmee River project). Corporate restorations are becoming more popular (e.g., Red Wing Shoes headquarters) (Perry 1994). Restoration and mitigation consultancies are on the rise. These developments point to a potential decrease in participatory/community-based projects.

Political

Should we be worried about whether restorations are in any sense democratic? Is there a problem, in an admittedly fictitious case, in having a terrific restoration completed with slave labor? Light and Higgs (in press) argue that restoration is not inherently democratic but has inherent democratic potential. To keep this latter potential in reach requires careful consideration of the political significance of restoration practice. This means asking continually, Who gains and who loses? Answering this question, and related ones, often reveals issues underlying a project. For example, if a corporation is the primary beneficiary of a restoration through an enhanced corporate image, this ought to color our perception of that restoration, but not necessarily undermine the worth of the project. Or, if a restoration is proceeding solely to satisfy a regulatory requirement, as in the case of many wetland mitigation projects, then we ought to take a closer look at the politics in restoration.

Aesthetic

Wilson (1991) points out that aesthetic considerations form a major part of people's appreciation of nature. The widespread and lavishly supported practice of gardening is an illustration of the significance of beauty. Landscape architecture has risen in this century to become a vital part of the construction and reconstruction of the built environment, and landscape design is a determining factor in recreation sites, homes, commercial complexes, and parks. Both gardening and landscape design have strong commitments to formal practices, canons of aesthetic taste, and popular and professional movements. With the rise of natural landscaping in the past several decades, ecological function and structure are important to the success of a project but usually remain subordinate to aesthetic considerations. It is not surprising that ecologically minded landscape architects, whose business it is to design landscapes, have found ecological restoration an attractive alternative and moved close to the center of this new practice. Aesthetic principles are important in restoration to the extent that they enhance public acceptance of restoration. However, public acceptance and aesthetic production easily overwhelm ecological fidelity. Some argue that beauty ought to be the final goal of restoration (Turner 1992), but in any case very little attention has been given to conceptual concerns about aesthetics in the restoration literature.

Moral

The rapid rise of environmental ethics of the past 15 years has demonstrated a plurality of moral perspectives about the environment but perhaps most clearly has shown that many of our actions proceed from an anthropocentric motivation; that is, we are guided by interests distinctly human. Alternatives, such as those associated with deep ecology, suggest a bio- or ecocentric view in which the primary moral subjects are nonhuman. An ecocentric perspective would argue that restoration is good insofar as it serves to enhance the lives of ecosystems from their own perspective. This is difficult for most of us to conceptualize, and it is especially challenging to restoration practice. Is restoration motivated primarily by a desire to help organisms and ecosystems realize their own ways of being, or are we driven by a desire to absolve ourselves of guilt over past environmental transgressions? The matter is not this simple, either, for there are many more categories of ethical thought to be invoked as alternatives to this rather stark dichotomy. These ethical positions challenge deeply held assumptions.

In summary, these six categories challenge and expand the domain of effective and efficient restoration. They build on the technological challenges raised in the previous section and together create a setting for expanding the conception of restoration. Figure 1 illustrates the nested relationship of effectiveness, efficiency, and expanded measure of good restoration.

A Process-oriented View of Good Restoration

An almost natural tendency exists for those who address the evaluative question in restoration to construct a set of objective criteria for measuring the worth of restoration. This applies not only to the matters of ecological fidelity and efficiency but also the expanded factors outlined above. Although perhaps far-fetched, the Holy Grail of the technocratic restorationist would be a numerical ranking system of restoration practice that includes performance criteria for community participation, cultural significance, political rectitude, and moral stature. This is exactly what I want to avoid, knowing full well that living in a technological culture molds us tightly to this way of thinking. The issues about the conflation of process and product hold here: How can we balance what is restored and how it is accomplished? My proposal as simple.

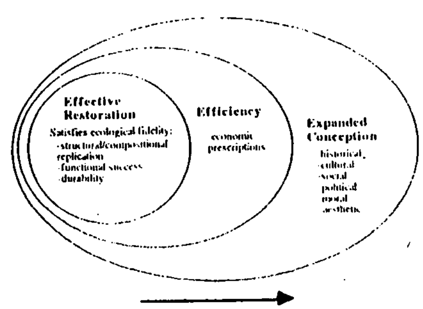

Figure 1. At the core of ecological restoration is a commitment to ecological fidelity. Successive layers of context are added to produce an expanded conception of good ecological restoration.

Develop an inclusive process for making decisions about the design, implementation, and management of restorations. By inclusive, I mean a reasonable balance of people who are long-term stakeholders in a landscape: environmentalists, restoration scientists, restoration consultants, amateur naturalists, landholders, corporations with vested interests, local governments, etc. For such groups to work together, they must be comprised of people who are committed to the restoration, not because they necessarily agree on the means or the specific end. As much as possible, people should be given ways of making the most use of their abilities. Sound ways of modeling options must be developed so that reasonable alternatives can be carefully evaluated. There are, of course, many techniques in mediation, negotiation, and participation available within and outside of environmental management, but these have been scarcely applied to restoration. This is, of course, only the briefest sketch of a process-oriented approach to restoration. Much work needs to be done on developing this further.

It is obvious how such a process embraces the expanded conception of restoration, but there is one benefit that deserves special attention. Nature and ecosystems are historically and culturally contingent ideas. There ought not be any single, fixed, correct restoration for any particular site, although the structure, composition, or function will often provide some tight guidelines. By bringing people with diverse interests together and by providing them with a voice in the conduct of restoration, the model will raise manifold assumptions for serious discussion, criticism, and negotiation. For example, in Jasper National Park, the largest of Canada's Rocky Mountain National parks, decisions about restoration may be avoided by letting "nature take its course." Some believe this is the best decision because it supposedly avoids any imposition of human value: nature runs its course. There are many complex assumptions being made in such a decision, such as the meaning of nature and the worth of human involvement, and these become buried under a patina of piety. Exposing such assumptions for scrutiny forces us to address many of the complicated, painful, mind-numbing issues that have in many cases been neglected in favor of easier decisions.

There are several risks in this process-oriented approach. Two come to mind. The first is that opening up cultural assumptions will produce restorations that are far more human than natural. Assuming for a moment that such a dichotomy is valid, I suspect the opposite reaction will prevail. Once assumptions are better identified and information is provided that matches the questions being asked, people will respond in many cases more sensitively than current practice would lead us to believe. In other words, we might expect a net gain in "naturalness." Second, in the absence of clear goals or principles that prevent human involvement in ecosystems, development will accelerate. This is a serious worry. So far, environmental protection has depended on a continuum of natural value, with remote mountain ecosystems as the arbiters of the wild end of the spectrum. Without this kind of model behind us, we may tend to produce and reproduce human intrusions and development. I see no easy way of preventing this, and certainly the force of contemporary capitalism coupled with population increases are corroding the system of protection that has been developed with such difficulty over the past century. By ignoring the political character of these landscapes, however, we are not contributing to creative solutions. As Alex Wilson (1991) suggested,

> . . . none of our relations with the natural world will change until we change the basic relations of power in the Canadian and U.S. societies. Without broad social empowerment and true democratic institutions—neither of which I believe exists in any systematic way in North America today—our connections to the natural world will continue to be characterized by greed and exploitation, the very values so rampant in our social lives (p. 16).

Restoration will become a much more prominent, well-funded practice in the next decade. For it to avoid becoming a passing fad, it must shake loose from some of its commitments (e.g., "indigenous" ecosystems) and turn self-consciously to an oppositional strategy regarding the dominant patterns of technological culture. Whether this happens, depends on the development of authentic engagements (Higgs 1991) between people and ecosystems; in other words, the development of a heightened "place awareness." Early signs of the commodification of ecological restoration are evident and suggest strongly that the best hope for answering the conceptual and practical questions of what is good ecological restoration lies in developing an effective process-oriented view of restoration.

One of the first and most effective strategies in this direction is to reconsider the very name *restoration*. It connotes a fixed, historic, and static notion of ecosystems (although this is what a few proponents, especially ecologists, want). A better alternative, perhaps, is *regeneration*, which gives open recognition to the tentative, developmental quality of sensitive human engagements with ecosystems. The dialectic between experience and

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[illegible] their activities and beliefs, it requires the counterweight of careful reflection (interpretation) in order to comprehend what we are doing through our constructive manipulations of ecosystems. I proposed that ecological restoration offers the prospect of generating healthier relationships between people and the ecosystems in which they live. Generation is a constructive process and when applied to ecosystems suggests that restorationists-as-regenerationists are thinking carefully about the future as well as the past. Regeneration involves merging what we have accomplished and practiced well, and sets this in the context of workable, creative, and faithful engagements with ecosystems.

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Contributed Papers

Assessing Risks to Biodiversity from Future Landscape Change

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Abstract: *We examined the impacts of possible future land development patterns on the biodiversity of a landscape. Our landscape data included a remote sensing derived map of the current habitat of the study area and six maps of future habitat distributions resulting from different land development scenarios. Our species data included lists of all bird, mammal, reptile, and amphibian species in the study area, their habitat associations, and area requirements for each. We estimated the area requirements using home ranges, sampled population densities, or genetic area requirements that incorporate dispersal distances. Our measures of biodiversity were species richness and habitat abundance. We calculated habitat abundance in two ways. First, we computed the total habitat area for each species in each landscape. Second, we calculated the number of habitat units for each species in each landscape by dividing the size of each habitat patch in the landscape by the area requirement and summing over all patches. Species richness was based on presence of habitat. Species became extinct in the landscape if they had no habitat area or no habitat units, respectively. We then computed ratios of habitat abundance in each future landscape to habitat abundance in the present for each species. We also computed the ratio of future to present species richness. We then calculated summary statistics across all species. Species richness changed little from present to future. There were distinctly greater risks to habitat abundance in landscapes that extrapolated from present trends or zoning patterns, however, as opposed to landscapes in which land development activities followed more constrained patterns. These results were stable when tested using Monte Carlo simulations and sensitivity tests on the area requirements. We conclude that this methodology can begin to discriminate the effects of potential changes in land development on vertebrate biodiversity.*

Evaluación de Riesgos para la Biodiversidad Debido a Cambios Futuros en el Paisaje

Resumen: *Examinamos los impactos en la biodiversidad de un paisaje debidos a posibles patrones de modificación del suelo. Nuestros datos de paisaje incluyen un mapa del área de estudio actual derivado de sensores remotos y seis mapas de distribuciones futuras del hábitat que resultan de diferentes escenarios de desarrollo del suelo. Nuestros datos de especies incluyen listas de todas las especies de aves, mamíferos, reptiles y anfibios del área de estudio, sus asociaciones de hábitat y los requerimientos de espacio para cada una de ellas. Estimamos los requerimientos de área usando rangos de hogar, densidades de poblaciones muestreadas o requerimientos genéticos de área que incorporan destancias de dispersión. Las medidas de biodiversidad fueron la riqueza de especies y la abundancia del hábitat. La abundancia del hábitat fue estimada en dos formas. Primero, estimamos el área total del hábitat para cada especie en cada paisaje. Segundo, calculamos el número de unidades de hábitat para cada especie en cada paisaje dividiendo el tamaño de cada parche de hábitat en el paisaje por el requerimiento de área y sumando para todos los parches. La riqueza de especies*

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(LARS) (Can. Spec. Publ. Fish. Aquat. Sci. No. 106, 1989), focused more on management of aquatic resources.

These symposia used a steering committee and a workshop-type format to successfully meet their objectives; we used their method. In the workshop at the Kempenfelt Centre, November 14–18, 1994, we sought to assess and synthesize the understanding of the linkages between habitat, production, and structure of aquatic and wetland communities, identify successful habitat restorations and enhancements, identify and fill important gaps in scientific knowledge, and provide recommendations for resource managers to effectively conserve, restore, and enhance aquatic habitat.

Forty-three background papers were prepared in advance of the workshop and seven discussion groups responded to challenges developed by the steering committee. This supplement includes the original research papers, case history papers, and perspectives either invited or developed at the workshop that survived peer review.

The challenge

In grappling with fundamental questions on how the environment affects animal activity, Fry (1947, p. 59) suggested that although our present understanding may be flawed, it needs to be expressed "for there is a great deal more value in having things corrected than there is in never stating them; the road to truth lies much through argument." These proceedings, particularly those papers that tried to integrate information or synthesize ideas, provide a good basis for argument. Hopefully, freshwater science, which now proceeds in an atmosphere of severe fiscal restraint, at least in Canada, can still address those uncertainties that impede successful ecosystem conservation and repair.

This supplement may provoke those who routinely promote, market, or implement habitat improvement techniques or technology with little or no evaluation of their relation to ecosystem performance. Minns et al. (1996) and Lester et al. (1996), particularly, indicate the process and rigour required to detect responses to change in a way that will benefit our ability to conserve and repair ecosystems. It is essential, in our view, to maintain an independent and continuing scientific process whereby remedial techniques are evaluated and uncertainties addressed; if society fails to support such programs, expensive and ineffective ecosystem and repair initiatives will inevitably result.

If habitat is "managed," it is axiomatic that all types of habitat needed for a species to complete its life cycle are important. These proceedings help focus on habitat features that man has affected most. The lack of initiatives that were successful in restoring or repairing aquatic ecosystems or its properties is, however, disconcerting. It may be simply that rehabilitation and enhancement efforts are too recent to yield results. Nevertheless, we suggest that society's ability to protect and rehabilitate will be least where scientific uncertainty and sampling variability are greatest.

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Underlying principles of restoration

A.D. Bradshaw

Abstract: The term restoration is used in many ways; however, it normally implies return to an original state. In ecological restoration, it should be thought of as applying to whole ecosystems. It must be remembered that options, such as rehabilitation or replacement, exist that may be more practicable than restoration. The components of restoration are the chemical and physical aspects of the habitat and the species themselves. Each of these may require specific treatment, but natural restorative processes should be used wherever possible; in fact, natural processes may be sufficient once the degrading influences have been removed. Because the process of restoration is progressive, the criteria of success are not easy to define. The most important point is that ecosystem development should be on an unrestricted upward path. From this, it follows that successful restoration is a serious test of our ecological understanding.

Résumé : Le terme restauration est utilisé dans plusieurs sens, mais il suppose normalement un retour à l'état initial. Dans le domaine de l'écologie, il faut voir la restauration comme s'appliquant à des écosystèmes complets et se souvenir que d'autres solutions, comme la rehabilitation et le remplacement, peuvent être plus réalistes. La restauration vise à la fois les aspects chimiques et physiques de l'habitat et les espèces elles-mêmes; chacun de ces volets peut exiger des mesures particulières, mais il faut autant que possible se fier aux mécanismes naturels de restauration. En fait, si on a éliminé les sources de dégradation, ces mécanismes sont souvent suffisants. Comme la restauration est un processus progressif, il peut être difficile de fixer des critères de réussite. Il faut avant tout se rappeler que l'écosystème doit se développer sans entrave dans le sens d'une amélioration. La réussite d'une telle opération met à rude épreuve notre compréhension de l'écologie. [Traduit par la Rédaction]

Introduction

There is a tendency for individual groups involved in the practical aspects of restoration to pay little attention to what others are doing, or have done. The reason is usually that they feel that their problem is special and has little connection with others, because of climate, terrain, species, or any of the many other ways one community can differ from another. Yet the strength of modern ecology is that it has been able to produce underlying principles of general application.

In restoration ecology it is clear that general principles are developing that are applicable widely, no matter whether the subject is the restoration of tundra, tropical forest, lakes, or farmland. Because the HabCARES workshop is mainly about aquatic systems and this paper is by an ecologist whose main experience is in terrestrial systems, the challenge is to show that generalizations are possible and can provide valuable guidance to restoration practice.

What is restoration?

We must be clear what is being discussed. Although words can change their meaning, it is important to examine what they have meant until recently (here using Oxford English Dictionary; Fowler and Fowler 1971). The relevant definition of *restoration* is "the act of restoring to a former state or position ... or to an unimpaired or perfect condition." To *restore* is "to bring back to the original state... or to a healthy or vigorous state." There is both the implication of returning to an original state and to a state that is perfect and healthy. This seems to be the way in which we continue to use the word on both sides of the Atlantic.

Rehabilitation is defined as "the action of restoring a thing to a previous condition or status." This appears rather similar to restoration, but there is little or no implication of perfection. Indeed in common usage, something that is rehabilitated is not expected to be in as original or healthy a state as if it had been restored.

Remediation is the act of remedying. To remedy is "to rectify, to make good." Here the emphasis is on the process rather than on the endpoint reached.

Reclamation is a term used by many practitioners, especially in Britain but also in North America. It is defined as "the making of land fit for cultivation." But to reclaim is given as "to bring back to a proper state." There is no implication of returning to an original state but rather to a useful one.

Replacement is, therefore, a possible alternative option. To replace is "to provide or procure a substitute or equivalent in place of" (although an alternative meaning is to restore).

Mitigation is a word often used when restoration is considered. It is important to note that it is nothing to do with restoration. To *mitigate* is "to appease... or to moderate the heinousness of something." So although mitigation can be an outcome of restoration it is a separate consideration.

Since the word restoration has been adopted for the title of this workshop, it will be used as the point of reference, despite its troublesome perfectionist implications (Francis et al. 1979).

To what are these words applied?

This problem must be addressed because here is where perhaps the greatest confusion lies about what we are doing. From our biological point of view we can apply it to ecosystems, habitats, communities, species, water or soil quality, or some other

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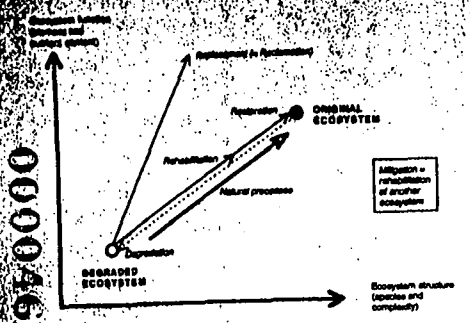
Fig. 1. The general different options in restoration ecology.



characteristic of the degraded or damaged area. All these are different, and therefore, their use has specific implications.

The word *ecosystem* covers the biological and nonbiological elements occurring together in a particular area. So it is all inclusive. However, because "system" is included, there is an emphasis on the overarching functions and interactions of these elements. So when the restoration of *ecosystems* is being referred to, the suggestion is that we are particularly interested in the restoration of the fundamental processes by which ecosystems work. This has been well argued by Cairns (1988).

It is common now to talk about *habitat* restoration; it is in the title of this workshop. Because habitat refers just to the place where organisms live, it tends to imply less than ecosystem. Its use, therefore, puts more emphasis on the restoration of place than of important ecological functions. We can also talk about restoration of *communities* or of *species*. In this case the emphasis is on just the plants and animals occurring in a particular place, or on a single species.

We also talk about restoration of *quality*. This is particularly true in discussions of soil or water restoration, perhaps because the species in these habitats are multifarious and their individual occurrences difficult to predict; therefore, the implication is different. It is the perceived attributes of what is in an area, or of a component of the environment, that are considered to be important. To what is referred depends on the particular situation; it could be either an important factor, such as biological oxygen demand or level of contaminants, or a derivative of well being such as species diversity.

Whatever we may think deserves attention, our intention should always be to focus on the restoration of functions, of processes, because without this the communities of organisms in which we are interested cannot persist. Our ultimate aim should be the restoration of the whole ecosystem, even if we sometimes emphasise some particular component or attribute (National Research Council 1992, Ch. 1).

Options in restoration

There are clearly many attributes to an ecosystem. These can usefully be simplified into two main components: structure and function. What has happened to a damaged ecosystem can then be represented graphically with these components as the two axes (Bradshaw 1987*a*) (Fig. 1). Both components will have suffered and will have to be restored. Rehabilitation, in which progress has been made but the original state not achieved, and reclamation, to something different, can be represented on the same figure.

This clarifies our options. In particular it points to the fact that restoration may not be easy. It may be possible, perhaps, to restore the functions fairly completely, but to achieve the original structure may be more difficult. This may not be so true in an aquatic ecosystem where, because of the smallness and consequent mobility of the individuals, the rate of reestablishment of populations can be rapid, but it will certainly be true in a forest ecosystem where the full age structure may be impossible to achieve in less than 500 yr. It may not be possible to achieve an original soil profile in less than 5000 yr, although the biological functions of a soil can perhaps be restored in less than 10 yr.

So in many situations, true restoration may be unrealistic. It may also be impossibly expensive. So we should realise that rehabilitation and replacement can be proper options. Both these alternatives, by offering something different, may provide an endpoint that is more valuable than what was there in the first place. Replacement is a particularly interesting option since it may allow restoration of a component, such as productivity, to a higher level than existed previously. In the heavily developed agricultural land of Britain, sand and gravel workings left to fill with water have contributed enormously to the diversity of wildlife and landscape in many areas. This is valuable reclamation; however, it is not true restoration although there may be restoration of particular attributes such as biodiversity.

It is, therefore, very important that when any work is undertaken, the different options and what they each might involve are clearly worked out and understood. Figure 1 can provide useful guidelines. The endpoint of full restoration, although it may seem ethically the most justifiable and, therefore, the most obvious to adopt, may in fact not always be the most sensible in practical or biological terms.

Components of restoration

To judge what is worthwhile attempting it is necessary to appreciate what it involves. In essence, no matter what ecosystem is being tackled, once the damaging process has been controlled, the crucial characteristic of any intervention is that it should relieve those factors that are restraining the redevelopment of the ecosystem required. Obviously this can involve many different elements, depending on the ecosystem and the degradation that has occurred.

Essentially three matters will need attention: (*i*) remodelling the physical aspects of the habitat; (*ii*) remodelling the chemical aspects, nutrients, and toxicity; and (*iii*) replacing missing species or removing undesirable exotics.

Exactly what is required will depend on what is wrong. For instance, acid land left after coal mining will require liming; raw inert materials left to be soils will require nutrients; lakes overcharged with phosphorus may require mud pumping; lost species may require reintroduction. There are now handbooks as well as papers on all these and other problems (e.g., for land,

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Coppin and Bradshaw 1982; Lyle 1987; Shaller and Sutter 1978; Williamson et al. 1982; for water, National Research Council 1992; Ryding and Rast 1989; for the Great Lakes, Francis et al. 1979). It is possible rationalize what is to be done (e.g., for terrestrial habitats, Bradshaw 1987*a*; for lakes, National Research Council 1992, Ch. 4). Attempts are now being made to put this rationale into logical decision trees (Maguire 1988). It is essential to identify the controlling factors that will not ameliorate naturally and then address these first.

Use of natural processes

These recommendations may suggest that each fault or deficiency has to be addressed if restoration is to be achieved. Yet we all know that, in the Great Lakes region, the preexisting vegetation and soils were repeatedly destroyed by the great ice sheets that covered much of North America. When these retreated, natural processes were able to build up ecosystems to their present day complexity of structure and function. The different processes, covered by the omnibus term "primary succession," have been well described recently (Miles and Walton 1993). These same processes are visibly at work in the secondary succession that follows present-day disturbances, whether in old fields, tropical forests, or other situations (Gray et al. 1987). They are processes of considerable power; they can bring about major changes in time scales as brief as decades and are particularly applicable to large ecosystems such as the Great Lakes.

With such a series of natural processes that can be harnessed to help restoration, we have to decide what part they should play in our work. It should be axiomatic that they should be used wherever possible, firstly because they cost nothing in themselves (although they may cost something to initiate); secondly, they are likely to be self sustaining because they originate from within nature (although they may need nurturing in some situations); and thirdly, they can be used on a large scale. Although it is clear that natural processes can eventually achieve full restoration, some may take a long time and need to be assisted. It is not possible to describe all the ways in which natural processes can be used, but some illustrations can be made.

Physical problems

Many degraded soils and deposited materials are compacted and have a high bulk density. Yet the changes that take place naturally on glacial moraines (Crocker and Major 1955), as well as on coal waste heaps and elsewhere, show that radical changes can be brought about by the growth of vegetation, the incorporation of organic matter, and the activities of soil fauna and flora. However, in some seriously compacted situations, natural recovery is so slow that mechanical treatment is necessary. In aquatic systems, physical treatments are widely undertaken.

Nutrient problems

One of the commonest problems of degraded terrestrial environments is lack of nutrients, particularly nitrogen. The soil nitrogen capital, normally at least 1000 kg N·ha^{-1}, can be rebuilt up by means of fertilizers, but this is expensive and involves returning many times. It is much simpler to introduce legumes, such as white clover (*Trifolium repens*), which can accumulate nitrogen at the rate of 100 kg N·ha^{-1}·yr^{-1}. However, calcium and phosphorus levels must be sufficient to maintain the growth of the clover (Roberts et al. 1982); although N-fixing species can often be chosen that do not have as special nutrient requirements as clover. By contrast, nutrients such as phosphorus cannot be conjured out the air and will remain deficient if not added.

In aquatic systems the problem is usually excess of nutrients. Once inputs into flowing systems are stopped, recovery is usually rapid. But this does not occur so readily in lakes. For lakes of limited size the removal of the nutrient-rich bottom muds may be possible. In other situations a totally different approach, using natural ecological processes that involve the manipulation of phytoplankton by manipulation of the zooplankton (Moss 1992; Hosper and Meijer 1993), can be more effective. The fact that assisting the growth of protective macrophytes or even the provision of bundles of twigs, to provide safe sites for the zooplankton, is effective, challenges our understanding of the mechanics of the freshwater ecosystem. Unfortunately, the size of the Great Lakes make both these approaches impractical; natural dispersal and loss may be the only answer.

Toxicity

This can be one of the most intractable problems, which natural processes by themselves cannot easily overcome, as witnessed by the persistent degraded and often completely bare areas contaminated by heavy metals in many places in the world (Ernst 1974). Yet restoration of the northern deciduous forests destroyed by the nickel smelters at Sudbury, Ont., illustrates both the problems and possibilities (Gunn 1995). Earlier work suggested that the combination of acidity and metal toxicity could only be answered by the use of metal-tolerant grasses. However, once the acidity is relieved by liming, the metal becomes less available and trees, which root through the surface soil into the less polluted horizons below, can be planted. Once such trees establish, the development of the ecosystem takes a new direction. Surface conditions are ameliorated sufficiently for natural recolonization to occur. In the end, elevated metal levels may remain, but a fully functional forest seems certain to develop. On a smaller scale a vigorous grassland ecosystem has been developed on lead–zinc mine tailings following an initial stimulus of sewage sludge and fertilizers (Johnson et al. 1976).

In aquatic habitats, once the toxic input has ceased, natural processes can lead to recovery even where the toxicity defies treatment. This is well demonstrated by the progressive reduction in metals in the Mersey Estuary that has occurred since inputs have been reduced over recent decades (National Rivers Authority 1995). Acid rain can be a serious problem because whole catchments are affected. To reverse the effects, liming of lakes has been carried out, but such localized treatment has usually had only short-term effects. The logical answer is to treat the source of the problem and lime the catchment rather than the lake. Work on this has so far been very promising (Howells and Dalziel 1992). It is important to note that except for liming and reintroduction of missing fish species, everything else can be left to natural processes.

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Because of the dispersal powers of many species it is easy to fall into the trap of thinking that natural processes can be relied on for all species. In terrestrial situations, if rapid establishment is required, sowing of the main plant species is always essential. It is then often presumed that other species will arrive on their own. But studies of the recolonization of chemical wastes over the last 100 yr show that several appropriate species are missing because their nearest populations are too far away (Gray et al. 1994). The herbaceous species of woodlands are notoriously poor at dispersal (Peterken 1974); therefore, it can be crucial to introduce the missing species by artificial means (Francis 1993). The comparisons made between intervention and leaving natural processes alone to achieve recovery at Mount St. Helens are particularly interesting (Franklin et al. 1988); intervention certainly leads to more rapid recovery, especially where destruction of the habitat has been most complete.

In aquatic systems the situation is different. Fish, of course, will often need transfer. But most of the important species are microscopic and easily dispersed. Natural dispersal processes are, therefore, usually effective, especially in streams and lakes where substantial transport processes exist. This may not be true, however, for new isolated water bodies. In one of the earliest and very successful attempts to create a new aquatic system for the conservation of wildfowl from a gravel pit, there was no need to introduce the wildfowl, but the water body was inoculated with aquatic plant and animal species by bringing in species-rich mud (Harrison 1974). This is now recommended practice (Andrews and Kinsman 1990). Note that it is inoculation that is suggested, not full-scale planting, since natural processes of species establishment and spread will take the developing ecosystem on to its mature state. The removal of species, usually of alien introductions such as the sea lamprey (*Petromyzon marinus*), is another problem altogether, unfortunately often impossible to rectify.

Engineering

All this leads us into the whole subject of ecological engineering (Mitsch and Jorgensen 1989) sometimes called bioengineering (Schlechtl 1980). The discipline is much wider than the restoration we are considering here, being described as the techniques of designing and operating the economy with nature (Odum 1989). But within it are many provocative examples of how ecological processes can be harnessed specifically for the purposes of restoration, particularly in civil engineering situations.

In any restoration situation it is important to become fully aware of the natural processes already occurring. This may mean detailed studies of primary succession in the damaged area or in analogous areas. The detail is important, as a mere record of species colonization may tell very little. In both aquatic and terrestrial situations it will be valuable to understand matters such as the origins of the immigrating species, the part played by safe sites for species establishment, the changes occurring in soil or water fertility and in microorganisms, and the effects of species interactions. It can be informative to study the factors that appear to be preventing succession (Gemmell 1975). There is a complementarity between academic and practically oriented ecological studies; this is discussed later.

The possibility of doing nothing

The contribution of primary succession and natural processes introduces an alternative possibility, the extreme option of actually doing nothing. This can be seen as the negation of restoration. If, however, natural processes of primary or secondary succession are powerful, they may be able to do all that is necessary. Certainly the forested fields of New England are witness to the power of old-field succession.

If restoration is used in a wide sense to include the restoration of biodiversity, then untreated areas may have an important place in the different strategies of restoration. In Britain, disused quarries are now recognised as being important additions to the countryside because, in their unrestored state, they provide havens for species that find it difficult to survive in the managed agricultural countryside (Ratcliffe 1974). Restrictions on ecosystem development can, indeed, be an advantage for some species.

Similarly, young lakes can be important. Gravel pits have allowed the development of previous threatened floras and the spread into Britain of the little ringed plover. In Indiana, strip mine pits and ponds have had an important role for wildlife, sufficient to make it important to develop methods of modifying them, but not destroying them, to increase their wildlife potential (Willard 1988).

The criteria of success

How far, then, should intervention go? Purists, whether among the ecological profession or the general public, may ask for everything to be restored completely. Even if actually impossible, to approach such perfection can be immensely difficult. It has lead to planners requiring the transfer, for restoration purposes, of mature forests, which is impracticable. It can lead to immense costs. Certain manipulations, however, such as the retention and replacement of original topsoils, may be the only way to achieve the appropriate endpoint, as in the Australian sand mining industry (Bradshaw and Chadwick 1980). Equally, the total removal of contaminated or highly eutrophic sediments may be the only way to restore the water quality and, therefore, the total ecosystems of some damaged lakes.

But if we are realistic, such major operations may be excessive or impossible in large systems such as the Great Lakes. What is important is to set off succession in the right direction and then leave it to continue itself; this may require preparatory work. Nobody thinks that there is anything wrong in planting small trees to reestablish a forest. But to achieve satisfactory growth it may be necessary to ensure that the soil is fertile or has the means to make it fertile such as by the inclusion of nitrogen-fixing species. This illustrates the importance of ensuring that the functions of the developing ecosystem are properly cared for.

But what are to be the criteria of success? Firstly, should the criteria be based on structure, and in particular the presence or absence of species, or on function, such as plant growth? There is no easy answer, since so much depends on what was the original particular value of the area, and therefore, what is seen to be critical. If the area was rich in wildlife, then the number of species might be the criterion; but if the area was mainly used for agriculture, then crop yield may be the most crucial criterion, as it is in the U.S. Surface Mining Control

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Table 1. A checklist of problems to be found in degraded terrestrial ecosystems, any of which may require treatment, by intervention or natural processes, if restoration is to be successful.

Category	Problem
Physical	
Texture	Coarse, fine
Structure	Compact, loose
Stability	Unstable
Moisture	Wet, dry
Nutrition	
Macronutrients	Nitrogen, others
Micronutrients	Deficient
Toxicity	
pH	Low, high
Heavy metals	High
Salinity	High
Organisms	
Plants	Absent, slow colonization, alien species
Animals	Absent, slow colonization, alien species

Note: A detailed checklist should be made for any habitat requiring restoration.

and Reclamation Act (SMCRA). It could, of course, be some much simpler criterion, such as the amount of heavy metal emanating from a mine site, since water quality down stream will be directly related to this figure.

Secondly, if reliance is being placed on the progressive effects of natural processes, what level has to be achieved? Should 75 or 90% of the preexisting species or plant yield be achieved? There can be no fixed criterion for these, although SMCRA expects 90%. Should metal burdens be reduced to 50, 10, or only 1% of what occurred previously? There are again no easy criteria, although for water there are World Health Organization and individual government standards. For a critical element such as phosphorus in lake water we may from experience take a value such as 100 $\mu g\ P \cdot L^{-1}$ as the critical level in recovery from hypertrophication (Ryding and Rast 1989). But this begs the question as to what is to be considered the original state; is it to be the water quality of 1930, 1950, or perhaps 1500, bearing in mind that human beings have long been part of the ecosystem? In a recent analysis of English lakes, Johnes et al. (1994) suggest the middle 1930s because this is after the full establishment of agriculture but before the advent of intensive agriculture.

Thirdly, once targets have been set, by when should they be achieved? Five years is taken as the period for bond release under SMCRA. But for many natural terrestrial processes such as the accumulation of soil nitrogen, it is not long enough. It can also not be long enough to judge whether interventions are adequate, such as the supply of phosphorus in face of soil phosphorus-fixing processes (Daniels and Zipper 1988). There is no easy answer, except that 3 years is certainly not long enough in either aquatic or terrestrial systems over which to judge success, particularly if restoration has involved major work. What has been done may well last for a few years and then collapse. It was, for instance, not possible to understand the changes taking place in the water quality of the Norfolk Broads, and how they could be combated, in less than a 10-yr study period (Moss 1989). It has taken a similar period of time to establish that a minimum of 1000 kg $N \cdot ha^{-1}$ is required for the restoration of temperate terrestrial ecosystems (Marrs et al. 1982).

It is certainly easier to require the presence or absence of particular species by a certain number of years. This does not need detailed understanding of functions and it is easy to specify. Yet this approach is fraught with dangers, especially if species have been artificially reintroduced. They may persist for a few years and then disappear because the restoration of underlying functions has not been addressed properly.

What is crucial is that the development of the ecosystem should be on an upward path in terms of structure and function (Fig. 1), and that no barriers to its long term further development can be envisaged. It is invaluable to have the potential limiting factors in the form of a check list, for example Table 1. This means that both the environment and the process of ecosystem development must be understood. We must also beware of taking any character as a surrogate for the whole development process. In salt marsh restoration for instance, despite its widespread use, the criterion of increased tidal flushing can be misleading, because of complexities in hydrology (Zedler 1988). Should we really put so much stress on biodiversity?

Restoration as an acid test of our understanding

This brings us to the final point, that there is a close relationship between ecological understanding and successful restoration. Indeed, restoration is an acid test of our ecological understanding (Bradshaw 1987*b*), because if we do not understand the processes at work in an ecosystem we are unlikely to be to able to reconstruct it so that it works.

But the relationship is reciprocal, since any attempt to reconstruct an ecosystem is a test of our knowledge of the ecosystem and will reveal any deficiencies in our theoretical knowledge. It is easy enough to take an ecosystem to bits and think that all the significant attributes have been identified. It is only when attempts are made to put it together again that it can be seen whether the bits have been identified correctly. We can learn from our failures.

There is, however, one problem. When restoration is apparently taking place because of the efforts expended, there is the possibility that it could actually be due to the self-restoring properties of the ecosystem, the processes involved in primary succession that we have already discussed. This confusion can be overcome by careful experiments, in which the effects of intervention are compared with suitable controls where there is no intervention.

This raises the role of experimentation in restoration. Such tests cannot be applied unless proper experiments are set up in which critical comparisons can be made. Comparison is an essential aspect of scientific ecology (Bradshaw 1987*c*). The efficacy of different forms of intervention can similarly only be examined in proper experiments, with good statistical design. It should be an essential part of every restoration programme that experimental testing of different aspects of the intervention are carried out. In terrestrial ecosystems this sort of experimentation is easy (Bradshaw and Chadwick 1980). In aquatic systems it is more difficult but equally necessary.

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Finally, it is essential that results are published in journals or reports that are readily available to everyone working in the field. Reviews, including failures as well as successes, are particularly important. It is only by exchange of information that science progresses and that new findings and ideas can be promulgated and developed. Not only should we not have to reinvent the wheel, but also there are generalizations to be made that will allow us to make predictions to guide future action. The development of the science of restoration should go hand in hand with achievements of successful restoration itself.

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Vertebrate herbivory in managed coastal wetlands: a manipulative experiment

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Abstract

Structural marsh management and nutria herbivory are both believed to strongly influence plant production in the brackish, deltaic marshes of coastal Louisiana, USA. Previous studies have tested the effects of structural management on aboveground biomass after implementing management, but very few studies have collected data before and after management. Thus, to test the effects of structural marsh management on *Spartina patens* (Ait.) Muhl. and *Scirpus americanus* Pers., the aboveground biomass of both species was estimated before and after the construction of shallow, leveed impoundments. The water level in each impoundment was managed with a single flap-gated culvert fitted with a variable crest weir. Additionally, the influence of nutria grazing on aboveground biomass was measured by nondestructively sampling fenced (ungrazed) and unfenced (grazed) plots in both managed and unmanaged areas. While there was no significant difference in *S. patens* production between managed and unmanaged areas, marsh management negatively affected *Sc. americanus* production. The two species also differed in their responses to grazing. Grazing dramatically reduced the sedge, *Sc. americanus*, while the grass, *S. patens*, remained at similar biomass levels in grazed and ungrazed plant stands. These findings support the belief that herbivory has a strong influence on plant production, but do not support the claim that management increases plant production in the deltaic marshes of Louisiana. Published by Elsevier Science Ltd.

Keywords: Wetland management; *Myocastor coypus*; Aboveground biomass; Nutria; Marsh

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1. Introduction

The extensive network of coastal marsh land in Louisiana is converting to open water at a rate of 56 km^2 per year (Barras et al., 1994). The key factors contributing to this loss include geologic subsidence, sea-level rise, and anthropogenic developments, such as dredging and levee construction, that have facilitated saltwater intrusion and reduced mineral sediment deposition (Gosselink, 1984). Vertebrate herbivores may compound the wetland loss problem by reducing the living plant matter that consolidates the marsh's upper peat layer, thus making the marsh vulnerable to additional erosion and fragmentation.

Historically, marsh management has been used as a method to combat wetland loss. Marsh management techniques encompass a wide range of activities from the installation of simple fixed-crest weirs in shallow channels to the construction of shallow, leveed impoundments fitted with elaborate water control structures. The results of management are highly variable and are influenced by habitat stability, marsh type, soil type, local hydrology, and the water-level management regime (Hartman and Cahoon, 1990).

As defined by Cahoon and Groat (1990), structural marsh management encompasses those techniques that 'make use of structures to manipulate local hydrology'. The use of impoundments, a form of structural marsh management, has become more widespread (Cahoon, 1994) in Louisiana, yet their impacts are not completely understood. The water level management guidelines employed by marsh managers in Louisiana call for dewatering impoundments in the spring, equilibrating water levels in summer, and increasing the water level inside impoundments in fall and winter. This is a regime with multiple objectives that do not always complement each other. The effectiveness of impoundments in enhancing and restoring habitat is the subject of a continuing debate because management objectives and success differ from project to project. Impoundments may slow wetland degradation by impeding saltwater intrusion, and can enhance open-water habitat by increasing submerged aquatic vegetation. Alternatively, impoundments can have a negative impact on coastal wetlands because they usually reduce sediment influx and tidal exchange (Boumans and Day, 1994), inhibit the movement of estuarine organisms (Rogers et al., 1994), reduce soil drainage (Mendelssohn et al., 1983), and alter the plant community composition (Day et al., 1986). To effectively manage wetlands, it is important to understand the processes that contribute to wetland degradation.

Vertebrate herbivory is one of the natural processes that influences the structure and function of wetland communities (Kerbes et al., 1990) and thus can influence the effectiveness of wetland management and restoration. Consumptive and nonconsumptive (i.e., trampling, defecation, feeding platform construction, trail formation) damage by wetland herbivores such as nutria (*Myocastor coypus* Molina) can enhance or reduce aboveground (Fuller et al., 1985; Taylor et al., 1994) and belowground biomass (Visser, 1989), alter species composition (Shaffer et al., 1992), and modify plant stand architecture (Lodge, 1991).

One of the most common wetland herbivores in Louisiana is the nutria, a rodent indigenous to South America. As in Europe (Gosling and Baker, 1989; Reggiani et al., 1995), Russia, Africa, the Middle East, and other regions of the United States (Kinler et al., 1987), nutria were brought to Louisiana to stock fur-farming operations. After a series of accidental escapes beginning in 1939, nutria dispersed into the surrounding coastal wetlands of southwest Louisiana (Evans, 1970). High reproductive rates and low natural predation enabled the nutria population to increase, and by 1962 Louisiana trappers annually harvested over 1×10^6 nutria (Lowery, 1974). Although nutria were first valued as a natural resource, they are now more commonly viewed as a problem species because of their damage to agricultural crops and levees and their disturbance to native habitats (Lowery, 1974; Gosling et al., 1988).

Nutria are generalist herbivores that forage primarily on the basal portion of stems, leaving the majority of aboveground tissue to decompose on the marsh surface. Their feeding habits are damaging because their foraging activity can result in large unvegetated patches of marsh and their intensive over-winter grubbing for roots and rhizomes overturns the marsh's upper peat layer (Kinler et al., 1987), thereby disrupting and weakening the root–soil matrix. Unvegetated patches of marsh with a weakened peat layer are vulnerable to subsequent erosion and may lead to additional marsh fragmentation and loss.

Grazing reduces plant growth when it is intensive with little recovery time (Oesterheld and McNaughton, 1991a; Turner et al., 1993) or when herbivory is coupled with flooding (Oesterheld and McNaughton, 1991b) and other sources of stress (Oesterheld, 1992). This is likely to be the case in the deltaic marshes of Louisiana where nutria forage in marsh plant communities already growing under stress from anoxia and sulfide toxicity induced by prolonged flooding and increased soil salinity (Burdick and Mendelssohn, 1987).

As emergent wetlands continue to convert to open water, it is imperative to critically test the effectiveness of commonly used water-level management regimes before relying on them to manage the region's existing coastal wetlands. Previous studies have examined the effects of management on marsh plant communities after implementing management, but very little data has been collected to contrast pre- and post management.

Understanding the processes that contribute to wetland degradation is also an important step in managing wetlands. Past studies (Linscombe et al., 1981; Fuller et al., 1985; Shaffer et al., 1992) of wetland processes have documented the effects of nutria grazing on plant growth, but have only speculated on the role of nutria in wetland loss. Nutria herbivory may be an additional factor that undermines the stability of Louisiana's deltaic wetlands.

In 1991, a detailed study was started to examine the effects of nutria herbivory on wetland vegetation as it relates to structural marsh management. The study was designed to address the following questions:

Does the aboveground biomass of *Spartina patens* (Ait.) Muhl. and *Scirpus americanus* Pers. increase in response to structural marsh management?

Does nutria herbivory significantly reduce the aboveground biomass of *S. patens* and *Sc. americanus*?

Is there a long-term change in the aboveground biomass of *S. patens* and *Sc. americanus* in response to structural marsh management and herbivory?

2. Methods

2.1. Study areas

The study was conducted in a 344-ha complex of emergent, mesohaline wetlands located 35 km south of New Orleans, Louisiana, USA (29°35′N, 90°05′W). These wetlands are typical of the tidally influenced, oligo-mesohaline marshes of the middle Barataria basin (Conner and Day, 1987) and lie within a region undergoing rapid land loss (Turner, 1987). Two pairs of experimental marshes were studied within the 344-ha complex. The area encompassing the northwestern pair of marshes was designated as Little Lake and the area encompassing the southeastern pair of marshes was designated as Three Bayou. A mosaic of *S. patens* and *Sc. americanus* (formerly classified as *Scirpus olneyi*) dominated the plant communities of all four marshes. *Juncus roemerianus* Scheele and *Distichlis spicata* (L.) Greene were also present in both areas but were more common in the Three Bayou area; thus, the Three Bayou and Little Lake areas were considered to be similar rather than identical. All four marshes were interspersed with shallow-water ponds ranging from 1 to 150 m in diameter and were bisected by several deeper (1–2 m) canals and smaller natural waterways.

2.2. Field experiments

The effects of structural marsh management on aboveground biomass were tested in two pairs of adjacent sites. One pair of sites (Little Lake area) consisted of a 177-ha marsh impounded 1 year before the study and an adjacent 79-ha unmanaged marsh. The impounded site was treated as unmanaged in 1991, the first year of the study, because the water control structure was open, allowing for water exchange. The second pair of sites (Three Bayou area) consisted of a 32-ha unmanaged marsh and an adjacent 56-ha marsh impounded in January 1992. A single flap-gated culvert with a variable crest weir was installed in each impoundment to control water level. Water-level management began in March 1992 for both managed areas and followed an annual water level management schedule that is commonly used in coastal Louisiana. The following description is a summary of this schedule. In March, the impoundments were drained by gravity flow by closing flapgates and setting the stoplogs 12 in. below average marsh elevation. The impoundments were drained in the spring in an attempt to enhance seed germination, to stimulate the growth of existing plants by improving the redox conditions in the rhizosphere, and to cause the drying and firming of sediments. In July, the flapgates were opened and the stoplogs were maintained at 12 in. below average marsh elevation to equilibrate the water levels inside and outside of the impoundments. The equilibrated water levels rehydrated the marsh and allowed for the ingress and egress of marine organisms. In October, the water level inside of the impoundments was increased by keeping the flapgates open and by setting the stoplogs 6 in. below average marsh elevation. The water level was increased in the fall and winter to provide consistent waterfowl habitat and to allow for hunter access.

Water level was measured hourly in each managed and unmanaged area with 800-series Omnidata data loggers and 2.5-psi pressure transducers. Interstitial water conductivity and temperature were also recorded on each data logger through a

noncontacting conductivity probe connected to a separate temperature sensor. The three sensors were placed in a perforated, 10-cm PVC stilling well, covered with nylon mesh and installed 15 cm below marsh surface. A global positioning system (GPS) was used to establish a National Geodetic Vertical Datum (NGVD) benchmark at each data logger site. The data logger elevations were subsequently calibrated to a common benchmark by using a geodimeter (Foote, unpublished data).

Five 9-m^2 exclosures (fenced and ungrazed) and five 9-m^2 control (unfenced and grazed) plots were constructed in each of the managed and unmanaged areas to test the effects of nutria grazing on aboveground biomass. Exclosure sites were selected by using a stratified random sampling scheme. The exclosures were constructed out of 5 × 5 cm wooden posts and 4 × 6 cm plastic-coated, weld-wire mesh. The wire mesh extended 1 m above marsh surface and was buried 30.5 cm below marsh surface to prevent nutria from burrowing into the exclosures. Two permanent 0.0625-m^2 subplots were established within each 9-m^2 plot. Logistics prevented the construction of extra fenced plots to control for cage effect; thus, each subplot was placed 0.5 m away from the edge of the 9-m^2 plot boundary. The noncentrality parameter (Montgomery, 1991, pp. 110–114) was used to run a power analysis (Lenth, 1987) for all significant variable differences. The experimental power values were ≥ 80% suggesting that there was an appropriate degree of sampling to detect real differences (Montgomery, 1991, pp. 110–114).

A combination of tagged-stem counts and stem height measurements (Hopkinson et al., 1980; Smith and Kadlec, 1985) was used to estimate the aboveground biomass of *S. patens* and *Sc. americanus*. By using nondestructive techniques, the same stem cohorts were followed over a long period of time, the number of stems lost between samplings was estimated, the number of new stems produced between samplings was determined, and a more accurate estimate of the aboveground biomass was calculated. In March 1991 all *S. patens* and *Sc. americanus* stems in each subplot were tagged with colored labeling tape (Smith and Kadlec, 1985; Morris and Haskin, 1990). One month later, all tagged stems that remained on each subplot were counted, all newly emerged stems were tagged with a different color of tape, and the total height of all tagged stems was measured. This sampling regime was repeated 10 times at 2–3 month intervals until December 1992. After the basic seasonal trends were established in 1991 and 1992, the sampling interval was extended to 6 months in 1993 and 1994.

During each sampling period, plant stems were collected to calibrate the stem height measurements. About 100 ungrazed stems of *S. patens* and of *Sc. americanus* were randomly selected from plant stands within 100 m of the experimental plots. Stems were clipped at the marsh surface and returned to the lab for subsequent measurements. The total height of all stems was measured to the nearest 0.5 cm, the stems were dried at 70°C to a constant weight and then weighed to the nearest 0.01 g. A linear regression equation was calculated from the height–weight relationship of these stems, then the regression equation was applied to the heights of tagged stems to estimate the aboveground biomass produced on the study plots. The R^2 values from the linear regressions ranged from 0.75 to 0.96 for *S. patens* and from 0.77 to 0.92 for *Sc. americanus*. The REG procedure of the Statistical Analysis System (SAS) was used to perform all regression analyses (SAS Institute, 1990).

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An analysis of variance fixed effects model was used to test for the effects of management and grazing on aboveground biomass. The *S. patens* data were transformed, where necessary, with either logarithmic or square-root transformations to meet the assumptions of homogeneity (Neter et al., 1989, pp. 142–151). The *Sc. americanus* data were transformed with rank transformations to meet the homogeneity assumption (Neter et al., 1989, pp. 142–151). Significant factor-level differences were isolated a posteriori by using Bonferroni pairwise comparisons (Neter et al., 1989, pp. 164–165).

Aboveground biomass estimates were also analyzed with repeated measures analysis of variance (Winer, 1971, pp. 261–308), where the within-subject effect was time and the between-subject effects were replicated area, managed/unmanaged treatment, grazed/ungrazed treatment, and subplot. The data were transformed with rank transformations and time points and class variables were collapsed when necessary to meet the homogeneity of variance and multivariate normality assumptions of repeated measures analysis. Mauchley's criterion was used to test for sphericity, and the univariate or multivariate method was selected depending on the acceptance of this assumption (Moser et al., 1990; Potvin et al., 1990; SAS Institute, 1991, pp. 274–278). Adjusted univariate tests were used if the sphericity assumption was mildly violated (Moser et al., 1990; Potvin et al., 1990). The Huynh–Feldt and Greenhouse–Geisser corrections gave similar results for the data. Tukey's test was used a posteriori to isolate significant differences between the Little Lake and Three Bayou areas (Montgomery, 1991, pp. 78–79). Bonferroni pairwise comparisons were used a posteriori to isolate significant differences at all other nested levels (Neter et al., 1989). When the sphericity assumption was dramatically rejected, the multivariate approach was selected and the significant class variables were identified by using the Wilks' Lambda F statistic (Seber, 1984, pp. 412–413; Potvin et al., 1990). Bonferroni pairwise comparisons were made a posteriori to identify significant factor-level differences. Differences are reported as significant at $P \leq 0.05$.

3. Results

3.1. Effects of marsh management on plant production

The style of structural marsh management used in this study altered the hydrology of managed sites by producing significantly lower water levels ($P \leq 0.05$) during the spring drawdown and by muting the daily tidal amplitude (Fig. 1) (Foote, unpublished data). Even though managed areas had lower water levels and more oxidized soils during the spring drawdown (Hargis, 1994), structural marsh management did not enhance the aboveground biomass of *S. patens*. When analyzed by sampling date, *S. patens* biomass estimates were similar between designated managed and unmanaged areas before management in April 1991 ($P = 0.8660$) and remained similar at every sampling date through October 1994 ($P = 0.2650$) (Fig. 2A). Similarly, there were no long-term effects of management on *S. patens* biomass as indicated by the nonsignificant interaction of time and management from 1991–1994 (Table 1).

Active marsh management negatively affected the aboveground biomass of *Sc.*

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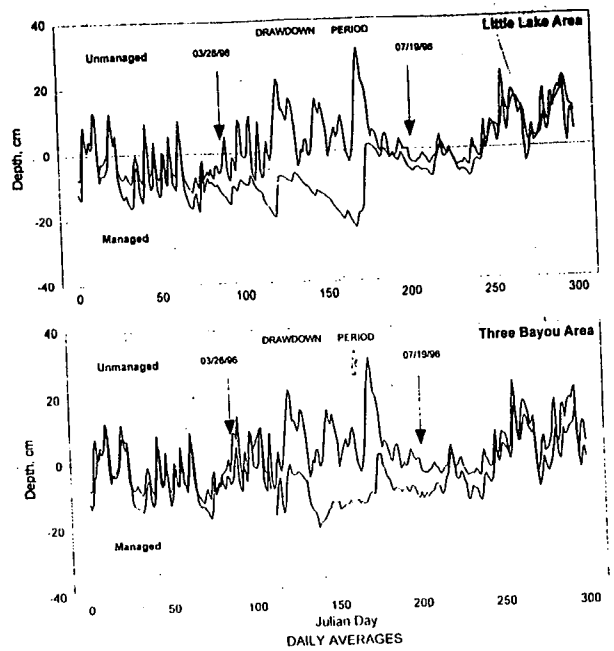

Fig. 1. Water depth of managed vs. unmanaged areas in 1993.

americanus. Significant differences in the *Sc. americanus* biomass of managed and unmanaged areas first appeared before management in October 1991 ($P = 0.0171$) (Fig. 2B) between the Little Lake pair of sites. Although significant, the difference in biomass production between managed and unmanaged sites was not consistent. In October 1991, a statistically greater amount of *Sc. americanus* biomass was produced in the Little Lake managed area as compared to the Little Lake control area, yet a similar difference in biomass occurred in the Three Bayou sites and was not significant. There was no consistent difference in biomass between impounded and unimpounded areas because production in the Little Lake impoundment was similar to the Three Bayou control area, and the biomass estimate for the Three Bayou managed area was comparable to that of the Little Lake control area. Significant differences between the amount of aboveground biomass in managed vs. unmanaged areas occurred again in July ($P = 0.0400$), October ($P = 0.0084$), and December ($P = 0.0193$) of 1992 (Fig. 2B). In July and October, planned comparisons indicated that the *Sc. americanus* aboveground biomass in the Three Bayou unmanaged area was three to four times greater ($P = 0.0242$ and $P =$

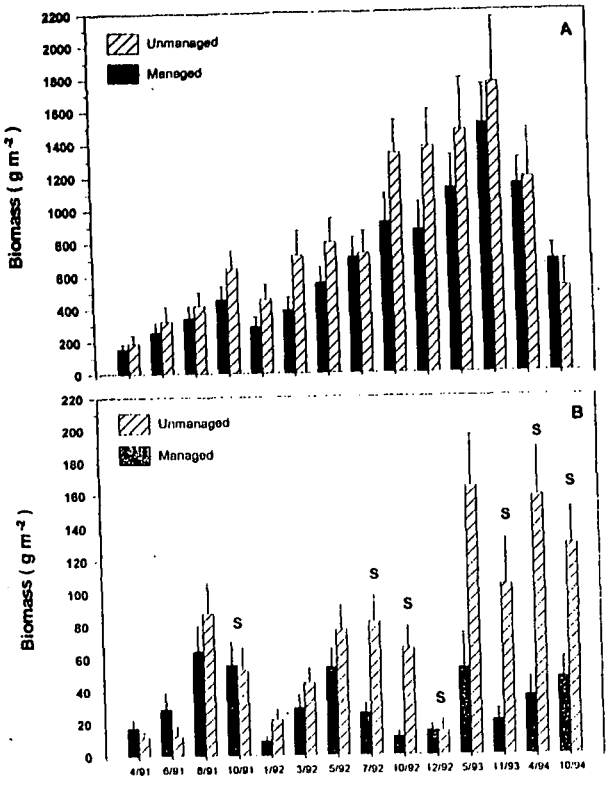

Fig. 2. Aboveground biomass response to management for (A) *S. patens* and (B) *Sc. americanus* in 1991–1994. Significant differences are denoted by S. Significant differences may not be visually apparent because the averages of untransformed data are presented for managed and unmanaged areas. Error bars represent ±1 SE. Note the unequal sampling intervals on the x-axis. Sampling occurred every 2 to 3 months in 1991–1992 and every 5 to 6 months in 1993–1994.

0.0087, respectively) than in the Three Bayou managed area. The aboveground biomass in the Three Bayou unmanaged area remained high throughout the year, then the annual senescence in December 1992 lowered the biomass estimate in this area to the lowest of all four areas and resulted in a statistically significant difference between the Three

Table 1
Repeated-measures analysis of variance (ANOVA) for the aboveground biomass of *S. patens*

Source of variation	*S. patens* aboveground biomass							
	1991		1992		1993		1994	
	df	*P*	*df*	*P*	*df*	*P*	*df*	*P*
Area	1	0.1542	1	**0.0210**	1	0.1968	1	**0.0004**
Management	2	0.5565	2	0.0575	2	0.6249	2	**0.0001**
Grazing	4	0.3874	4	0.0705	4	0.5628	4	**0.0027**
Subplot	*	*	8	0.1281	8	0.2487	8	**0.0001**
Error	72		64		44		60	
Time	3	**0.0001**	2	0.9093	1	0.1865	1	**0.0001**
Time × area	3	0.4613	2	**0.0211**	1	0.8372	1	0.2372
Error	70		128		44		60	
Time × management	6	0.7516	4	0.2519	2	0.5926	2	0.0867
Error	140		128		44		60	
Time × grazing	12	0.0554	8	**0.0033**	4	0.7529	4	0.4285
Error	185		128		44		60	
Time × subplot	*	*	16	0.0922	8	0.1327	8	0.8762
Error	*		128		44		60	

*Variable was collapsed to meet the assumptions for repeated-measures analysis.
The 1994 data were analyzed by using repeated-measures ANOVA under the split-plot framework because the assumptions of homogeneity and multivariate normality did not hold. The assumption of equal correlation was not a problem because there were only two time points in 1994.
Significant *P*-values are in boldface type.

Table 2
Repeated-measures analysis of variance (ANOVA) for the aboveground biomass of *S. americanus*

Source of variation	*Sc. americanus* aboveground biomass							
	1991		1992		1993		1994	
	df	*P*	*df*	*P*	*df*	*P*	*df*	*P*
Area	*	*	1	**0.0004**	1	0.3892	1	0.1601
Management	1	0.1127	2	0.5457	2	0.4443	2	**0.0001**
Grazing	2	0.2513	4	**0.0331**	*	*	4	**0.0001**
Subplot	*	*	8	0.9869	*	*	8	0.6040
Error	76		64		76		60	
Time	2	0.5580	4	**0.0001**	1	0.2074	1	0.9991
Time × area	*	*	4	0.5433	1	0.9837	1	0.4504
Error	75		61		76		60	
Time × management	2	0.8315	8	0.9442	2	**0.0163**	2	**0.0470**
Error	75		122		76		60	
Time × grazing	4	**0.0001**	16	**0.0001**	*	*	4	**0.0365**
Error	150		187		76		60	
Time × subplot	*	*	32	**0.0001**	*	*	8	0.6586
Error	*		226		*		60	

*Variable was collapsed to meet the assumptions for repeated-measures analysis.
The 1994 data were analyzed by using repeated-measures ANOVA under the split-plot framework because the assumptions of homogeneity and multivariate normality did not hold. The assumption of equal correlation was not a problem because there were only two time points in 1994.
Significant *P*-values are in boldface type.

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Bayou managed and unmanaged areas. In 1993 and 1994, the effect of time on *Sc. americanus* aboveground biomass differed (Table 2) between managed and unmanaged areas. When analyzed by month, these differences were evident in both pairs of managed and unmanaged areas in November 1993 ($P = 0.0085$), April 1994 ($P = 0.0001$) and October 1994 ($P = 0.0002$) (Fig. 2B) when the unmanaged areas produced a significantly greater amount of *Sc. americanus*.

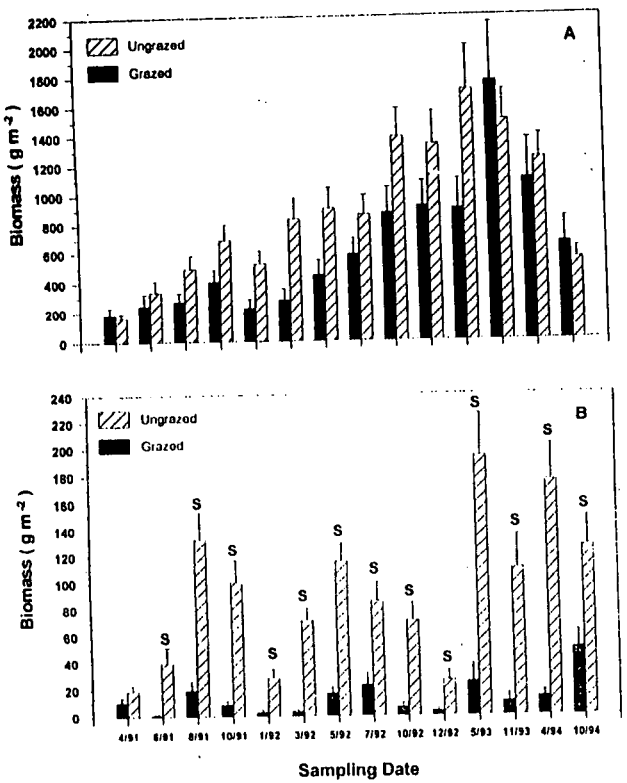

Fig. 3. Aboveground biomass response to herbivory for (A) *S. patens* and (B) *Sc. americanus* in 1991–1994. Significant differences are denoted by S. Significant differences may not be visually apparent because the averages of untransformed data are presented for grazed and ungrazed areas. Error bars represent ± 1 SE. Note the unequal sampling intervals on the x-axis. Sampling occurred every 2 to 3 months in 1991–1992 and every 5 to 6 months in 1993–1994.

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3.2. Nutria grazing effects on plant production

Nutria grazing had no significant effect on the available aboveground biomass of *S. patens* from April 1991 ($P = 0.8660$) to October 1994 ($P = 0.2650$) (Fig. 3A). Although grazed and ungrazed plots were similar when analyzed by sampling date in 1992, there was a difference in the biomass change over time between grazed vs. ungrazed plots as shown by the significant interaction of time and grazing (Table 1). The aboveground biomass in grazed plots gradually increased from January 1992 to a peak estimate in December 1992 (Fig. 3A). Rather than a gradual increase in 1992, aboveground biomass growth in ungrazed plots reached a plateau from March to July and then ascended to a peak in October.

Nutria grazing significantly reduced the aboveground biomass of *Sc. americanus*. There was no significant difference ($P = 0.0813$) between grazed and ungrazed plots when the experiment was initiated in April 1991; however, aboveground biomass estimates were significantly greater in ungrazed plots by June 1991 ($P = 0.0012$) and remained so on every subsequent sampling occasion through October 1994 ($P = 0.0013$) (Fig. 3B). The greater amount of biomass in ungrazed plots contributed to long-term differences in *Sc. americanus* growth between grazed and ungrazed plots as indicated by the significant interaction of time and grazing in 1991, 1992 and 1994 (Table 2).

4. Discussion

4.1. Effects of marsh management

Under the water-level management regime used in this study, marsh management did not enhance the production of *S. patens* and *Sc. americanus*. The lack of a management effect on *S. patens* in this study may be related to the soil conditions of the study area. Hargis (1994) characterized the soils of the study area by taking monthly measurements of interstitial soil salinity, redox potential and sulfide concentrations of managed and unmanaged sites from 1991 to 1993. The soils of the experimental areas were mesohaline, strongly reduced, and contained high sulfide concentrations. Hargis (1994) reported that overall there was no significant difference in root zone soil salinity, redox potential and sulfide concentrations between the managed and unmanaged areas from 1991 through 1993. The water level data indicate that the water level management regime used in this study significantly lowered water levels in the managed areas during spring drawdown (Foote, unpublished data). Although managed marsh soils were more oxidized during the low water period, the level of oxidation was not enough to significantly alter the soil chemistry of the managed marsh (Hargis, 1994); thus, *S. patens* production remained unchanged in these areas. Elevated soil sulfide concentrations are characteristic of reduced soil in brackish and saline marshes (Mitsch and Gosselink, 1993); however, the soil sulfide concentrations measured in both the managed and unmanaged areas of this study from 1991–1993 (Hargis, 1994) are considered limiting to photosynthesis as reported by Pezeshki et al. (1991).

In a comparative study of soil chemistry and plant production in managed and unmanaged coastal marshes, Flynn et al. (1990) attributed a reduction in *S. patens* production to reduced soils. When sufficient soil drainage was attained, Flynn et al. (1990) found that managed marshes had lower interstitial salinity, more oxidized soils, and correspondingly greater *S. patens* production.

Contrary to what we expected, management did not enhance the growth of *Sc. americanus*. The unmanaged marsh areas clearly produced a greater amount of *Sc. americanus* in July 1992, October 1992, November 1993, April 1994 and October 1994. In December 1992, aboveground biomass in the Three Bayou managed area was greater than the unmanaged area, but these results are misleading. The observed differences were not a result of increased plant production in managed areas but were due to the senescence of the greater *Sc. americanus* biomass in the unmanaged area that accentuated the difference between the two treatments.

The distribution of *Sc. americanus* has been positively associated with increased water levels (Nyman et al., 1993; Broome et al., 1995). The increased production of this species in unmanaged plant stands may be related to the greater mean water depth and tidal amplitude of unmanaged marsh. Broome et al. (1995) noted that *Sc. americanus* reached optimum growth levels with 10 cm of water above marsh surface while *S. patens* attained its greatest abundance with water levels 10 cm below marsh surface. Hess et al. (1975) also found that impoundments which maintained a water level slightly below marsh surface or 5 to 10 cm above marsh surface provided optimum growth conditions for *Sc. americanus*. Depending on the hydrologic manipulations implemented under management, changes in *Sc. americanus* production and changes in a preferred food source (Chabreck et al., 1981) of nutria may affect the subsequent impact of nutria herbivory on coastal marsh.

4.2. Nutria grazing effects on plant production

The presence of clipped *S. patens* stems on our unfenced experimental plots confirmed that nutria graze on *S. patens* shoots; however, grazing was insufficient to reduce the aboveground biomass of this species. This is not surprising because the aboveground tissue of *S. patens* is not a preferred food source in brackish marsh (Chabreck et al., 1981). The similarity in biomass that we observed between grazed and ungrazed *S. patens* stands was also reported in a separate, parallel study that focused on interactions between fire and herbivory (Taylor et al., 1994).

Nutria indirectly affect aboveground biomass production by grubbing for roots and rhizomes over winter. Grubbed *S. patens* stands show that nutria digging disrupts the structure of the marsh root zone leaving behind mixed stands of dead, rootless stems and living, intact stems. Root herbivory removes belowground biomass and subsequently thins the aboveground stand via stem mortality. The signs of nutria grubbing and grazing were visually evident in the grazed *S. patens* stands, but the impact was not statistically significant for aboveground biomass. In this study, the early spring growth of *S. patens* in 1992 was more gradual on grazed plots than ungrazed plots. Although aboveground biomass estimates were similar between grazed and ungrazed plots, there was a significant interaction of time and grazing in 1992, indicating that nutria herbivory had

some effect on *S. patens*. Without the necessary data, it can only be speculated that belowground herbivory may have contributed to the changes in the aboveground biomass growth curve.

Nutria herbivory reduced *Sc. americanus*, the preferred food source of nutria in brackish marsh (Chabreck et al., 1981). These results agree with Linscombe et al. (1981) who also reported that nutria grazing reduced the aboveground biomass of *Sc. americanus* in brackish marsh. The aboveground biomass data collected in this study clearly demonstrate that nutria grazing suppresses *Sc. americanus*. Stem height and stem density data collected from the same experimental plots (Johnson and Foote, unpublished data) suggest that nutria grazing alters the architecture of plant stands in brackish marsh. After *Sc. americanus* was protected from grazing in fenced plots, *Sc. americanus* steadily increased in stem density and height in ungrazed stands and was accompanied by a significant increase in the height of *S. patens* (Johnson and Foote, unpublished data). While the stem height of *S. patens* increased significantly, the stem density remained similar between grazed and ungrazed stands (Johnson and Foote, unpublished data). The similarity in biomass and stem density between grazed and ungrazed stands, and the difference in stem height suggest that the structure of the two stands is different. Nutria herbivory may be a link in the chain of processes leading to marsh erosion if the changes to the plant stand architecture are severe.

Over-winter grubbing of the marsh surface and intensive grazing of *Sc. americanus* patches create openings in the plant stand that facilitate the sheet flow of surface water. Erosion of these areas creates interior ponds that facilitate interior marsh break-up (Hillbricht and Ryszkowskik, 1961) and further exacerbate the submergence of *S. patens*.

5. Conclusions

Historically, the Barataria Basin has had some of the highest rates of wetland loss in Louisiana. To retain the remaining wetlands, the plant production of these marshes must be maintained and enhanced if possible. Is structural marsh management the answer? The style of structural marsh management used in this study was not successful in enhancing plant production. The aboveground biomass of *S. patens* remained unchanged between managed and unmanaged sites and the aboveground biomass of *Sc. americanus* was greater in unmanaged marsh.

Coastal wetland loss in Louisiana is the result of a combination of many factors. Nutria herbivory is one of the factors that reduces the biomass of select species in brackish marsh, and should not be overlooked when formulating wetland management plans. In this study, nutria herbivory significantly reduced the aboveground biomass of *Sc. americanus* and additional unpublished stem height and stem density data suggest that herbivory may affect the plant stand architecture of brackish marsh. If severe enough, reductions in plant biomass and alterations to plant stand structure may facilitate marsh erosion and fragmentation, thus contributing to wetland loss.

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Spatial variation of copper and lead concentrations of water hyacinth plants in a wetland receiving urban run-off

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Abstract

Copper and lead concentrations of roots of water hyacinth, *Eichhornia crassipes* (Mart.) Solms, in an urban wetland in Sydney, Australia ranged between 145 ± 15 and 1110 ± 145 μg g^{-1} dry mass for lead; and between 14.7 ± 7.0 and 303 ± 108 μg g^{-1} dry mass for copper, (mean ± sd, $n = 6$). Considerable variation at the scale of individual plants was found, about 20% relative standard deviation within a site of about 3 m radius. Samples of single or few plants are therefore unlikely to allow assessment of the pollution status of a wetland. Copper and lead had similar spatial distribution. Metal concentrations in the sediments, roots and leaves declined exponentially with increased distance from the inflow to the wetland. Distance from an inflow explained much of the variation in metal concentrations, up to: 87% for Pb and 85% for Cu in roots; 54% for Cu in leaves; 88% for Pb; and 45% for Cu in sediments. The decline in metal concentration over distance was steeper for roots than sediments. Concentrations of metals were greater for fine secondary roots than for coarse primary roots. The median and range of metal concentrations in root portions and sediments were as follows (μg g^{-1} dry mass): Cu fine: 21.0, 12.3–259; Cu mixed: 53.3, 18.8–296; Cu coarse: 60.8, 29.7–327; Cu sediment: 263, 190–377; Pb fine: 121, 21.8–843; Pb mixed: 257, 41.4–1270; Pb coarse: 265, 77.5–1160; Pb sediment: 1170, 590–1870. Regressions of $\log_e$-transformed metal concentrations of roots and leaves on $\log_e$-transformed metal concentrations in adjacent sediment were significant for copper in leaves and roots, and highly significant for lead in roots. This study highlights the need for estimation of

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RAINFALL EFFECTS ON PLANT–HERBIVORE PROCESSES IN AN UPLAND OAK FOREST

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Abstract. We examined the patterns of foliar chemistry and insect herbivory in white oak (*Quercus alba*), chestnut oak (*Q. prinus*), and red maple (*Acer rubrum*) trees occupying an upland oak forest on the Walker Branch Watershed in Tennessee. Different size classes of each species were sampled to evaluate life cycle changes in foliar N and phenolic chemistry and their corresponding influence on insect herbivory. Oak trees had consistently higher foliar N and hydrolyzable tannin concentrations, and they experienced greater herbivore damage than did red maple trees; maple trees had higher condensed tannin levels. Foliar chemistry and herbivore damage were usually quite similar for all size classes. However, condensed tannins, and occasionally total phenolics, were higher in well-insolated mature trees than in shaded understory conspecifics, fitting the pattern expected through plant carbon/nutrient balance relationships.

Rainfall fluctuations during 1992–1994 significantly influenced plant–herbivore processes. Foliar N and phenolic concentrations were reduced in all species during the much drier summer of 1993, relative to 1992. The summer drought in 1993 was apparently severe enough to restrict carbon allocation to plant phenolics. In contrast, foliar N levels in oaks were somewhat elevated by the end of the wet 1994 growing season. Total phenol and hydrolyzable tannin levels remained quite low in 1994, when carbon may have been preferentially allocated to growth rather than differentiation, as N uptake increased during the wet summer following drought. Nevertheless, carbon allocation to condensed tannins was quite high for all species during the wet summer. Insect herbivore damage was directly correlated with rainfall totals over the 3-yr period. Herbivore damage on oaks was reduced during the 1993 drought, principally because of less impact by leaf skeletonizers. Insect feeding on oaks and maples was elevated during the wet 1994 summer, when strip feeding by lepidoptera larvae was at its highest. Our findings suggest that herbivore damage at Walker Branch appears to be largely dependent on the response of specific insect feeding guilds to moisture-related changes in foliar N and plant phenolics.

Key words: feeding guilds; foliar chemistry; forests; herbivory; insects; maples; nitrogen; oaks; phenolics; plant defenses; rainfall; tannins.

INTRODUCTION

Considerable evidence has accumulated linking herbivore damage with the levels of plant phenolics (i.e., tannins) in hardwood tree species (Feeny 1976, Schultz and Baldwin 1982, Coley et al. 1985, Coley 1986, Rossiter et al. 1988, Schultz 1988, Tuomi et al. 1988, Coley and Aide 1991, Herms and Mattson 1992, Tuomi 1992, Dudt and Shure 1994). One source of this evidence concerns the inverse correlations observed between levels of plant phenolics and herbivore damage along resource gradients of light or nutrients (Mole et al. 1988, Landsberg and Ohmart 1989, Shure and Wilson 1993, Dudt and Shure 1994). Changes in plant carbon/nutrient balance and growth/differentiation balance provide possible explanations for the phenotypic expression of plant phenolics across these resource gradients (Herms and Mattson 1992). Both hypotheses suggest that plants preferentially allocate carbon for growth when conditions are favorable, whereas carbon will often accumulate and be used for differentiation products, such as defenses, when high light or low nutrients promote photosynthesis in excess of growth (Bryant et al. 1983, Chapin et al. 1987, Muller et al. 1987, Mole et al. 1988, Fajer et al. 1992, Herms and Mattson 1992). The more inclusive growth/differentiation balance hypothesis predicts that any environmental factor that slows growth more than photosynthesis will increase the resource pool of carbohydrates available for allocation to secondary metabolites such as tannins (Herms and Mattson 1992, Tuomi 1992). However, the presence of counteradaptations among certain insect species has prompted debate concerning the efficacy of these phenolic compounds as putative defenses against herbivore populations (Bernays 1981, Faeth 1985, Bernays et al. 1989).

The lack of consistent correlations between plant defenses and insect herbivory has prompted a reconsideration of factors other than plant defensive chemistry in possibly regulating herbivore populations (Landsberg and Ohmart 1989). Insect herbivores may be limited by other aspects of foliar chemistry, including leaf water content (Scriber 1984), toughness (Coley 1983), and especially nitrogen content (Mattson 1980, White 1984). Evidence supporting the importance of natural enemies in limiting insect herbivores is also accumulating (Faeth et al. 1981, Schowalter et al. 1986, Hunter and Schultz 1993, Marquis and Whelan 1994, Cornell and Hawkins 1995). In addition, climatic conditions such as drought may operate indirectly on herbivore populations through their effects on plant foliar chemistry. However, establishing predictions concerning the response of plant phenolics and insect herbivores to drought has proven difficult (Gershenzon 1984, Mattson and Haack 1987*b*, Larsson 1989, Ayres 1993). Earlier evidence suggested that drought and other stresses promoted outbreaks of herbivorous insects because of elevated plant nutrient levels (White 1984), lowered plant defenses (Rhoades 1985), or the development of a more suitable abiotic environment (Rhoades 1983, Mattson and Haack 1987*b*). More recent evidence (Mattson and Haack 1987*b*) implies a nonlinear response of insects to plant stresses such as drought, that are strongly specific to each insect feeding guild (Larsson 1989). These varied findings suggest a need for further evaluation of herbivore responses to these possible regulatory mechanisms.

The current study offered an opportunity to examine plant–herbivore processes throughout the life cycle of several important tree species occupying a mature upland oak forest in Tennessee. Our specific objectives involved (1) determining the levels of foliar N and plant phenolics in different size classes of tree species present within the forest; (2) evaluating the temporal changes in foliar chemistry over a 3-year period involving quite different rainfall regimes; (3) examining the type and extent of insect herbivore damage for different size classes of each tree species; and (4) assessing whether the responses of insect herbivores to rainfall-mediated changes in plant host chemistry are feeding-guild specific. We hoped, through our efforts, to provide much greater understanding of the spatio-temporal dynamics of plant–herbivore processes within a temperate deciduous forest. This type of information should prove important in assessing the mechanistic basis for future alterations in plant–consumer processes as a result of climate change effects on temperate forests.

METHODS

Study area

We conducted the study at the Walker Branch Watershed on the Oak Ridge National Laboratory site near Oak Ridge, Tennessee, USA. The project is part of a large-scale Throughfall Displacement Experiment (Hanson et al. 1995), which is examining the long-term impact of climate-induced rainfall modification on eastern deciduous forests. The overall study area consists of a 1.8-ha plot (80 m downslope × 240 m across slope) established on a south-facing slope at the top of the watershed. The plot has been subdivided into three contiguous 80 × 80 m subplots for the purposes of the experiment. The specific site was selected because of its uniform slope, consistent soil type, and relatively homogeneous vegetation distribution. A nearby meteorological station (~0.5 km away) provides continual rainfall data. Time domain reflectometers (TDR) are being used to follow changes in soil water content and soil matric potential at 310 locations within the 1.8-ha study area (Hanson et al. 1995). Paired TDR rods were inserted in the soil in April 1992 (0–35 cm and 0–70 cm depths at each location) and monitored at 2–4 wk intervals, thereafter.

The Walker Branch Watershed has been extensively studied over the past 25 years concerning its stand composition, hydrology, soils, and biogeochemistry (Johnson and Van Hook 1989). The climate is typical of the humid Southern Appalachians, with an annual precipitation of 140 cm and mean annual temperature of 13.3°C. Soils on the watershed are primarily typic Paleudults, quite acid (pH 4.2–4.6), cherty, infertile, and highly permeable (Garten and Taylor 1992, Garten 1993). The vegetation is characterized as an upland oak forest with a basal area of 20–25 m^2/ha, mean canopy height of 22 m, and a leaf area index (LAI) of 5.0 (Hutchison et al. 1986). Stand composition within the study area consists of white oak (*Quercus alba*), chestnut oak (*Q. prinus*), and red maple (*Acer rubrum*) as overstory dominants. Red oak (*Quercus rubra*), yellow poplar (*Liriodendron tulipifera*), black gum (*Nyssa sylvatica*), and sourwood (*Oxydendrum arboreum*) are important subdominant species. Dogwood (*Cornus florida*) occupies the forest understory.

The 1.8-ha experimental area was established prior to the initiation of our study in 1992. The actual Throughfall Displacement Experiment began in mid-July 1993, but had no real effect on the vegetation through 1994. This factor enabled us to combine trees from all three 80 × 80 m subplots to characterize plant–herbivore processes over a 3-yr (1992–1994) period.

Field sampling

We used white oak, chestnut oak, and red maple trees for sampling purposes. Nine individual trees of each of three diameter size classes (<2.5 cm dbh, ≥2.5 cm <10 cm dbh, ≥10 cm dbh) were permanently marked for each species from within each 80 × 80 m subplot. These size classes approximate seedling, sapling, and mature trees. However, the "seedling" size category was restricted to those trees containing sufficient foliage to enable sampling; most (71.6%) were <1.5 cm in diameter. We randomly selected three individuals of each size class from the bottom, mid, and top sections

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TABLE 1. Models of three-way factorial designs used for ANOVA in our Walker Branch Watershed, Tennessee, study. We used Model A when comparing the three tree species on any date, and Model B to test individual species responses over the 3-yr study.

Source (Model A)	df	Source (Model B)	df
Species	2	Date	2
Size class	2	Size class	2
Species × Size class	4	Date × Size class	4
Elevation	2	Elevation	2
Species × Elevation	4	Date × Elevation	4
Size class × Elevation	4	Size class × Elevation	4
Species × Size × Elevation	8	Date × Size × Elevation	8
Error (trees)	216	Error (trees)	216

Note: Model A was used for ANOVA in Tables 3, 4, and 6, and in Figs. 2–5; Model B was used for ANOVA in Table 5 and Fig. 6. Species comparisons (Model A) in July (smallest size class not sampled) used 1 df for Size class, 2 df for Species × Size class and Size class × Elevation interactions, and 161 df for the Error term.

of each 0.64-ha subplot to monitor for topographic effects on plant–herbivore processes. In total, 243 trees (81 trees per species) were thus permanently tagged in June 1992 for use throughout the study. Tree sampling occurred in late August 1992, and in early July and late August of 1993 and 1994. The smallest size class was not sampled in July because of the limited number of leaves available each growing season.

Sampling consisted of obtaining 10 leaves from each tree on each sample date. Hand sampling of leaves was possible from smaller trees. We used extension pole cutters to remove two small branches (five leaves per branch) from larger trees. The cutters enabled us to sample up to a height of 14 m. All leaves were randomly selected to avoid visual biases in herbivory determinations. The 10 leaves were bagged, placed in styrofoam containers, and returned to the laboratory for processing. These sampling procedures, as well as the subsequent herbivory and plant chemical analyses, follow earlier studies (Shure and Wilson 1993, Dudt and Shure 1994).

Herbivory and plant chemistry

All leaves sampled in late August of each year were photocopied prior to chemical analysis. Each photocopy indicates the cumulative leaf area damaged or removed by fungal pathogens and different types of insect herbivores throughout the growing season (Hargrove et al. 1984). We used a magnetized digitizer (Micro-plan II, Laboratory Computer Systems, DCS Services, Natick, Massachusetts, USA) to determine total leaf area and percentage of leaf area damaged annually by fungi and different insect feeding guilds, including strip feeders, pit feeders, leaf skeletonizers, leaf miners, leaf rollers, and leaf galls (Coulson and Witter 1984). Interannual differences in insect damage reflect changes in herbivore abundance as well as consumption rates.

Plant chemical assays were performed to determine foliar N content, total phenols, and condensed and hydrolyzable tannin concentrations. The 10 leaves sampled from each tree were composited and oven-dried at 35°C for 48 h, ground to powder in a Wiley Mill (1.27 mm mesh size), and frozen at −15°C until analyzed. Low drying temperatures (<40°C) minimize the irrevocable fixing or denaturing of tannins that occurs at higher temperatures (Swain 1979). A pilot study comparing freeze-drying vs. oven-drying procedures yielded no consistent differences for the species being studied (D. J. Shure, *unpublished data*). Nevertheless, drying conditions can influence the extractability of certain phenolics (Lindroth and Pajutee 1987). Subsamples of the powdered material were analyzed for foliar N content using procedures (Leco Furnace, model-FP428) through the Plant and Soil Analysis Laboratory at the University of Georgia.

We used a 50% methanol extraction procedure as a precursor for plant phenolic analyses (Bate-Smith 1977, 1981). The Folin-Denis technique was used to assay for total phenolics (Swain and Hillis 1959). Hydrolyzable tannins (ellagitannins only) were measured under an N_2 environment using an acetic acid–sodium nitrate procedure (Bate-Smith 1972). Condensed tannins were estimated as proanthocyanidins using a butanol–HCl technique (Bate-Smith 1975, 1981). Total phenolic assays used tannic acid for standard curves, and are expressed as percentage (dry mass) of tannic acid equivalents (TAE). Hydrolyzable tannins are reported as milligrams (dry mass) of hexahydroxydiphenoylglucose equivalents (Bate-Smith 1981) and condensed tannins as percentage dry mass Quebracho tannin equivalents. The possible limitations in these and other procedures for phenolic analyses have been reviewed (Martin and Martin 1982, Mole and Waterman 1987, Wisdom et al. 1987, Hagerman 1988) and are considered elsewhere (Shure and Wilson 1993).

Data analysis

We used three-way (3 × 3 × 3) factorial designs for the ANOVA in our data sets (Table 1). Most ANOVAs included either species (white oak, chestnut oak, and red maple; Model A) or time (1992, 1993, 1994; Model B), along with tree diameter size classes and slope position (up, mid, and down-slope) as main effects.

TABLE 2. Monthly rainfall totals (cm) on the Walker Branch Watershed, Tennessee, during the 1992–1994 summers, in relation to average values ($\bar{X}$ ± 1 SE) recorded over a 13-yr period (1982–1994).

Year	June	July	August	Total
1992	10.2	13.0	8.6	31.8
1993	4.1	5.1	9.3	18.5
1994	19.4	12.8	9.0	41.2
1982–1994 average	10.1 ± 2.12	11.7 ± 1.13	9.8 ± 1.62	31.6 ± 3.15

These ANOVAs were performed for each chemical parameter and for total herbivory, as well as for damage by different insect feeding guilds. Exceptions to this basic design included analyses of the July N and phenolic chemistry data sets (smallest size class omitted), data analysis of fungal damage on leaves of each species (two-way ANOVA), and comparisons of N content across all five sample dates (unbalanced one-way ANOVA). All ANOVAs were nested to account for replicate samples (trees). Data from the three 80 × 80 m subplots were combined in all analyses (no subplot effect). Restricted least significant difference tests were used to locate pairwise differences when ANOVAs were significant (Carmer and Swanson 1973). Statements about main effects have been tempered when interaction terms proved significant.

RESULTS

Rainfall

Moisture relationships at Walker Branch varied over the 1992–1994 summers (Table 2). Precipitation in 1992 closely approximated the 13-yr average for the study area. Soil water content (0–35 cm) in 1992 averaged 12.9–21.9%, and the mean soil matric potential remained above −0.32 MPa from June through August (P. Hanson, *unpublished data*). A fairly severe midsummer drought developed in 1993. The total rainfall in June and July 1993 (9.2 cm) was lower than that of any other year since 1982. Soil water content averaged 7.3–14.0% (Hanson et al. 1995) and soil matric potential reached −1.41 MPa during the dry summer. In contrast, precipitation exceeded the long-term average over the early part of the 1994 summer. Soil water content averaged 18.0–23.2% from June t gust, whereas soil matric potential never dr −0.11 MPa during the wet summer. This tern thus offered an opportunity to compar bivore processes over a sequence of relativ dry, and wet summers.

Foliar chemistry

Leaf N concentrations varied significantl and among tree species (Fig. 1, Table 3). N els averaged ~2.0% dry mass in chestnu oak trees in late August 1992, and were s lower (~1.6%) in red maple. Similar co were present in early July 1993. In contra concentrations dropped significantly (8–1 three species as the drought progressed d Levels were again ~2.0% (oaks) and 1.6% early July 1994. However, less seasonal curred during the wet (1994) growing se estingly, foliar N concentrations were us similar when we compared tree size clas species on each date (Table 3). Elevational in foliar N levels were also generally lacki sample date. However, foliar N levels in c trees often increased from upslope to down this trend being significant at the end of t in 1993 (Table 3). No trends were presen species.

Leaf phenolic concentrations varied among species and, to some extent, amon size classes (Table 4). Total phenolics in A were relatively similar in all three specie However, larger white oak trees contained si

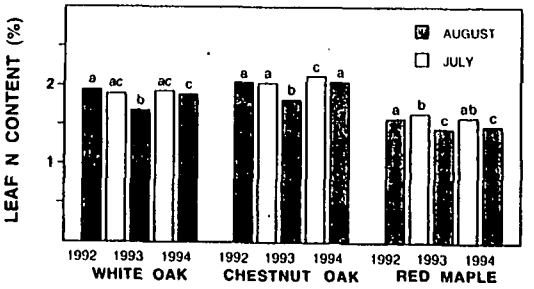

FIG. 1. Nitrogen content in t centage dry mass) of different tree pled on the Walker Branch Watersh see, in August 1992 (average yea August of 1993 (dry), and 1994 (s represent all trees sampled for each the entire study area. Different le means for a particular species indi cant differences, as determined fr ANOVA (white oak, F = 35.0, d chestnut oak, F = 26.3, df = 4, 313 F = 18.2, df = 4, 346; all F values at P < 0.0001).

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RESULTS

Rainfall

Moisture relationships at Walker Branch varied over the 1992–1994 summers (Table 2). Precipitation in 1992 closely approximated the 13-yr average for the study area. Soil water content (0–35 cm) in 1992 averaged 12.9–21.9%, and the mean soil matric potential remained above −0.32 MPa from June through August (P. Hanson, *unpublished data*). A fairly severe midsummer drought developed in 1993. The total rainfall in June and July 1993 (9.2 cm) was lower than that of any other year since 1982. Soil water content averaged 7.3–14.0% (Hanson et al. 1995) and soil matric potential reached −1.41 MPa during the dry summer. In contrast, precipitation exceeded the long-term average over the early part of the 1994 summer. Soil water content averaged 18.0–23.2% from June through August, whereas soil matric potential never dropped below −0.11 MPa during the wet summer. This rainfall pattern thus offered an opportunity to compare plant–herbivore processes over a sequence of relatively average, dry, and wet summers.

Foliar chemistry

Leaf N concentrations varied significantly over time and among tree species (Fig. 1, Table 3). Nitrogen levels averaged ~2.0% dry mass in chestnut and white oak trees in late August 1992, and were significantly lower (~1.6%) in red maple. Similar concentrations were present in early July 1993. In contrast, foliar N concentrations dropped significantly (8–14%) in all three species as the drought progressed during 1993. Levels were again ~2.0% (oaks) and 1.6% (maple) in early July 1994. However, less seasonal decline occurred during the wet (1994) growing season. Interestingly, foliar N concentrations were usually quite similar when we compared tree size classes of each species on each date (Table 3). Elevational differences in foliar N levels were also generally lacking on each sample date. However, foliar N levels in chestnut oak trees often increased from upslope to downslope, with this trend being significant at the end of the drought in 1993 (Table 3). No trends were present for other species.

Leaf phenolic concentrations varied consistently among species and, to some extent, among different size classes (Table 4). Total phenolics in August 1992 were relatively similar in all three species (Fig. 2). However, larger white oak trees contained significantly

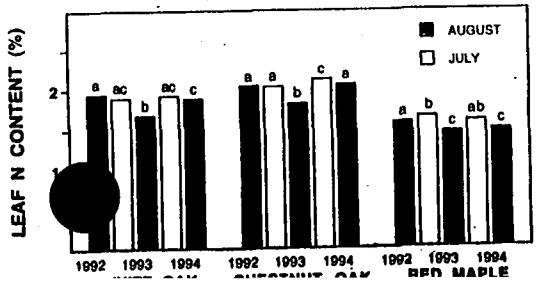

FIG. 1. Nitrogen content in leaves (percentage dry mass) of different tree species sampled on the Walker Branch Watershed, Tennessee, in August 1992 (average year), July and August of 1993 (dry), and 1994 (wet). Means represent all trees sampled for each species in the entire study area. Different letters above means for a particular species indicate significant differences, as determined from one-w[illegible] ANOVA (white oak, $F = 35.0$, df = 4, [illegible] chestnut oak, $F = 26.3$, df = 4, 313; red ma[illegible] $F = 18.2$, df = 4, 346; all F values significa[illegible] at $P < 0.0001$).

TABLE 3. Results of three-way factorial ANOVAs of foliar N content in tree species sampled on the Walker Branch Watershed, 1992–1994. The *F* values are presented for main effects and their interactions, with levels of significance indicated.

Date	Main effects			Interactions		
	Species (S)	Size (SC)	Elevation (E)	S × SC	S × E	SC × E
August 1992	236.0**	2.89	1.14	0.25	1.58	1.20
July 1993	63.4**	1.03	1.28	0.02	0.69	0.93
August 1993	92.3**	3.67*	7.41**	2.03	2.52*	0.65
July 1994	98.0**	0.40	1.71	1.19	0.70	0.02
August 1994	254.5**	1.98	1.44	1.62	0.55	1.00

Note: Variance components and their degrees of freedom in all ANOVAs are as in Table 1 (Model A).
* $P < 0.05$; ** $P < 0.01$.

higher levels of total phenolics than did smaller size classes (Table 4). This pattern was absent for chestnut oak and red maple. Hydrolyzable tannins in 1992 were significantly higher in white oak leaves than in chestnut oak and especially in red maple leaves. Hydrolyzable tannin concentrations in all species were similar among size classes. In contrast, condensed tannins were generally higher in maple than in oak leaves, and higher in mature overstory than in understory conspecifics for all three species; many of these differences were significant (Table 4, Fig. 2). These patterns of leaf phenolics were present when reexamined in early July 1993 (Fig. 3). However, total phenolics were considerably higher in white oak leaves than in other species.

Species differences persisted at the end of the 1993 and 1994 growing seasons (Figs. 4 and 5). Total phenolics remained significantly higher in white oak trees than other species. Oak leaves again contained significantly higher hydrolyzable tannins whereas maple trees allocated more carbon to condensed tannin production (Table 4). This reciprocal response in allocation of hydrolyzable vs. condensed tannins was thus consistent on all sample dates (Table 4). However, the higher levels of total phenolics (white oak) and condensed tannins in overstory vs. understory conspecifics was less evident at the end of the drought in 1993 and during 1994 (Figs. 4 and 5, Table 4). Hydrolyzable tannins were significantly higher in mature than understory white oak trees during the wet 1994 summer.

The pronounced year-to-year differences in phenolic production appear to be weather related (Fig. 6). Eight of the nine measures of plant phenolics were reduced during the drier 1993, in comparison to the more normal 1992 summer, and most differences were significant. Results for the wet 1994 growing season were varied. Total phenolics and hydrolyzable tannins remained low in 1994, whereas condensed tannin production was significantly higher for all species during the particularly wet summer. Leaf phenolics exhibited no clear upslope-to-downslope patterns throughout the study, even when differences were significant (Table 4).

TABLE 4. Results of three-way factorial ANOVAs of total phenolics and hydrolyzable (H) and condensed (C) tannins in tree species sampled at Walker Branch, 1992–1994. The *F* values are presented for main effects and interactions, with levels of significance indicated.

Date	Measure	Main effects			Interactions		
		Species (S)	Size (SC)	Elevation (E)	S × SC	S × E	SC × E
1992							
August	Phenolics	10.9**	8.16**	2.25	7.13**	0.36	0.70
	Tannins, H	101.4**	0.35	13.09**	1.15	3.91**	1.27
	Tannins, C	17.5**	13.29**	2.85	1.18	0.97	1.80
1993							
July	Phenolics	42.4**	1.39	4.39*	1.54	2.71*	0.80
	Tannins, H	212.4**	0.36	10.11**	1.83	4.75**	0.67
	Tannins, C	33.4**	12.95**	0.51	2.53	2.11*	0.71
August	Phenolics	264.4**	0.22	3.43*	1.11	0.91	0.38
	Tannins, H	157.0**	3.98*	0.77	4.42**	3.02	1.52
	Tannins, C	44.6**	2.46	0.20	0.91	0.70	2.13
1994							
July	Phenolics	50.6**	3.04	4.34*	3.25*	2.85*	0.53
	Tannins, H	324.0**	6.52*	3.94*	4.49*	0.61	1.90
	Tannins, C	22.1**	0.27	3.62*	2.03	1.46	0.15
August	Phenolics	61.6**	5.04**	0.08	5.46**	0.77	0.77
	Tannins, H	550.2**	10.57**	2.31	5.17**	1.30	1.10
	Tannins, C	40.5**	13.02**	5.29**	2.12	1.41	1.11

Note: Variance components and their degrees of freedom in all ANOVAs are as in Table 1 (Model A).
* $P < 0.05$; ** $P < 0.01$.

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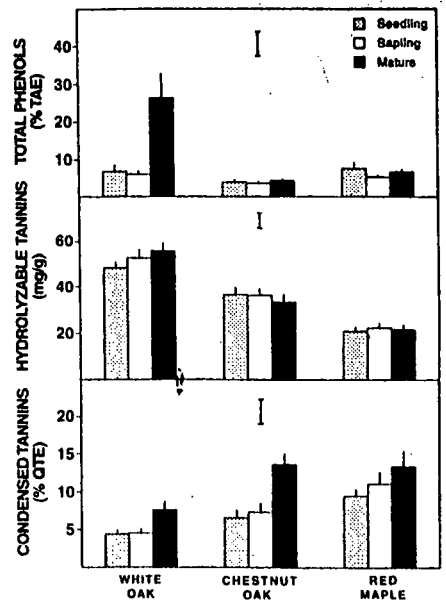

FIG. 2. Levels of phenolic chemistry (means + 1 SE) in leaves of tree species sampled at Walker Branch in August 1992. Diameter size classes sampled are presented as seedling, sapling, and mature trees. Total phenols are expressed as percentage of tannic acid equivalents (TAE), hydrolyzable tannins as milligrams of hexahydroxydiphenoylglucose equivalents per gram of leaf tissue, and condensed tannins as percentage of Quebracho tannin equivalents (QTE). The interval at the top of each graph is the least significant difference ($P < 0.05$), which indicates where significant differences exist among all means presented.

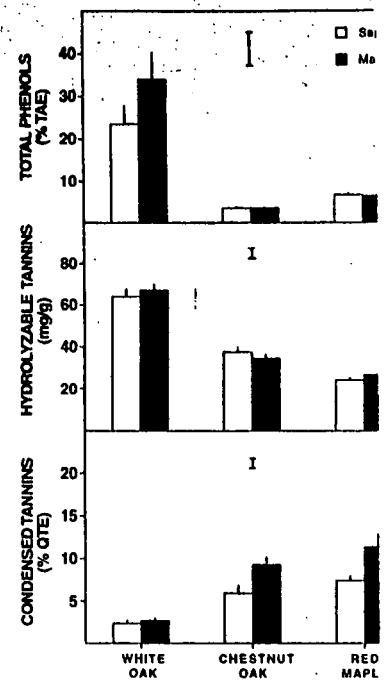

FIG. 3. Levels of phenolic chemistry (means + leaves of tree species sampled at Walker Branch in Ju Total phenols, hydrolyzable tannins, and condensed are expressed as in Fig. 2. The interval at the top graph is the least significant difference ($P < 0.05$) indicates where significant differences exist among a presented.

Insect herbivory

Insect herbivory varied significantly among species and over the 3-yr study (Tables 5 and 6). Total leaf area damaged was significantly higher on oak than on maple trees throughout the study; white oak leaves always had significantly more damage (Table 6). Herbivore damage was significantly reduced on white oak trees during the drier 1993 summer than that of 1992 (Table 6). A similar trend for chestnut oak was not significant. Damage on maple trees was identical in both years. In contrast, the extent of insect damage was significantly higher on all species during the wet summer of 1994. No significant differences emerge we compared total damage on different size cla trees of each species during any year (Table 6)

Tree species at Walker Branch differed some the relative importance of insect feeding guilds 5 and 6). Strip feeders (i.e., Lepidoptera larvae) the greatest damage on all three tree species thro the study (Table 5). Leaf skeletonizers were a portant herbivores on white oak and chestnut oa but not on red maple (Table 5). Adhesive skelet which feed mainly within the cover afforded a hesing two leaves together, caused much of t letonizing damage on both oak species. Leaf was significantly more important on oak than o trees, whereas pit feeding was greater on mapl (Tables 5 and 6). Leaf galls and leaf rollers ac for <0.1% of the leaf area damaged on any throughout the study.

Insect feeding guilds varied in their resp

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TABLE 4. Results of three-way factorial ANOVAs of total phenolics and hydrolyzable (H) and condensed (C) tannins in tree species sampled at Walker Branch, 1992–1994. The F values are presented for main effects and interactions, with levels of significance indicated.

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	[illegible]ins, C	22.1**	0.27	3.62*	2.03	1.46	0.15
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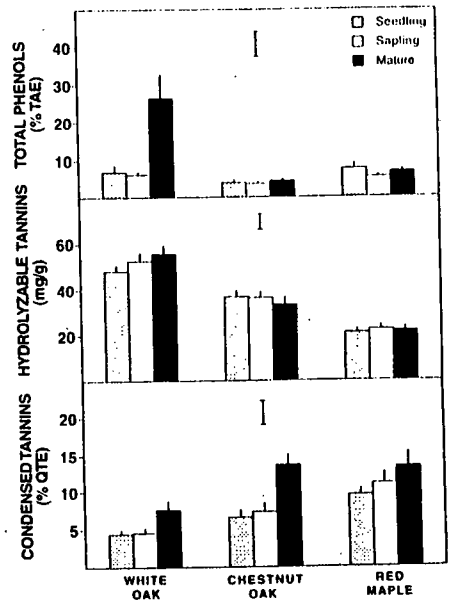
	Tannins, C	40.5**	13.02**	5.29**	2.12	1.41	1.11

Note: Variance components and their degrees of freedom in all ANOVAs are as in Table 1



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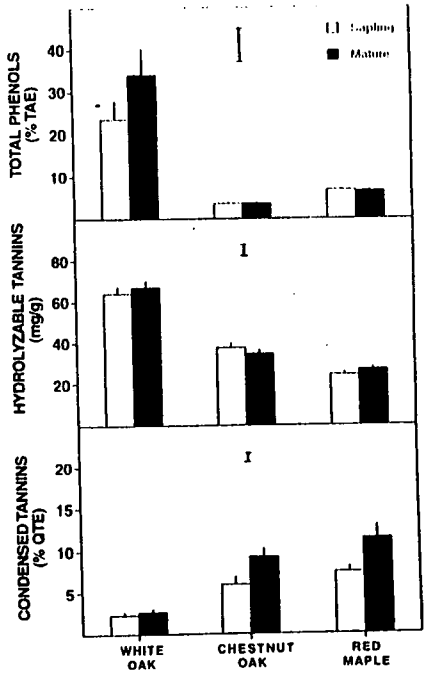

FIG. 3. Levels of phenolic chemistry (means + 1 SE) in leaves of tree species sampled at Walker Branch in July 1993. Total phenols, hydrolyzable tannins, and condensed tannins are expressed as in Fig. 2. The interval at the top of each graph is the least significant difference ($P < 0.05$), which indicates where significant differences exist among all means presented.

Insect herbivory

Insect herbivory varied significantly among species and over the 3-yr study (Tables 5 and 6). Total leaf area damaged was significantly higher on oak than on maple trees throughout the study; white oak leaves always had significantly more damage (Table 6). Herbivore damage was significantly reduced on white oak trees during the drier 1993 summer than that of 1992 (Table 6). A similar trend for chestnut oak was not significant. Damage on maple trees was identical in both years. In contrast, the extent of insect damage was mer of 1994. No significant differences emerged when we compared total damage on different size classes of trees of each species during any year (Table 6).

Tree species at Walker Branch differed somewhat in the relative importance of insect feeding guilds (Tables 5 and 6). Strip feeders (i.e., Lepidoptera larvae) caused the greatest damage on all three tree species throughout the study (Table 5). Leaf skeletonizers were also important herbivores on white oak and chestnut oak trees, but not on red maple (Table 5). Adhesive skeletonizers, which feed mainly within the cover afforded after adhesing two leaves together, caused much of the skeletonizing damage on both oak species. Leaf mining was significantly more important on oak than on maple trees, whereas pit feeding was great[illegible]ple trees (Tables 5 and 6). Leaf galls and leaf [illegible]ccounted for <0.1% of the leaf area damaged [illegible]ly species throughout the study.

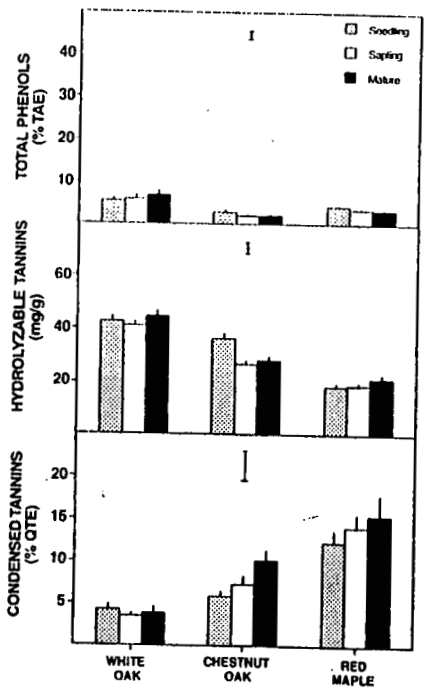

FIG. 4. Levels of phenolic chemistry (means + 1 SE) in leaves of tree species sampled at Walker Branch in August 1993. Total phenols, hydrolyzable tannins, and condensed tannins are expressed as in Fig. 2. The interval at the top of each graph is the least significant difference ($P < 0.05$), indicating where significant differences exist among all means presented.

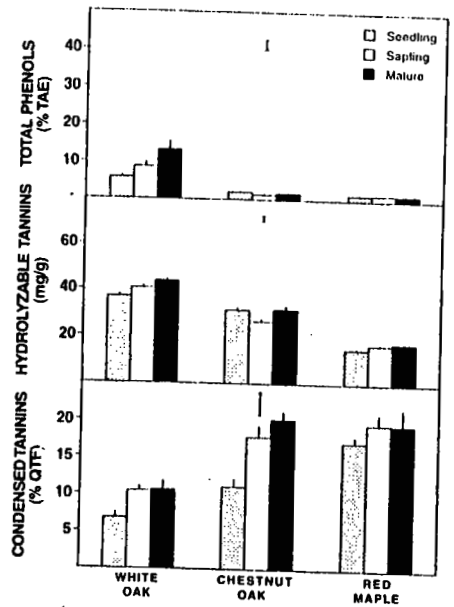

FIG. 5. Levels of phenolic chemistry (means + 1 SE) in leaves of tree species sampled at Walker Branch in August 1994. Total phenols, hydrolyzable tannins, and condensed tannins are expressed as in Fig. 2. The least significant difference ($P < 0.05$) interval is depicted as in Fig. 2.

moisture changes during the study (Table 5). Strip feeding remained unchanged on all three tree species when comparing 1992 and 1993. In contrast, skeletonizing, pit feeding, and leaf mining were all reduced during the drought in 1993, and nearly all differences were significant. However, strip feeding was greater on all tree species during the wet 1994 growing season. Skeletonizing, pit feeding, and mining damage showed no clear increase during the wet year (Table 5). Only skeletonizing on chestnut oak trees was significantly elevated in 1994.

Fungal damage

The level of fungal damage differed between tree species and in response to rainfall variation (Table 7). Damage was considerably higher on maple than oak 1992 and the trend for red maple was significant (Table 7). Damage levels on red maple and chestnut oak leaves were highest during the wet 1994 summer.

DISCUSSION

Patterns of foliar chemistry

The tree species selected for study represent slow-growing canopy dominants occupying a rather nutrient-poor upland oak forest (Garten 1993). Thus these species should, in theory, employ relatively high levels of foliar phenolics in minimizing herbivore damage and subsequent tissue replacement costs (Coley et al. 1985). In fact, the three species actually exhibited quite different constitutive patterns of foliar N and plant phenolics. Oak trees maintained higher levels of foliar N and hydrolyzable tannins, whereas maple leaves were especially low in N content, but higher in condensed tannin production. Nevertheless, foliar N levels in all three species were relatively low for trees occupying temperate deciduous forests (Feeny 1970, Mattson 1980, Coley and Aide 1991). In contrast, species stud-

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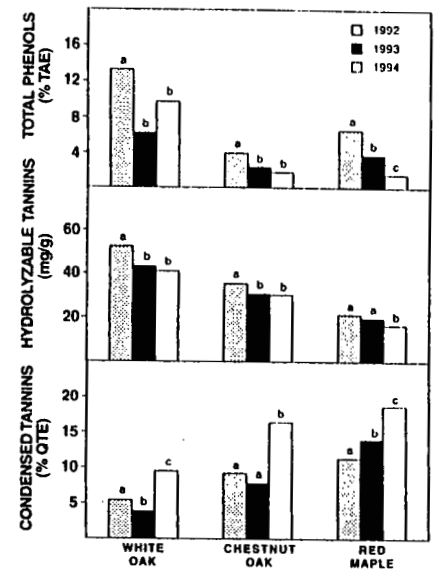

FIG. 6. Levels of phenolic chemistry in leaves of tree species sampled at Walker Branch in August of 1992 (average rainfall), 1993 (dry), and 1994 (wet). Means reflect all trees sampled for each species in the study area. Total phenols (TP), hydrolyzable tannins (HT), and condensed tannins (CT) are expressed as in Fig. 2. Means with different letters are significantly different. The F values derived from three-way ANOVA (Model B, Table 1, Date) for white oak were: TP, 4.8; HT, 21.4; CT, 33.8; for chestnut oak: TP, 20.8; HT, 5.7; CT, 39.3; and for red maple: TP, 57.2; HT, 10.5; CT, 16.5. All F values were significant at the $P < 0.01$ level.

within the Southern Appalachian Mountains in North Carolina (Shure and Wilson 1993). Tannin concentrations in maple trees at Walker Branch were actually comparable to those in conspecifics occupying highly insolated forest openings at the North Carolina site. Therefore, the species studied at Walker Branch were relatively low in foliar N and generally high in phenolic components.

Studies to date have rarely evaluated life cycle changes in foliar chemistry of forest tree species. Thus, very little information is available to test the relative fit of the carbon/nutrient balance or growth/differentiation balance hypotheses as plants shift from understory to canopy positions and potentially exploit nutrients available at different soil depths. Interestingly, our findings showed minimal variation in foliar N concentrations for different size classes of all three species class differences may reflect existing constraints on plant N uptake in a nutrient-poor habitat (Garten 1993).

Leaf phenolic contents often exhibited size class differences that appeared to be directly correlated with available sunlight. Mature canopy-dwelling trees generally contained higher levels of condensed tannins and occasionally total phenolics (white oak) than did conspecifics occupying the shaded understory. These canopy trees receive greater rates of photosynthetically active radiation (Denslow et al. 1990), which can lead to the metabolic accumulation and storage of poorly translocatable phenolic compounds, such as the more structurally based condensed tannins (Mole et al. 1988). This response should prove especially true in N-limited habitats where growth is limited more than photosynthesis, and where buildups of secondary metabolites are expected (Mattson 1980, Bryant et al. 1983, Larsson et al. 1986, Chapin et al. 1987, Tuomi et al. 1988, Herms and Mattson 1992). In contrast, understory trees are light limited; thus, a similar accumulation of carbon-based differentiation products is prevented. The buildup of condensed tannins in canopy-dwelling conspecifics thus fits the carbon/nutrient balance hypothesis and further supports the trend of strong positive correlations between light availability and plant phenolic production (Langenheim et al. 1981, Waterman et al. 1984, Larsson et al. 1986, Bryant et al. 1987, Mole et al. 1988, Herms and Mattson 1992, Shure and Wilson 1993, Dudt and Shure 1994). In contrast, hydrolyzable tannins generally failed to show this canopy/understory relationship. The lack of size class differences in hydrolyzable tannin concentrations may reflect the ease of maintenance of similar constitutive levels of this more mobile category of tannins that are purported to be especially effective against insect herbivores (Zucker 1983).

Emerging patterns suggest a differential utilization of hydrolyzable vs. condensed tannins by forest tree species (Rossiter et al. 1988, Shure and Wilson 1993). Results from our upland oak forest indicate a clear difference between oaks and maples in their synthesis of hydrolyzable vs. condensed tannins. These observed differences in tannin production may represent adaptive trade-offs in phenolic utilization against insect herbivores or microbial pathogens (Zucker 1983). For example, condensed tannins were especially high in all species when fungal pathogens might have been particularly pronounced during the wet 1994 growing season. This was especially true for maple trees, which exhibited much greater susceptibility to fungal damage than did oaks throughout the study. Past reports of seasonal increases in condensed tannins and corresponding decreases in hydrolyzable tannins (Baldwin et al. 1987, Shure and Wilson 1993) could be related to changing pressures of herbivore vs. pathogen pop-

TABLE 5. Annual leaf area damaged (%) by feeding guilds of insect herbivores on tree species (size classes combined) sampled at Walker Branch Watershed during 1992–1994. The *F* values were determined through three-way ANOVA (see Table 1, Model B), with different letters indicating means that are significantly different. Totals ($\bar{X}$ ± 1 SE) include all six guilds.

Guild	1992	1993	1994	*F*
White oak				
Strip feeders	6.85[b]	6.54[b]	8.42[a]	2.83†
Skeletonizers	4.52[a]	3.11[b]	4.07[ab]	3.64†
Pit feeders	0.25[a]	0.17[b]	0.13[b]	4.42*
Miners	0.56[a]	0.12[b]	0.10[b]	25.36**
Total	12.4 ± 0.59[a]	10.1 ± 0.57[b]	13.0 ± 0.82[a]	4.37*
Chestnut oak				
Strip feeders	4.47[a]	4.99[a]	5.56[a]	1.57
Skeletonizers	3.66[b]	2.44[b]	4.94[a]	8.44**
Pit feeders	0.15[a]	0.09[b]	0.09[b]	3.47*
Miners	0.31[a]	0.09[b]	0.07[b]	14.85**
Total	8.6 ± 0.53[b]	7.7 ± 0.59[b]	10.7 ± 0.78[a]	6.25**
Red maple				
Strip feeders	4.93[b]	5.38[b]	7.47[a]	5.42**
Skeletonizers	0.33[a]	0.24[a]	0.22[a]	1.76
Pit feeders	0.56[a]	0.26[b]	0.31[b]	36.92**
Miners	0.07[a]	0.02[b]	0.01[b]	4.14*
Total	6.0 ± 0.52[b]	6.0 ± 0.64[b]	8.0 ± 0.61[a]	3.87*

* $P < 0.05$; ** $P < 0.01$; † $P = 0.06$.

mobilization of hydrolyzable tannins might prove to be especially effective. The progressive increase in total incidences of herbivore damage over time facilitates the spread of microbial pathogens within leaves as foliar concentrations of condensed tannins are accumulating. Tree species may thus develop seasonal separation in the relative production of constitutive levels of different categories of tannins, and may possibly rely on induced accumulations when herbivores or pathogens are especially numerous (Rhoades 1979). Further research is needed to distinguish whether these tannin differences are adaptive or simply reflect passive accumulations under contrasting microenvironmental conditions.

Plant responses to moisture regimes

Plant populations exhibit a wide variety of responses in adjusting to alterations in moisture availability (Hsiao 1973, Gershenzon 1984, Horner 1990, Chapin 1991, Louda and Collinge 1992). The initial stages of drought may promote increases in foliar nutrients and soluble carbohydrate concentrations (Hsiao 1973,

TABLE 6. Results of three-way factorial ANOVAs of damage by different insect feeding guilds on tree species sampled on the Walker Branch Watershed during 1992–1994. The *F* values are presented for main effects and their interactions, with levels of significance indicated.

Year	Guild	Main effects			Interactions		
		Species (S)	Size (SC)	Elevation (E)	S × SC	S × E	SC × E
1992	Total	35.91**	0.66	0.25	1.06	1.58	1.09
	Strip	9.48**	1.62	0.74	0.77	1.95	0.62
	Skeletonizers	51.12**	0.12	0.29	1.88	1.87	1.68
	Pit	50.17**	2.94	3.50*	0.79	1.66	1.11
	Miners	20.96**	1.49	3.61*	1.50	1.99	0.59
1993	Total	13.25**	1.06	1.37	1.32	1.11	1.02
	Strip	2.47	0.90	0.18	0.78	0.43	0.95
	Skeletonizers	63.75**	0.31	5.97**	2.54*	2.76*	0.60
	Pit	14.69**	0.95	2.11	0.37	1.40	0.80
	Miners	4.23*	1.30	0.70	1.10	1.47	1.54
1994	Total	11.82**	0.98	0.48	6.19**	0.77	2.05
	Strip	3.84*	0.40	1.36	4.09**	0.94	1.60
	Skeletonizers	52.76**	3.29*	0.82	5.46**	0.43	1.42
	Pit	43.40**	1.40	0.73	2.53*	2.04	2.22
	Miners	13.66**	2.68	0.78	1.13	0.94	1.95

Note: Variance components and their degrees of freedom in all ANOVAs are as in Table 1 (Model A).

* $P < 0.05$; ** $P < 0.01$.

TABLE 7. Annual leaf area damaged (%) by fungal pathogens utilizing tree species sampled on the Walker Branch Watershed during 1992–1994. Data were obtained from all trees of each species ($N = 27$) present on the central 80 × 80 m subplot of the study area.

Type species	1992	1993	1994	*F*
White oak	0.22	0.10	0.11	0.94
Chestnut oak	0.17	0.09	0.21	0.98
Red maple	8.61[a]	2.75[b]	9.97[a]	8.31**

Note: The *F* values were determined through two-way ANOVA (Date, df = 2; Size class, df = 2; Date × Size class, df = 4; Error, df = 72), with different letters indicating means that are significantly different.

** $P < 0.01$.

Hsiao et al. 1976, White 1984, Mattson and Haack 1987*a*, *b*, Louda and Collinge 1992) through plant osmotic adjustments in establishing drought tolerance (Kramer 1983). However, the potential for roots to absorb nutrients will gradually decline as water stress develops (Chapin 1991). Thus, moderate drought will reduce growth more than photosynthesis (Kozlowski 1982, Kramer 1983, Wardlaw 1990), enabling carbohydrates to accumulate in plant foliage. Part of this excess pool of carbohydrates may be allocated preferentially to root development, thereby permitting root : shoot biomass ratios to increase adaptively until carbon fixation becomes limited as water stress progresses (Bradford and Hsiao 1982, Schulze et al. 1987, Chapin 1991). Any excess carbon remaining in leaves during moderate drought is available for storage or use in the production of secondary metabolites for possible defensive purposes (Gershenzon 1984, Herms and Mattson 1992). Ultimately, severe drought stress will reduce photosynthetic rates and the overall quality of leaf tissues (Ehleringer and Cook 1984, Chapin 1991). Leaf contents may also undergo resorption if leaf senescence occurs in response to drought (Killingbeck 1996).

These findings suggest a nonlinear response of plant phenolic production to increasing intensities of water deficits (Mattson and Haack 1987*a*, Horner 1990). Secondary metabolites, including phenolic compounds, should increase in leaves as N uptake rates and growth are curtailed during the transition from mild to moderate drought. However, the concentrations of these secondary metabolites should ultimately decrease, either because of a limitation in photosynthetic enzymes available for carbohydrate production, a reduction in the activity of enzymes involved in phenolic biosynthesis, or through resorption (Gershenzon 1984). Recent validation of this nonlinear response (Horner 1990) fits the major tenets of the carbon/nutrient and growth/differentiation balance hypotheses and offers a possible resolution of the long-standing enigma of inconsistent responses of plant phenolics to moisture [illegible] Ayres 1993). Past studies were apparently conducted at varying intensities of soil water stresses.

Tree species studied at Walker Branch exhibited similar responses to rainfall fluctuations over the study period. The changes in foliar chemistry during wet or dry summers were consistent for all size classes of trees of each species, and generally fit the patterns expected concerning shifts in resource allocation from growth to differentiation (Herms and Mattson 1992). Foliar N concentrations at Walker Branch normally decrease throughout the growing season, following peak levels in early spring (Garten 1993). Nevertheless, the decline in foliar N in oaks and maple trees during the midsummer drought in 1993 reached levels well below those present by late August in 1992 and 1994. The direct correlation observed between rainfall and foliar N levels should be expected, given the relatively low soil N levels present in the study area (Garten 1993). Any drought-induced shift to water uptake from deeper, more nutrient-impoverished soil strata would further reduce foliar N concentrations.

Nearly all measures of foliar phenolic chemistry were lower during the much drier growing season of 1993 than of 1992. The consistency of this response probably reflects the presence of severe soil water deficits in 1993. The reduction in foliar N levels during drought should have increased phenolic concentrations if photosynthetic rates had remained high and growth had ceased (Mattson and Haack 1987*b*, Horner 1990, Herms and Mattson 1992). Instead, the magnitude of the drought was apparently sufficient to limit either carbon production or phenolic biosynthesis (Gershenzon 1984). Either mechanism would promote declines in phenolic production as the possibility of carbon allocation to differentiation products, such as secondary metabolites, was limited. Early resorption and leaf senescence may not have occurred, because the timing of autumn litterfall was quite similar during wet and dry years at Walker Branch (Paul Hanson, *personal communication*).

The differential response of phenolic compounds during the wet 1994 summer is more difficult to reconcile. The failure of total phenol and hydrolyzable tannin levels to rebound following drought might reflect a preferential utilization of carbon for growth over differentiation as soil N uptake increased during high rainfall in 1994 (Bryant et al. 1983, Herms and Mattson 1992, Tuomi 1992). The fact that annual bole diameter growth of mature trees was 50.4% (white oak), 51.6% (chestnut oak), and 95.3% (red maples) higher in 1994 than in 1993 (Paul Hanson, *unpublished data*) supports this contention. In addition, any reduction in carbon production and subsequent storage during the 1993 drought would diminish [illegible]on pool available for phenolic production dur[illegible]ext growing season. Haukioja and Neuvonen ([illegible]), Tuomi et al. (1988), and Marquis and Whelan (1994) have documented the [illegible]

delayed expressions of carbon and nutrient shortages through a second or subsequent year. The combination of shortages of stored carbon and high soil N availability in 1994 may have limited carbon allocation to differentiation products such as tannins, or may have promoted adaptive trade-offs in the relative production of different categories of phenolics. The occurrence of especially high levels of condensed tannins in all species in 1994 may represent such a trade-off, because fungal damage was greater on maple and, to some extent, chestnut oak trees during the wet than during the dry summers (Zucker 1983). Induced responses of this type would reflect optimal defense (Rhodes 1979, Zangerl and Rutledge 1996) if further fungal damage were restricted. However, the speculative nature of these explanations points out the need for further experimental validation of the mechanistic basis for plant phenolic responses under varying moisture regimes.

Insect herbivory

Insect herbivore damage on the Walker Branch Watershed varied among species and in response to rainfall fluctuations. Insect damage on oak trees exceeded average levels reported for broadleaf tree species occupying temperate deciduous forests (Schowalter et al. 1986, Coley and Aide 1991), but were comparable to or less than levels reported for oak seedlings and saplings in Missouri forests (Sork et al. 1993, Marquis and Whelan 1994). The high levels of leaf stripping and skeletonizing damage on oaks occurred despite relatively low levels of foliar N (Coley and Aide 1991, Garten 1993) and high concentrations of total phenolics and/or hydrolyzable tannins. In contrast, insect damage was quite low on red maple foliage, as a result of the absence of leaf skeletonizing. The especially low foliar N levels in maple trees at Walker Branch may prevent skeletonizers from utilizing maple tissue. Foliar N levels can significantly influence insect feeding (Fox and McCauley 1977, Mattson 1980, Scriber and Slansky 1981, White 1984, Mattson and Scriber 1987), particularly because of the metabolic constraints imposed by much lower N concentrations in leaf than in insect tissues (Mattson 1980, Ayres 1993). In fact, the incidence of insects feeding on leaves containing N concentrations <2% is generally quite limited (Fox and McCauley 1977).

Few, if any, studies have evaluated herbivore damage at different life cycle stages of forest tree species (Schowalter et al. 1986). Methodological constraints have often limited studies to smaller seedlings or saplings without including mature conspecifics. No patterns emerged when we compared insect damage on different size classes of oaks or maple species. Instead, tannin levels in mature trees of each species apparently failed to reduce insect feeding, unless herbivore densities were greater on the more-insolated overstory conspecifics (Schupp and Feener 1991). Nevertheless, the overall absence of differences in herbivore pressure from early to late stages of forest tree development fails to support earlier predictions that acquired resistance should produce lower damage levels in mature trees (Karban 1987).

Considerable difficulty has existed in predicting the overall response of insect herbivores to moisture fluctuations (Gershenzon 1984, Mattson and Haack 1987*a*, Larsson 1989, Louda and Collinge 1992, Ayres 1993, Stowe et al. 1994). This difficulty seems to be largely a product of the varied responses of specific insect herbivores to changing ratios of foliar nutrients and plant phenolics as water stress increases (Bazzaz et al. 1987, Louda and Collinge 1992). Insect damage should increase during the initial stages of drought, if foliar nutrients and soluble carbohydrates accumulate through plant osmotic adjustments (Stowe et al. 1994). However, herbivores may become limited if secondary metabolites accumulate as moderate water stress retards growth more than photosynthesis (Horner 1990, Herms and Mattson 1992). The extent of this impact might depend on the relative ability of insect detoxification systems to handle the possible buildup of carbon-based defenses. Ultimately, severe water stress should limit photosynthesis as well as nutrient and water uptake, thereby rendering plant foliage largely unsuitable for insect herbivores (White 1984, Louda and Collinge 1992). Direct insect mortality should thus occur during severe droughts.

The level of insect damage on the Walker Branch Watershed was directly correlated with rainfall totals during the 3-yr study. Foliar N concentrations appeared to be quite important in regulating consumption by insects during these rainfall fluctuations. For example, the reduction in skeletonizing damage on oak trees during the 1993 drought occurred when foliar N levels declined below 2.0%. This drop in consumption during drought occurred despite a concomitant reduction in foliar phenolics in both oak species. The combination of low foliar N and possibly low leaf water content (Scriber 1984) in oaks may have caused sufficient insect mortality or reduced feeding to limit skeletonizing damage during the severe midsummer drought. The relative absence of skeletonizers from N-limited maple foliage provides support for this assertion. Thus, leaf skeletonizers at Walker Branch may be particularly sensitive to rainfall-related effects on foliar N concentrations.

Foliar chemistry appeared to be more favorable for insect herbivores during the wet 1994 growing season

chestnut oaks. The allocation of considerable carbon to condensed tannin production in all species in 1994 may have proved more important in limiting fungal damage than insect herbivory. These results suggest that insect damage on our study area at Walker Branch involves the response of specific feeding guilds to weather-related effects on concentrations of foliar N, and probably to a lesser extent on plant phenolics. Louda and Collinge (1992) also reported guild-specific insect responses following soil water manipulations, and Larsson (1989) has clearly articulated why the actual response of insect herbivores to plant stress should be feeding-guild specific. Thus, a guild approach seems advisable in future attempts at isolating causal mechanisms for changes in consumption by insect herbivores during climatic fluctuations.

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DENSITY-DEPENDENT PROCESSES IN MEADOW VOLES: AN EXPERIMENTAL APPROACH[1]

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Abstract. Patterns of population dynamics are determined by the interaction between density-dependent and density-independent processes. To examine the responsiveness of various demographic and behavioral processes to population density, we maintained replicate meadow vole (*Microtus pennsylvanicus*) populations at low, medium, and high densities inside field enclosures in southeastern New York. Density was manipulated by removing subadults during biweekly live-trapping sessions. Under higher density conditions voles exhibited: (1) a truncated breeding season; (2) reduction in growth rates of individuals; (3) increase in age (but not size) at sexual maturity; and (4) reduction in movement distances of individuals. Extremely large-bodied voles were most frequent in low-density enclosures and least common in high-density ones. Survival rates of adults were delayed density-dependent. Reproductive rates during the middle of the breeding season and survival rates of juveniles and subadults were not affected by vole density. We conclude that vole populations are stabilized by density-dependent reductions in reproductive rate and recruitment, but destabilized by density-independent survival rates of young, and by density-dependent compression of individual movements, which accomodates population growth. The time delay in the effects of density on survival of adults may provide a mechanism for vole cycles in which lagged density-dependent mortality plays a central role.

Key words: age at sexual maturity; breeding season length; density vs. individual performance; density vs. space use; enclosure; field experiment; individual growth; movement distance vs. density; reproductive rates; survival rates.

INTRODUCTION

The arvicolines (microtine) rodents are perhaps best known for their population cycles. Many populations fluctuate in size an order of magnitude or more, with 2–4 yr between peaks (Krebs and Myers 1974, Hansson and Henttonen 1988, many others). In attempting to explain this unusual pattern of population dynamics, ecologists have searched unsuccessfully for features unique to arvicolines (Elton 1942, Chitty 1967, Finerty 1980, Cockburn 1988, Batzli 1992). The predominant approach has been to treat the vole cycle as a single, unitary phenomenon, and to provide a unifying hypothesis to explain most or all phases, i.e., increase, peak, decline, and low phases, as well as their rhythm (reviewed by Cockburn [1988]; see also Lidicker [1988]). There is widespread disagreement among researchers on arvicolines about the accuracy and utility of the resulting models, and because they are specifically intended to explain vole cycles, the models have limited applicability to animal populations in general.

Any pattern of population dynamics, including a cycle, is caused by an interplay between density-dependent and density-independent processes. Unfortunately, relatively little attention has been paid by vole ecologists to disentangling which population processes are more or less sensitive to population density. Density-dependent processes, acting with little or no delay, tend to stabilize population size, and density-independent processes will destabilize it (Royama 1992). Thus, density-independent, or delayed density-dependent processes should be important in strongly fluctuating populations.

Many investigators have monitored demography and space use of freely fluctuating vole populations. It is often claimed that rates of natality, mortality, or dispersal are not density dependent (Krebs and Myers 1974, Finerty 1980, Gaines and McClenaghan 1980, Bondrup-Nielsen 1987), only weakly so (Krebs and Myers 1974, Mihok et al. 1985), or delayed density-dependent (Schaffer and Tamarin 1973, Stenseth and Anonsen 1988, Hanski et al. 1991, 1993, Turchin 1993). For instance, reproductive rates may remain high even in high-density populations (Batzli and Pitelka 1971, Lidicker 1973, Rodd and Boonstra 1984), and survival rates can be low at either low or high density (Krebs et al. 1973, Boonstra and Rodd 1983, Mihok et al. 1985). Sharp declines in numbers can follow a period of high or only moderate density (Krebs and Boonstra 1978). Emigration rates are not observed to be density dependent (Gaines and McClenaghan 1980, Lidicker and Stenseth 1992). It is argued that vole demography is sensitive to the phase of the cycle (Krebs et al. 1973, Krebs and Myers 1974, Chitty 1987), but not necessarily to density per se.

However, the effects of density itself on demographic processes can be difficult to determine in freely fluctuating populations for three primary reasons. First,

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establishing cause-and-effect relationships is problematic. Investigators may apply correlational methods to assess the relationship between density and rates of natality, mortality, and dispersal, but often it is difficult to determine the polarity of the causal relationship and to eliminate spurious correlations caused by unmeasured factors and unknown time lags. Second, many vole populations pass through density levels very quickly, making the effects of current density on current or future demographic performance difficult to detect. Finally, time-series approaches to examining the strength and timing of density dependence in population growth rates (Hanski et al. 1993, Turchin 1993) rarely allow exploration of the demographic or behavioral mechanisms of any observed density dependence.

In this study we used an experimental approach to examine the relationship between population density and demographic and behavioral processes in meadow voles (*Microtus pennsylvanicus*). By maintaining vole populations at different levels of density through time, we attempted to isolate density and its immediate consequences as causes of variation in demographic processes. We do not attempt to explain vole cycles, but rather ask which demographic processes will act to maintain vole populations near an equilibrium, and which may be responsible for wide divergences from equilibrium.

Materials and Methods

Study site and experimental design

We performed our experiment in a fertile, mesic, old field on the property of the Institute of Ecosystem Studies in Dutchess County, southeastern New York (41°50′ N, 73°45′ W). The field had been mown every 1–2 yr since abandonment from corn cultivation in the early 1970s. Mown vegetation was not removed, and the field had a well-developed litter layer. Dominant plants included the grasses *Bromus inermis*, *Poa pratensis*, *Arrhenatherum elatius*, and *Phleum pratense* and the forbs *Galium mollugo*, *Solanum carolinense*, *Glecoma hederacea*, *Oxalis repens*, *Potentilla* spp., *Hieracium pratense*, and *Solidago* spp.

We employed a randomized block design to study the effects of vole density on demography, individual performance, and space use. In May and June 1990 we constructed nine 40 × 40 m fenced enclosures. Fences were made of 1.3 m wide galvanized hardware cloth (1.3-cm mesh), with 0.5 m belowground and 0.8 m aboveground. The nine enclosures were divided into three blocks. Blocks 1 and 2 were contiguous, and were separated from block 3 by a hedgerow (see Ostfeld and Canham 1993: Fig. 1). The plant species composition of blocks 1 and 2 were similar, whereas block 3 was more mesic and had a higher percentage cover of sedges (*Carex* spp.) and goldenrods (*Solidago* spp). The three enclosures within each block were assigned randomly to either a low, medium, or high vole-density treatment giving us three replicates of each density level. Enclosures were closely juxtaposed and experienced similar abiotic and biotic conditions. Mammalian and avian predators were not excluded by the fences.

Monitoring and manipulating vole populations

Live-trapping grids were established in June 1990 within each enclosure. In addition, two 0.16-ha unenclosed (control) trapping grids were established adjacent to the enclosures in August 1991. Each grid consisted of 25 trap stations 7.5 m apart, with 5 m between the outermost trap stations and the fence. Initially, one Longworth live trap was placed at each station; when vole density grew such that ≥80% of traps contained voles on any single trapping day, a second trap was placed at each station within that enclosure. Thus, for most of the study, high-density enclosures had two traps per station. Traps were supplied with crimped oats and cotton batting, and were covered with a masonite board for protection from rain and snow. Traps were set for two consecutive nights every 2nd wk from June 1990 to April 1992. Due to cold temperatures, one scheduled trapping session was missed in December 1990, and one in December 1991. All small mammals captured (except shrews) were given individually numbered metal eartags on first capture. On all captures we recorded tag number, body mass, sex, reproductive condition, and trap station. Females were considered reproductive if they had enlarged nipples, an open vulva, or were obviously pregnant. Males were considered in breeding condition if their testes were scrotal rather than abdominal. All small mammals were released at the point of capture after handling. Traps were locked open between trap sessions. In addition to meadow voles, low numbers of shrews (*Blarina brevicauda* and *Sorex cinereus*), white-footed mice (*Peromyscus leucopus*), meadow jumping mice (*Zapus hudsonius*), and eastern chipmunks (*Tamias striatus*) were captured. Since these species are granivorous or insectivorous, none of them competes directly with folivorous meadow voles for food.

In late June 1990 the vole density in all enclosures was reduced to two breeding pairs by removing adults and independent young. Vole density was subsequently managed at three different levels. In designated high-density enclosures we neither introduced nor removed voles throughout the remainder of the experiment. In low- and medium-density enclosures vole numbers were regulated by removing subadults (20 to 30 g) during the biweekly every-second-week trapping sessions. The subadult class is the primary age of dispersal in meadow voles (Gaines and McClenaghan 1980, Lidicker 1985). Approximate vole density was ascertained on day 1 of each trapping session, and targeted voles were removed and released several kilometres away on day 2. For medium-density enclosures, voles were removed whenever ≥15 adult plus subadult voles were captured on day 1. For low-density enclosures, voles were removed whenever ≥5 adult plus subadult voles were captured on day 1. During some seasons, rapid population growth in low- and medium-density enclosures necessitated trapping each week in order to maintain targeted densities. We avoided removing adults (>30 g) in order to reduce disruption of social organization, which is dominated by interactions among adults (Wolff 1985). We did not remove dependent young (juveniles, defined as <20 g) in order to minimize direct impacts on endocrine and behavioral state of lactating females.

Capture probabilities of voles averaged 86% over the study, and therefore we used the minimum-number-alive method (Krebs 1966) to estimate vole density.

Statistical analyses

Our general approach was to test for the effects of vole-density treatment (low, medium, high) on various demographic and behavioral features. We were interested in the effects of density on: (1) reproduction (proportion of adult females and males in breeding condition); (2) recruitment (rate of appearance of unmarked individuals); (3) survival of juveniles, subadults, and adults (instantaneous survival rate per 14 d); (4) growth in body mass of different age categories (percentage growth rate per day); (5) median mass (in grams) at sexual maturity for both sexes (minimum body mass at which half the individuals are in breeding condition); (6) frequency distribution of body mass; and (7) movement distances (in metres) of both sexes and all age classes (distance between successive captures 2 or 4 wk apart). Movement distances were used as an indicator of home range size. These parameters were measured for each trapping session, every 2 wk, to account for seasonal and annual changes. Therefore, we used repeated-measures analysis of variance (SAS Institute 1987) to analyze the effects of density treatment on population and individual performance. Because the three enclosures at each density level maintained independent populations of voles, we used the enclosures, not individual voles, as the unit of replication. Percentages for reproduction and survival were subjected to an angular transformation before analysis. We also used ANOVA to test for effects of season and block.

Results

Effects of the density manipulation

Within 2 mo of the establishment of the enclosures (i.e., August 1990), vole densities in the three experimental treatments had begun to diverge, and for the remainder of the study average densities were distinctly different (Fig. 1). For part of the summer of 1991, density in one of the high-density enclosures declined

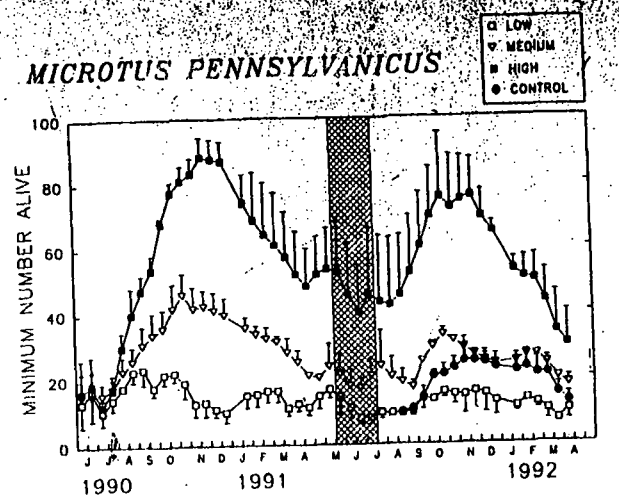

FIG. 1. Population densities (minimum number alive per 0.16 ha) of voles in the three density treatments (fenced populations) and controls (unfenced). Values are means (± 1 SE) for the three replicates of each density level and the two replicate control grids. Shading indicates the drought period (<40% of long-term monthly mean rainfall). Sampling every 2nd wk gives some months three samples.

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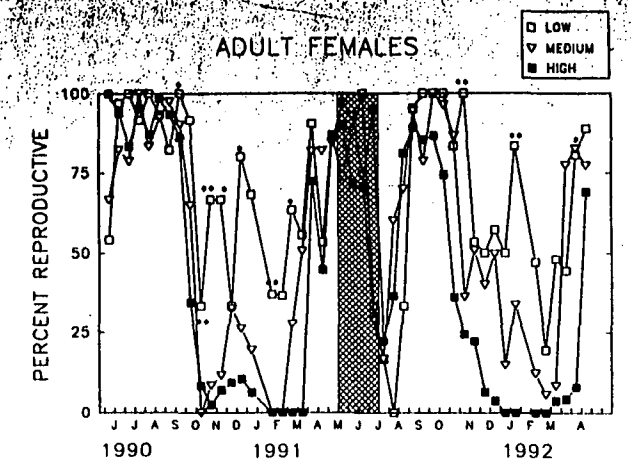

FIG. 2. Percentage of adult vole females in breeding condition, as indicated by condition of the vulva (perforate or nonperforate). Values are means for the three replicates of each density level. For the entire study, repeated-measures ANOVA showed statistically significant effects of density ($F_{2,6}$ = 27.02, P = 0.001), time ($F_{19,228}$ = 11.74, P < 0.0001) and density × time ($F_{90,270}$ = 1.96, P < 0.0001). For individual trapping sessions, statistically significant effects of density on proportion reproductive (angular transformed) are indicated by * = P < 0.05, ** = P < 0.01. Shading indicates the drought period. Sampling every 2nd wk gives some months three samples.

to a level similar to those in the medium-density enclosures, but it then increased substantially in the autumn. Populations in all three high-density enclosures declined gradually in the winter of 1991–1992. The unfenced control grids maintained density levels quite similar to those in the medium-density enclosures (Fig. 1). On the 11 trapping grids we captured a total of 3271 individuals 11 601 times over the course of the study.

Reproduction and recruitment

Vole density had a strong effect on reproductive activity of both females and males in the autumn, winter, and spring of both years, but not in summer (Figs. 2 and 3). For both sexes, a high proportion of individuals in low-density treatments remained in breeding condition even in winter, which typically is considered the nonbreeding season for this species (Tamarin 1977). In medium-density enclosures, voles of both sexes continued to breed later in the autumn, and returned to breeding condition earlier in the spring, than did those in high-density enclosures (Figs. 2 and 3).

During May and June 1991, rainfall was <40% of the long-term (1951–1989) monthly mean for this site. For females but not males, breeding activity dropped sharply in response to this drought (Figs. 2 and 3). The abrupt decline in breeding activity occurred in all enclosures, irrespective of population density. A delay of ≈2 mo was observed between the onset of the drought and the decline in breeding, presumably as a result of a lag in drying of the vegetation, which serves as food and cover for voles (Batzli 1985).

Differences among treatments in reproductive activity appeared to cause the strong density effect on per capita recruitment (Fig. 4). For most of the study, recruitment rates were highest in low-density enclosures, intermediate at medium-density, and lowest in high-density enclosures. However, the differences were statistically significant primarily in autumn, winter, and spring. For ≈2 mo following the 1991 drought, recruitment rates dropped sharply for all density treatments.

Survival rates

For juveniles and subadults there were no statistically significant effects of population density on survival rates during any of the individual trapping sessions, nor overall (repeated-measures ANOVA; juveniles: $F_{2,6}$ = 0.04, P = 0.958; subadults: $F_{2,6}$ = 1.34, P = 0.329). For adult voles, significant effects of density on survival rates began to appear in autumn and winter 1991–1992, ≈16 mo after the density manipulation began (Fig. 5). During this period, survival

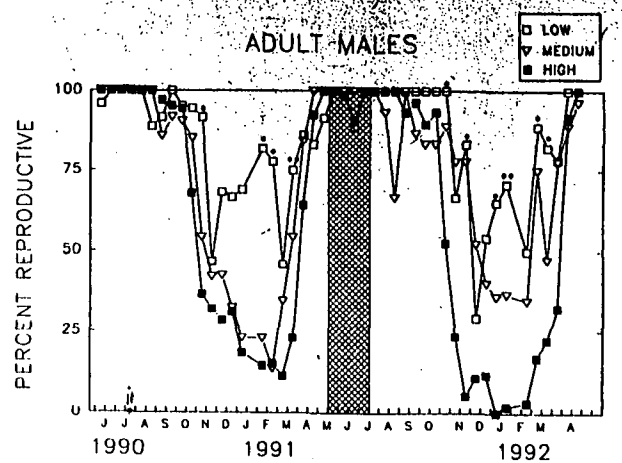

FIG. 3. Percentage of adult vole males in breeding condition, as indicated by position of the testes (scrotal or abdominal). Values are means for the three replicates of each density level. For the entire study, repeated-measures ANOVA showed statistically significant effects of density ($F_{2,6}$ = 8.49, P = 0.018), time ($F_{19,228}$ = 19.35, P < 0.0001) and density × time ($F_{90,270}$ = 2.23, P < 0.0001). For individual trapping sessions, statistically significant effects of density on proportion reproductive (angular transformed) are indicated by * = P < 0.05, ** = P < 0.01. Shading indicates the drought period. Sampling every 2nd wk gives some months three samples.

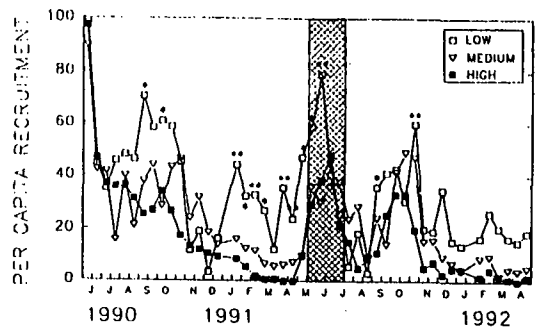

FIG. 4. Per capita recruitment by vole density treatment. Values are means for the three replicates of each density level. For the entire study, repeated-measures ANOVA showed a marginally significant effect of density ($F_{2,6}$ = 4.40, P = 0.067), and highly significant effects of time ($F_{19,228}$ = 16.26, P < 0.0001) and density × time ($F_{90,270}$ = 1.58, P = 0.003). For individual trapping sessions, statistically significant effects of density on per capita recruitment are indicated by * = P < 0.05, ** = P < 0.01. Shading indicates the drought period. Sampling every 2nd wk gives some months three samples.

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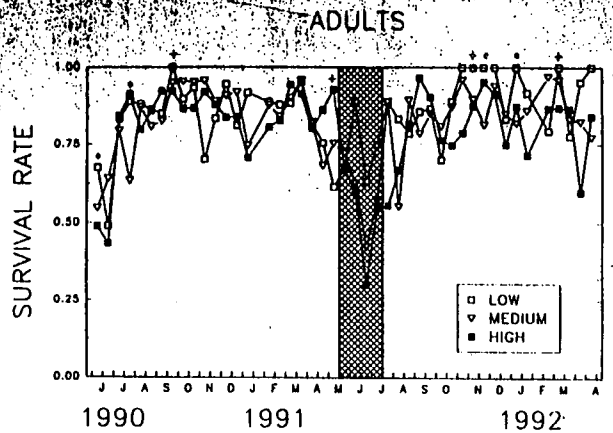

FIG. 5. Survival rates (instantaneous survival rate per 14 d) for adult voles in the density treatments. Values are means for the three replicates of each density level. See text for overall statistical results. For individual trapping sessions, statistically significant effects of density on survival rates are indicated by † = $P < 0.10$, * = $P < 0.05$, ** = $P < 0.01$. Shading indicates the drought period. Sampling every 2nd wk gives some months three samples.

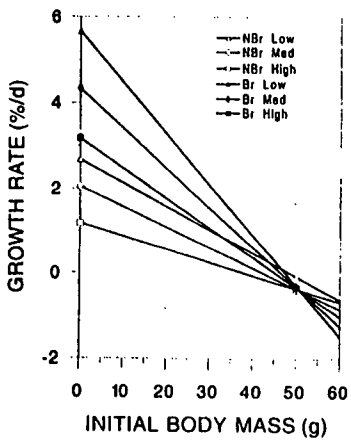

FIG. 6. Growth rates (percentage mass growth per day) for individual voles as a function of body mass, density treatment, and breeding season. Shown are least-squares regression lines describing the relationship between growth rate (calculated between every 2nd wk trapping sessions) and initial mass for the three density treatments and both nonbreeding (NBr) and breeding (Br) seasons.

rates were always highest in low-density enclosures, and usually lowest in high-density enclosures. Over the course of the study the effect of density on survival rates of adults was marginally significant (repeated measures ANOVA, $F_{2,6} = 4.23$, $P = 0.071$).

Survival rates varied significantly over time ($F_{14,588} = 5.93$, $P < 0.0001$), being higher during nonbreeding seasons (November–April) than during breeding seasons (May–October). Survival rates of adults declined during the 1991 drought, with voles in high-density treatments appearing to be most strongly affected, and those in low-density treatments least affected (Fig. 5). However the effect of density on survival was not statistically significant during that period.

Individual growth rates and body mass

Vole growth rates varied consistently with body size, season and density (Fig. 6). Regardless of season or density, growth rates (percentage mass growth per day) declined as body mass increased, converging on zero growth at ≈45–50 g (Fig. 6). Because of the convergence in growth rates with increasing body mass, growth rates of adults (>30 g) were not significantly affected by density. Density had a significant effect on growth rates of individuals <30 g during the nonbreeding season (i.e., juveniles and subadults; repeated-measures ANOVA, $F_{2,6} = 6.63$, $P = 0.030$), and a marginally significant effect during the breeding season ($F_{2,6} = 3.94$, $P = 0.081$). In both the breeding and non-

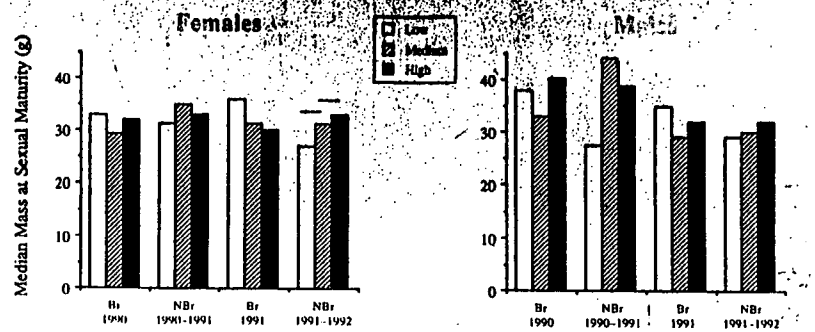

FIG. 7. Median mass at sexual maturity for vole females and males for the different density treatments and seasons. Only for females in the nonbreeding season (NBr) of 1991–1992 was there a significant effect of density (see *Results: Individual growth rates and body mass*). Horizontal lines above bars span mean values not significantly different by Tukey test.

breeding seasons the growth rates of juveniles and subadults were highest in the low-density enclosures, intermediate at medium density, and lowest in the high-density enclosures.

Although growth rates were affected by population density, density had a minimal effect on the body mass at which voles achieved sexual maturity (Fig. 7). A statistically significant effect of density was observed only for females in the 1991–1992 nonbreeding season ($F_{2,6} = 6.02$, $P = 0.037$). However, because individual growth rates were slower at higher densities, we infer that the age of sexual maturity increased with increasing population density.

We expected our experimental protocol (removing voles in the 20–30g mass class) to directly affect the frequency distribution of body mass in low- and medium-density treatments. The predicted effect was to increase the degree of bimodality in mass distribution by decreasing frequencies of medium-sized voles. However, during the breeding seasons of 1990 and 1991, when the majority of removals were made, all three density treatments showed similar bimodal distributions in body mass; low- and medium-density enclosures did not appear to show an underrepresentation of 20–30g voles compared to high-density enclosures (Fig. 8). In nonbreeding seasons, none of the treatments showed bimodal mass distributions. Nevertheless, we did not compare means or distributions across density treatments statistically, but only qualitatively.

There was a clear effect of population density on mass distributions in categories <20g and >30g. In both breeding and nonbreeding seasons of both years the low-density enclosures had greater proportions of juvenile voles, which reflected the higher recruitment rates in these enclosures (Fig. 4). Medium-density enclosures had the greatest frequencies of moderately large voles (≈40–50g), and low-density enclosures had the highest frequencies of very large voles (>50g). Very few extremely large voles occurred in high-density enclosures, particularly during nonbreeding seasons (Fig. 8).

Movement distances

Movement of voles between successive captures 2–4 wk apart was strongly affected by density (Table 1). The average movement distances declined significantly from 11.5 ± 2.7 m (mean ± 1 SD) at low density to 8.6 ± 2.0 m at medium density and 6.8 ± 1.6 m at high density (with all pairwise differences significant at $P < 0.05$). Movement distances also varied significantly with age class (Table 1), in the rank order juveniles (8.2 ± 2.6 m) ≤ subadults (8.4 ± 2.6 m) < adults (10.3 ± 3.1 m). However, all age classes responded similarly to the density treatments, as indicated by a statistically insignificant density × age interaction (Table 1). Movement distances also differed between sexes, with males moving significantly farther than females (Tukey's HSD test, $P < 0.05$). Movement of females appeared to be more sensitive to the density treatment (see the density × sex interaction term, Table 1).

DISCUSSION

Extent of density dependence

Most demographic and behavioral processes we examined were affected by our manipulation of vole density. We found that high density caused: (1) shorter breeding seasons; (2) lower rates of recruitment; (3) slower individual growth rates to lower modal body mass; (4) older age (but generally not greater mass) at sexual maturity; (5) reduced survival rates of adults, but only after ≈16 mo had elapsed after divergence of density conditions; and (6) reduced movement dis-

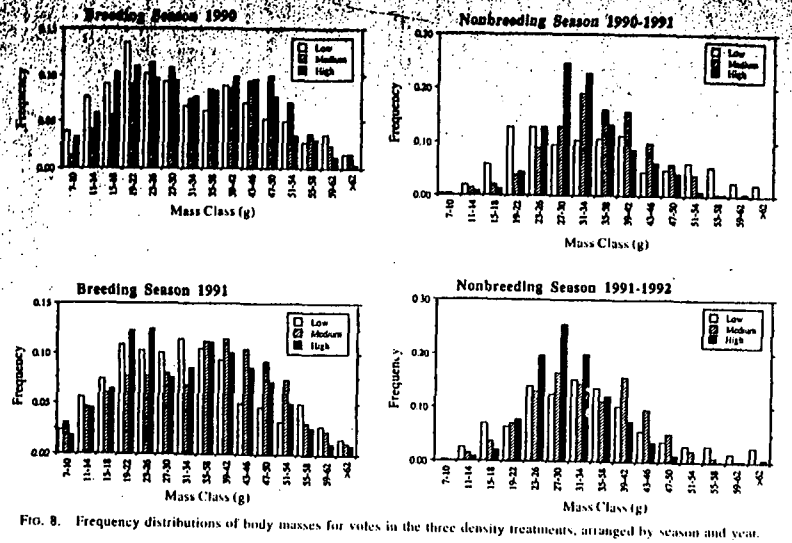

FIG. 8. Frequency distributions of body masses for voles in the three density treatments, arranged by season and year.

tances. In nearly all parameters, medium-density treatments were intermediate between high- and low-density treatments. The density treatments did *not* affect: (1) reproductive activity in the summer breeding season; (2) reproductive response to drought conditions; and (3) survival rates of juveniles and subadults.

Studies of freely fluctuating vole populations have given mixed results regarding the strength of density dependence in demographic and behavioral processes. Several studies have found shortened breeding seasons following periods of peak density (Kalela 1957, Krebs et al. 1969, Batzli and Pitelka 1971, Hansson and Henttonen 1985, Bernshtein et al. 1989), but others have not (Hoffman 1958, Krebs and Myers 1974, MacLean et al. 1974). Individual growth rates were affected by the phase of the cycle (highest during increase phase, lowest during decline phase), but not density in *Microtus pennsylvanicus* (Krebs et al. 1973). Mass at sexual maturity increased with increasing density in *M. townsendii* (LeDuc and Krebs 1975), and was highest at peak density in *M. pennsylvanicus* (Keller and Krebs 1970), but was unrelated to density in several other arvicoline species (Krebs 1964, Keller and Krebs 1970).

TABLE 1. *Results of three-way analysis of variance for effects of Density, Age (juvenile, subadult, or adult), and Sex (male or female) on movement distances between successive vole captures on 2-wk intervals. Enclosures were used as the unit of replication, thus all individual vole movement data within a Density × Age × Sex grouping were averaged prior to analysis.*

Source of variation	df	F	P
Model	13, 40	8.50	0.0001
Density	2, 40	35.17	0.0001
Age	2, 40	8.14	0.001
Sex	1, 40	4.42	0.042
Density × age	4, 40	1.34	0.271
Density × Sex	2, 40	3.53	0.039
Age × Sex	2, 40	3.52	0.039

The effects of population density on survival rates are controversial. In their review, Krebs and Myers (1974) reported that survival rates of voles vary consistently with the phase of the cycle, but not with density per se. However, other studies of voles (e.g., Erlinge et al. 1984, Hansson 1987, Hanski et al. 1991, 1993, Korpimäki 1993) have argued that density-dependent mortality occurs in areas dominated by generalist predators, and that specialist predators cause delayed density-dependent mortality.

Suppression of movement at high density has been observed for several vole species (Abramsky and Tracy 1980, Gaines and Johnson 1982, Desy et al. 1990, Sandell et al. 1991*a*). However, Taitt and Krebs (1981), Taitt et al. (1981), Bondrup-Nielsen (1986) and Jones (1990) have reported that movement distances decrease

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with increasing food availability, but are not necessarily (or only secondarily) responsive to population density. However, these studies did not control for the effects of increasing local density in response to increased food availability. In our populations food quantity was reduced in high-density enclosures relative to medium- and low-density grids (Ostfeld 1994). Therefore, the smaller movement distances we observed in the former must have been caused by high density, and not by food availability, which would have caused the opposite effect. Our data support the conclusion of Desy et al. (1990) that movement distances in voles are primarily affected by density, and only secondarily by food availability.

Few prior population studies have manipulated vole density, and all have consisted of short-term removals. Several (Redfield et al. 1978, Boonstra and Rodd 1983, Porter and Dueser 1986) manipulated density of one sex per study plot, and therefore (intentionally) altered sex ratios as well as total density. Boonstra (1977) and Rodd and Boonstra (1984) removed adult *M. townsendii* and *M. pennsylvanicus*, respectively, during the autumn and spring preceding expected spring declines. In both studies the effects of temporary reductions in density were modest. Survival rates of adult males and females were improved in *M. townsendii* (Boonstra 1977), but generally not in *M. pennsylvanicus* (Rodd and Boonstra 1984). Reproductive condition of both female and male *M. pennsylvanicus* was largely unaffected (Rodd and Boonstra 1984). Movement distances of *M. pennsylvanicus*, but not of *M. townsendii*, increased after experimental removals (Boonstra 1977, Rodd and Boonstra 1984). Inconsistencies between these results and those of the present study are difficult to interpret due to different experimental procedures: in the prior studies adults (not subadults) were removed, removal periods were brief, and trapping grids were not enclosed.

Density dependence and cycle-phase dependence

Some of the confusion regarding the importance of density dependence in vole population dynamics exists because the focus has been predominantly on effects of the cycle phase (i.e., low, increase, peak, decline), rather than effects of density per se (Frank 1957, Krebs et al. 1973, Schaffer and Tamarin 1973, Krebs and Myers 1974, Tamarin 1983, Cockburn 1988, Hansson 1989). In our view, the focus on cycle phase has been helpful but insufficient for elucidating the mechanisms of population change for the following reasons. First, in freely fluctuating populations detecting direct effects of density is difficult or impossible because comparisons of populations at the same or different density levels are confounded by seasonal conditions and recent history. Second, a focus on the effects of cycle phase limits the applicability of resulting models to less cyclic populations (Sandell et al. 1991*b*). Third, the implication of the focus on cycle phase is that vole populations respond to the direction and rate of density change rather than to current density, an assumption without supporting evidence. Animals are likely to experience directly the effects of current and recent density, but not necessarily the current rate of change in population size. Fourth, because increase and decline phases are defined based on whether or not gains exceed losses, conclusions regarding the effects of cycle phase on rates of gain and loss may be circular. Finally, if the effects of density involve substantial time lags, a demographic or behavioral response to density may be correlated with, but not caused by, the present cyclic phase.

An example of potential confounding of correlation with causation is the Chitty Effect, which is the occurrence of especially heavy voles particularly during the peak of a multiannual cycle (Chitty 1952, Boonstra and Krebs 1979, reviewed by Lidicker and Ostfeld [1991], Wolff [1993]). The Chitty Effect has been interpreted as an outcome of natural selection favoring large, and ostensibly dominant, individual voles during periods of population growth and at high density (Chitty 1967, but see Chitty 1987). Under our experimental conditions, especially large voles were substantially less frequent under high- than low-density conditions (Fig. 7), suggesting that high density per se is not the cause of the Chitty Effect. Apparently, conditions favorable for both individual body growth (Fig. 6) and population growth occurred in the low-density enclosures, but our manipulation prevented population growth while allowing body growth to large size. Our data support the conclusions of Lidicker and Ostfeld (1991) and Wolff (1993) that large-bodied voles are produced during periods that are especially favorable for growth and survival (often low-density periods), and that their predominance during population peaks results from conditions preceding, not during, the peak.

Stabilizing and destabilizing effects

A critical effect of high and medium density was to reduce the length of the breeding season, and therefore the number of generations per year (Figs. 2–4; Ostfeld et al. 1993). In addition, by reducing individual growth rates while not affecting mass at sexual maturity, high- and medium-density conditions increased age at sexual maturity and therefore slowed the potential rate of population growth (Cole 1954). The effects of density on reproduction and body growth were immediate and constant through time. These two density-dependent processes should be strongly stabilizing influences on population dynamics.

However, several experimental results revealed destabilizing processes. First, population density did not affect reproductive activity during the height of the breeding season (summer), which could lead to seasonal, rapid population growth even in high-density populations. Second, the density-independent response to drought (Fig. 2; see also Ostfeld et al. 1993) could

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contributes to erratic population fluctuations. Third, survival rates of juveniles and subadults were unresponsive to population density, which would act against the regulation of population growth. Fourth, the compression of movements with increasing density acts to accomodate density buildups, and therefore is not stabilizing. Spacing behavior previously has been considered a strong stabilizing force in vole population dynamics (e.g., Boonstra and Rodd 1983, Stenseth 1986). The emphasis has been on the effects of spacing behavior on population density rather than vice versa. However, if spacing behavior and social organization are highly responsive to density (Ylönen et al. 1988), then their stabilizing effects may be weak or absent in fluctuating populations (Heske and Bondrup-Nielsen 1990).

Survival rates of adults in the medium- and high-density enclosures declined significantly relative to low-density conditions beginning ~16 mo after the densities diverged (Fig. 5). Because delayed density-dependence can cause population cycles or chaos (May 1976, Ostfeld 1992, Hanski et al. 1993, Hornfeldt 1994), factors influencing adult survival rates may be of particular importance to vole population dynamics. The causes of the delayed effect of density on adult survival are not entirely clear. High and medium vole density caused a winter-spring decrease in aboveground plant biomass relative to low density, but the effect was ephemeral (Ostfeld 1994). Plant biomass recovered and was equivalent across density treatments by autumn 1991 when the effect of density on survival became evident (Ostfeld 1994). Therefore, we do not believe the delayed density-dependent survival was due to vole-resource dynamics (see also Ostfeld et al. 1993). Although our experiment manipulated only population density directly, we recognize that resource levels, social interactions, dispersal, and possibly age structure and predation rates also may have been affected indirectly.

Populations of voles differ radically in their tendency to fluctuate through time (Henttonen et al. 1985, Taitt and Krebs 1985, Ostfeld 1988). We suggest that future research should focus on the indirect effects of differences in vole density, and on differences among populations in the strength of density dependence in demographic and behavioral features.

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SOCIOECOLOGY OF A TERRESTRIAL SALAMANDER: JUVENILES ENTER ADULT TERRITORIES DURING STRESSFUL FORAGING PERIODS[1]

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Abstract. When adults of a species defend feeding territories, juveniles may benefit from access to those territories during periods when prey decline between territorial spaces. Adults may either deny or allow such access, thus impacting the foraging success of the juveniles. We examined a dense population of the terrestrial red-backed salamander (*Plethodon cinereus*) in which male and female adults hold territories (cover objects on the forest floor that act as patches of moisture and prey during rainless periods) that should be attractive to juveniles as the surrounding leaf litter dries. The purpose of our research was to determine whether adults of *P. cinereus* exclude juveniles from their territories, as they do conspecific adults, and to explore how juveniles respond to adult territoriality.

We found that adults were uniformly distributed intrasexually under cover objects but positively associated intersexually, during the summer when courtship does not occur. Juveniles entered territories of some adults during dry weather, when foraging in the leaf litter was difficult due to desiccation, but moved back into the leaf litter (out of territories) during rainy periods, when prey were more available. Adults ingested significantly larger prey than juveniles but food niche overlap was large between juveniles and adults, suggesting that competition for limited prey occurs when they share territories during rainless periods.

In laboratory experiments, juveniles were attracted to territorial pheromones of adult males and females, and males were less aggressive toward such juveniles than toward intruding adult males. Adults were more tolerant of juveniles with which they had cohabited previously in the forest than of juveniles that were "strangers"; in turn, juveniles spent more time near and less time escaping from previously cohabiting adults than from adult "strangers." Thus, adults appeared to tolerate territorial intrusions by juveniles but were more tolerant of some juveniles than of others.

We examined several hypotheses that may explain why adults might allow certain juveniles into their feeding territories during stressful periods. Our data best fit a "kin recognition" hypothesis. Kin recognition is known to occur in other species of salamanders and, in our study, adults and juveniles that had previously cohabited on the forest floor were more benign toward each other than were those that had not cohabited. Our data do not favor the "no competition" hypothesis because juveniles entered adult territories just when both adults and juveniles were able to ingest fewer prey (dry weather). Our results do not favor the hypothesis that juveniles sneak into adult territories undetected because juveniles move into adults' territories when adults are present, and histological evidence suggests that juveniles possess glands used in social communication. We do not favor the hypothesis that adults habituate to cohabiting juveniles because habituation is not likely to occur between food competitors when the adults can easily defeat the juveniles. The hypothesis of "dear enemy" (neighbor) recognition, which occurs between territorial adults of this species, is unlikely to be correct because juveniles do not act as territorial neighbors.

Adults appear to act as time minimizers during territorial defense. Juveniles, whether or not related to those adults, appear to act as energy maximizers, moving from leaf litter to cover objects as prey availability shifts.

Key words: aggression; feeding territories; food niche overlap; juvenile salamanders; kin recognition; pheromones; Plethodon cinereus; *Plethodontidae.*

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Induced plant defenses breached? Phytochemical induction protects an herbivore from disease

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Abstract. Although wound-induced responses in plants are widespread, neither the ecological nor the evolutionary significance of phytochemical induction is clear. Several studies have shown, for example, that induced responses can act against both plant pathogens and herbivores simultaneously. We present the first evidence that phytochemical induction can inhibit a pathogen of the herbivore responsible for the defoliation. In 1990, we generated leaf damage by enclosing gypsy moth larvae on branches of red oak trees. We then inoculated a second cohort of larvae with a nuclear polyhedrosis virus (LdNPV) on foliage from the damaged branches. Larvae were less susceptible to virus consumed on foliage from branches with increasing levels of defoliation, and with higher concentrations of gallotannin. Defoliation itself was not related to any of our chemistry measures. Field sampling supported the results of our experiments: death from virus among feral larvae collected from undefoliated trees was also negatively correlated with defoliation. In 1991, defoliation and gallotannin were found to inhibit the virus. In addition, gallotannin concentrations were found to be positively correlated with defoliation the previous year. Compared with previous results that demonstrated a deleterious effect of defoliation on gypsy moth pupal weight and fecundity, the inhibition of the virus should confer an advantage to the gypsy moth. Since leaf damage levels increase as gypsy moth density increases, and since leaf damage inhibits the gypsy moth virus, there is the potential for positive feedback in the system. If phytochemical induction in red oak can inhibit an animal pathogen such as LdNPV, it suggests that induction in red oak is a generalized response to tissue damage rather than an adaptive defense against herbivores.

Key words: *Lymantria dispar* – Wound-induced response – Nuclear polyhedrosis virus – Tannins

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Wound-induced responses in plants have been the subject of much research over the past twenty years (Green and Ryan 1972; Haukioja and Niemela 1977, 1979; Edwards and Wratten 1982, 1983; Schultz and Baldwin 1982; Raupp and Denno 1984; Bergelson et al. 1986; Hartley and Lawton 1987; Rossiter et al. 1988; Hartley and Firn 1989; Renaud et al. 1990) and, despite a number of recent reviews (e.g. Karban and Myers; and papers in Tallamy and Raupp 1991), there seems to be little consensus as to the ecological and evolutionary implications of phytochemical induction (Edwards and Wratten 1983, 1985, 1987; Baldwin and Schultz 1983; Fowler and Lawton 1985; Bergelson et al. 1986; Bergelson and Lawton 1988; Hartley and Lawton 1990). Simply put, there is no general agreement as to whether wound-induced responses are good for plants, good for herbivores, or linked evolutionarily in any way (Tallamy and Raupp 1991).

One approach to determining the ecological significance of induction is to view the consequences of induction as a balance between positive and negative forces (Faeth 1985, 1991; Hunter 1987, 1992a). The strength of this approach is that it reconciles studies which demonstrate deleterious effects of defoliation on herbivores with those that suggest that previous herbivory can be advantageous. Both may be occurring simultaneously, the final outcome may depend upon the specifics of the system involved, and "who wins" may not be constant over time or space. Moreover, an emphasis on balance has led to the incorporation of a third trophic level, the natural enemies of herbivores, into the investigation of induction (Price et al. 1980; Faeth 1987, 1991; Raupp and Sadof 1991).

Despite a well developed literature (e.g. Bell 1981; Kuc 1981, 1987; Agrios 1988), the impact of plant pathogens on phytochemical induction is often ignored in the debate on the ecological significance of wound-induced responses (see Karban et al. 1987; Karban and Myers 1989; and papers in Tallamy and Raupp 1991 for notable exceptions). Yet several studies have shown that the effects of phytochemical induction on herbivores and

[illegible] 1981; Hare 1983; [illegible] 1987; Hammond [illegible] 1991). Indeed, Hartley and Lawton (1990) have suggested that phenolic induction by herbivorous insects on birch may be directed primarily at invading plant pathogens, rather than the herbivores responsible for the defoliation (Edwards and Wratten 1983, 1985, 1987; Edwards et al. 1991; Wratten et al. 1990).

That wound-induced responses can influence both herbivores and plant pathogens simultaneously led us to predict that induction could act directly against the pathogens of herbivores. If induction in some plant species is a general response to invasion, and therefore not pathogen-specific, herbivores may benefit from induction by the inhibition of their own pathogenic organisms. The result would be a balance between positive and negative effects of induction (Faeth 1985; Hunter 1987), direct deleterious forces acting on the herbivore and indirect beneficial forces acting through inhibition of the herbivore's pathogens.

This paper describes a two year field and laboratory study in which we measured the effects of wound-induced changes in leaf quality, generated by an insect herbivore, on a naturally occurring pathogen of that herbivore. Our results suggest that induction can have a much greater impact on herbivore pathogens than it does on the herbivore itself.

The system

We chose to investigate the effects of induction on an herbivore pathogen with the gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), one of its major host plant species, red oak, *Quercus rubra*, and the gypsy moth nuclear polyhedrosis virus (LdNPV). This system is suitable for a number of reasons. First, the gypsy moth is known to induce chemical changes in the foliage of red oak (Schultz and Baldwin 1982) which can decrease gypsy moth larval growth rate and adult fecundity (Rossiter et al. 1988). Second, the species-specific LdNPV is considered one of the most important of many forces influencing population dynamics of the gypsy moth, and is associated with population collapse (Doane 1970; Wallner and McManus 1981). As such, LdNPV is a major ecological force, and its inhibition could have significant effects on gypsy moth dynamics and evolution. Finally, previous work has shown that the efficacy of LdNPV varies with the host plant species (Keating and Yendol 1987; Keating et al. 1989, 1990) and host plant individual (Schultz et al. 1990) on which the virus particles are consumed. The pathogenicity of the virus is therefore susceptible to inter- and intra-specific variation in leaf quality. The gypsy moth-oak-LdNPV system, regarded as having dynamics typical of many forest defoliators (Anderson and May 1980; Turchin 1990) has, therefore, many of the ecological characteristics required for an investigation of a more general question: what is the potential impact of induction on herbivore pathogens?

Although the gypsy moth is univoltine, [illegible] LdNPV is a twice-yearly event (Woods and Elkinton 1987). Some neonate larvae are infected as they eclose in spring, consuming the resting stage of the virus (polyhedral inclusion body, hereafter, PIB) from the egg mass surface where it has overwintered. When infected larvae die in the tree canopy, they release PIBs onto foliage which are then consumed by the same generation of larvae. Consumption of PIBs on foliage occurs at approximately the third larval instar (Woods and Elkinton 1987) and it is during this period alone that variation in foliage quality can influence the efficacy of the virus (Keating and Yendol 1987). Neither food quality before nor after infection influences mortality, and only the quality of foliage entering the gut in concert with the virus influences infection (Schultz et al. 1992). Larvae infected in the third instar die before pupation, releasing PIBs into the environment. Successful overwintering of the virus appears to be dependent upon its association with egg masses (Murray and Elkinton 1989; Woods et al. 1989) which may protect the PIBs from ultra-violet radiation and other environmental degradation.

Methods

Bioassay of viral efficacy on foliage damaged in the current year

In the spring of 1990, we generated a range of defoliation levels on 17 red oak trees by bagging varying numbers of gypsy moth larvae on branches. Trees were between 2 and 4 m in height, growing in a west-facing mixed hardwood stand on Berks shaley silt loam (Braker 1981). The phenolic chemistry of trees of this age falls within the range for mature red oaks (Kleiner et al. 1989; Schultz et al. 1990; results below) and responds to defoliation by induction (Rossiter et al. 1988). Thirty-one trees were chosen in all, 17 for this experiment and 14 for the unmanipulated field trial described below. The thirty-one trees were not a random sample - we selected every tree in the stand with sufficient canopy volume on which to place a bag for gypsy moth, and on which the remaining canopy was accessible from the ground for accurate "outside bag" defoliation estimates. Trees were assigned to either the bioassay or the field trial alternately (as near as possible) within the stand.

Bags of plastic window screen, 60 cm × 30 cm, were placed on the largest branch at breast height on each of the 17 trees just prior to natural gypsy moth larval eclosion. Second instar larvae were introduced into bags when the natural field population was also in 2nd instar. Each tree (bag) was assigned a different density of larvae, ranging from 0.25 to 0.90 larvae per leaf (leaf counts were made prior to the introduction of larvae). We used a broad range of larval densities rather than replicated categories (an ANOVA approach) in order to associate both defoliation and larval mortality with the various chemical analyses of foliage using multiple regression analysis (see analysis and chemical methods below). Previous observations had suggested that the densities chosen would generate realistic defoliation levels by the third instar. Densities were assigned to trees by random lottery.

Introduced larvae were used solely to generate leaf damage, and were not used subsequently in any experiment. To ensure that we had approximated the realistic range of defoliation at the time larvae would normally ingest LdNPV with foliage (i.e. the 3rd instar, Woods and Elkinton 1987), we removed all bags as feral larvae entered 3rd instar, and made defoliation estimates from bagged branches and throughout the rest of the canopy on each tree. The methods for the defoliation estimate have been published previously (Hunter 1987). Briefly, leaves were assigned to one of seven damage classes, representing per cent leaf area missing. Damage level was then calculated by multiplying the number of leaves in each class by the mid point of that class, and dividing by the total number of leaves in the sample. Damage estimates for bags were made by examining every leaf (N varied between 35 and 52), and canopy-wide estimates were made by examining 30–40 leaves haphazardly on each of the three largest remaining branches and pooling the results (e.g. Hunter 1992b).

The distribution of damage generated inside bags approximated the natural distribution of damage on the same population of trees (varying between 18% and 72% leaf area removed outside, and between 14% and 55% leaf area removed inside) from which we concluded that our treatments had generated a fairly realistic range of gypsy moth defoliation at 3rd instar. Since there was also a significant correlation between the densities of larvae we had introduced into bags and the defoliation levels that resulted ($p = 0.017$, d.f. = 1.15, r-sqd = 0.33, Fig. 1) we concluded that defoliation inside bags was, at least in part, due to our treatments.

We selected a sub-sample of 5 trees from the 17 for laboratory bioassays with virus. The five trees chosen represented a gradient from moderately high to low natural damage (47%–24%), but avoided the extremes of the distribution. Chemistry samples (see methods below) were taken from inside and outside bags on all 17 trees.

The methods to bioassay the effect of variation in foliage quality on viral efficacy have been published previously (Keating and Yendol 1987; Keating et al. 1989). Briefly, leaves from inside bags on the 5 bioassay trees were placed in water piks in the field and returned to the laboratory on ice for use the same day. The polyphenolic chemistry of red oak foliage in water piks is known to remain stable for at least 48 h (Kleiner 1991). The foliage was surface-sterilized (10% sodium hypochlorite solution for 10 mins and three 1 min rinses with distilled water), and 8 mm diameter discs were punched from the leaves and presented to gypsy moth larvae on agar blocks in individual cells. Each disc was dosed with 20,000, 40,000 or 65,000 PIBs, or distilled water as a control. The LdNPV (Hamden isolate) was prepared according to the methods of Magnoler (1974), and the doses chosen were known to bracket the LD50 (dose required to kill 50% of larvae) on red oak (Keating and Yendol 1987).

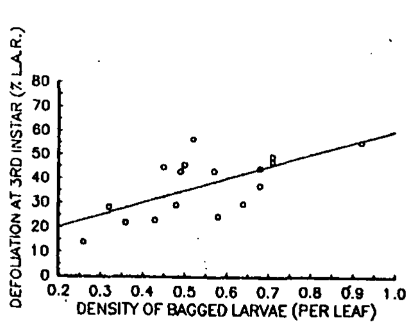

Fig. 1. Levels of defoliation generated within bags on red oak trees by the introduction of varying densities of gypsy moth larvae

Table 1. The mean mortality of gypsy moth larvae inoculated with virus on red oak foliage in the 1990 and 1991 bioassays. Percent mortalities were arcsine square-root transformed prior to analysis and back-transformed data are presented here. Means in columns [illegible] ANOVA (SAS Inst.). Dose is measured in PIBs per larva. N = number of trees.

1990					1991				
Dose	N	Mortality (SD)	Min	Max	Dose	N	Mortality (SD)	Min	Max
20,000	5	23.42ᵃ (8.90)	8.57	37.50	20,000	10	15.32ᵃ (6.49)	2.78	29.66
40,000	4	34.13ᵃ (3.84)	30.00	43.59	50,000	10	34.62ᵇ (6.78)	20.61	55.92
65,000	5	26.48ᵃ (8.80)	12.49	50.00	80,000	10	36.57ᵇ (6.89)	18.94	53.31

Larvae for the bioassay were obtained from APHIS, USDA, Otis, Mass. Egg masses were sterilized in 10% formalin before hatch and larvae were reared on a wheatgerm based diet (BioServ, Frenchtown, NJ) through the end of second instar. Immediately before moult to 3rd instar (based on head capsule slippage), larvae were removed from diet and starved for 24 h to moult and to void their guts. This ensured that larval guts were empty so that no remaining diet components could influence viral efficacy.

Forty larvae were treated per dose per tree. Each tree (defoliation level) therefore had 4 sets of 40 larvae (3 dosed with virus and 1 with water, a total of 20 groups of larvae). One set of 40 larvae was mishandled after dosing, leaving 14 treatment groups and 5 control groups remaining. Larvae were given 24 h to consume the entire leaf disc and therefore the entire dose of virus. Larvae failing to consume the whole disc were discarded. The remainder were transferred individually to artificial diet for 17 days at 25° C, 16:8 light:day. All larvae infected at 3rd instar died by day 17 under these conditions (Keating and Yendol 1987). Subsets of dead larvae were stained and checked for PIBs. This experiment was repeated in 1991 as part of the comparison of within- and between-year induction (below).

Analysis. Mortality in control groups (distilled water) was less than 3% and not associated with LdNPV. These data were not used in any further analysis. Dose was not a significant predictor of mortality from virus (analysis of variance in mortality, dose within tree, $F = 1.91$, d.f. = 2,7, $p = 0.22$, Table 1). Despite previous work which suggested that our doses were appropriate (Keating and Yendol 1987), we failed to bracket the LD50 viral dose and gypsy moth mortalities varied from 8% to 50% across treatments. Moreover, it appears that variation in leaf quality masked the effect of viral dose (note the large variation in mortality within a dose in Table 1, and see Results, below). Consequently, we have used mean mortality ($N = 3$ doses) weighted by the reciprocal of the variance in stepwise multiple regression analyses (Proc Stepwise, SAS Inst. 1985) relating mortality to measures of defoliation and chemistry among trees. Associations between chemistry and defoliation on the 17 treatment trees were investigated with general linear models (SAS Inst. 1985). Transformations were dose ($\log_e$), mortality (arcsin square-root) and per cent defoliation (arcsin square-root) for this and all following experiments.

Bioassay of viral efficacy on foliage damaged in the previous year

To compare the magnitude of wound-induced inhibition of virus by defoliation in the previous and current year, we repeated the laboratory bioassay in 1991 on a subset of the 17 trees used in 1990.

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[illegible] in other [illegible] (Keating et al. 1988). The [illegible] in 1991 were not a random sample of the 1990 trees. We chose the ten largest trees because they had had the smallest proportion of their canopies protected by bags from natural gypsy moth defoliation in 1990 and were therefore, we assumed, the most likely to exhibit across-year induction. Our research agenda was serendipitous: 1990 was the peak year of a moderate gypsy moth outbreak at our study site, and natural defoliation levels were much lower in 1989 (pre-experimental survey) and in 1991 (defoliation measured directly).

The ten trees were bagged with a similar range of larval densities as in 1990 to generate variation in defoliation, and the foliage was treated identically to that in 1990. Viral doses were changed, however, since the results from 1990 suggested that wound-induced variation in leaf quality (below) was high enough to mask the effects of viral dose. In 1991, doses were 20,000, 50,000 and 80,000 PIBs per larva (with distilled water control). The design was therefore 40 larvae per dose per tree (30 treatment groups and 10 control groups). Defoliation and chemistry measures (below) were taken as before, but in 1991, we could relate larval mortality to defoliation measured the previous year as well as current year defoliation. All other aspects of experimental design were as before.

Analysis. Again, mortality in the control groups (distilled water) was insignificant and was not used further in analysis. By broadening the range of viral dose in 1991 (above), we found a significant relationship between dose and gypsy moth mortality (analysis of variance in mortality, dose within tree, F = 18.90, d.f. = 2, 18, $p<0.001$, Table 1). We therefore generated LD50s (the dose of virus estimated to kill 50% of larvae) using Probit analysis (Sas Inst. 1985). The single measure of LD50 for each tree was then associated with defoliation (1990 and 1991) and tree chemistry (1991) in multiple regression analysis (Proc Stepwise, Sas Inst. 1985).

Field evaluation of wound-induced inhibition of LdNPV

To see whether natural mortality of feral gypsy moth larvae from virus was related to natural defoliation levels within a year (a field test of the 1990 bioassay), we carried out field sampling in 1990 on 14 additional trees (see methods for experiment 1) at the same site. Thirty to 50 larvae were collected haphazardly from each tree while in the 4th instar. By this age, larvae would have been exposed to any naturally-occurring virus on foliage (Woods and Elkinton 1987). Larvae were returned to the laboratory and fed individually on artificial diet (25° C, 16:8 light:day) to death or pupation. Subsets of dead larvae were stained and examined for PIBs as before. Since peak natural infection occurs in the 3rd instar, and since larval movement between trees is restricted primarily to neonate larvae or those in the 5th instar and beyond (Wallner and McManus 1981), we have assumed that larvae dying from virus from these 14 trees consumed their PIBs on those trees. Natural defoliation estimates were made as before. In addition, between thirty and forty leaves were removed haphazardly from each of the three largest branches for chemical analysis (below).

We attempted to replicate the field test of defoliation-induced inhibition of LdNPV in 1991, but natural gypsy moth populations at the site collapsed (above), and sample sizes of 4th instar larvae per tree were simply too low to relate them to measurements of defoliation or chemistry. As a result, we could not repeat the field test of viral inhibition, nor can we compare within- and between-year induction effects on feral larvae.

Analysis. All associations between larval mortality from virus, defoliation, and chemistry measures on the 14 sample trees were assessed by stepwise multiple regression (Sas Inst. 1985). Mortalities were weighted by the number of larvae sampled per tree (per cent mortalities calculated from trees with lower larval densities may have higher error).

[illegible] of foliage chemistry

Although our primary objective was to determine whether defoliation per se could influence viral efficacy, we were interested in linking the induction effect to a particular measure of foliage chemistry. Since the gypsy moth prefers host plants in which the allelochemicals are almost exclusively phenolics (Barbosa and Krischik 1988) and since previous studies of red oak induction have focussed on polyphenolic compounds (Rossiter et al. 1988), which have also been linked to pathogen inhibition (Keating et al. 1988, 1990), we limited our analyses to general measures of oak tannin chemistry. We stress, however, that our results are purely correlative, and should be interpreted cautiously.

Leaf samples were collected from bags and trees as described above. Ten to 15 leaves from each bag (those remaining after sampling for bioassays) and 20–40 leaves from outside bags (collected haphazardly from the three largest branches) were flash-frozen in liquid nitrogen in the field, stored at −40° C, lyophilized and ground to a fine powder. Extracts were prepared by prewashing 200 mg of powder in diethyl ether and extracting at 45° C for 3 h in 10 ml of 70% acetone. Acetone was removed by evaporation under reduced pressure, and distilled water added to the aqueous extracts to a constant 10 ml volume. Proanthocyanidins, total phenolics and protein were assayed using methods described in Rossiter et al. (1988). Ability of phenolic extracts to bind protein was measured using the radial diffusion assay with BSA as standard protein (Hagerman 1987).

Potassium iodate-reactive phenolics were assayed to estimate gallotannins (hydrolyzable tannins) using a method developed by Bate-Smith (1977) and modified by Schultz and Baldwin (1982). The potassium iodate reagent is sensitive to terminal galloyl residues, which provide the hydroxyls capable of interacting with proteins and other biologically-significant molecules (Bate-Smith 1977). In contrast, the alternative rhodanine assay for polymerized galloyl esters (Inoue and Hagerman 1988) estimates all galloyl residues present, including those incapable of participating in complexing. Moreover, ellagic acid, which is present in oak extracts, interferes with the rhodanine assay (Inoue and Hagerman 1988; Schultz and Schofield, unpub. observations). When tannic acid or gallic acid are used as standards, the potassium iodate and rhodanine assays give comparable estimates of relative gallotannin contents at the concentrations typical of red oak (Schultz and Schofield, unpub. observations); potassium iodate becomes less useful at very low gallic acid concentrations.

We recognize that there are limitations in these chemical analyses, but since we were interested in comparing red oak induction with previous studies using older methods, and since we were looking for general correlative trends rather than specific active compounds, we consider our methods a reasonable compromise. Perhaps most important, we focussed on analyses that have been highly predictive of viral inhibition in previous studies, have been shown to reflect biological activity of oak leaves (Keating et al. 1988; Schultz et al. 1990), and are known to change during damage by the gypsy moth (Schultz and Baldwin 1982; Rossiter et al. 1988).

Results

Bioassay of viral efficacy on foliage damaged in the current year

Defoliation inside bags and foliage hydrolysable tannin concentrations were the only significant predictors of gypsy moth mortality from virus in our 1990 bioassay. Defoliation was the first variable selected by stepwise multiple regression, and as defoliation levels generated inside bags increased on the 5 bioassay trees, mortality from virus decreased (r-sqd = 0.76, d.f. = 1,3, $p<0.05$,

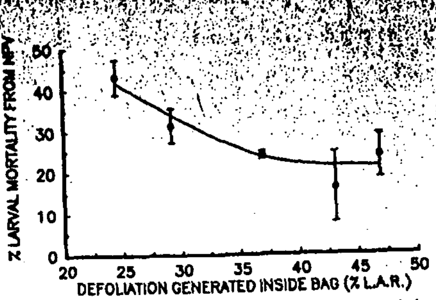

Fig. 2. Viral-induced mortality of gypsy moth in 1990 and the defoliation level of the associated foliage. Points are the means of three doses, each point representing an individual tree (see text for details) and bars are standard deviations. Data were transformed before analysis (see methods). The curve was fitted by least means square analysis (Axum Graphics, TriMetrix)

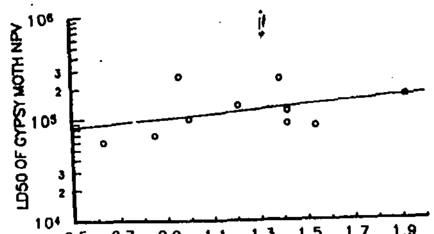

Fig. 3. The LD50 of gypsy moth virus in 1991 and the gallotannin content of the associated foliage. Gallotannin concentration is reported as per cent tannic acid equivalents per mg leaf disc. Each point represents an individual tree. Data were transformed before analysis (see methods)

Fig. 2). Hydrolysable tannin concentration of foliage was the second (and last) variable selected by the stepwise procedure, and was marginally significant ($p=0.08$). The combined regression suggests that the combination of high defoliation levels and high hydrolysable tannin concentrations are related to viral inhibition (r-sqd = 0.96, d.f. = 2,2, $p=0.038$). The equation of the line is:

Mortality = 98.16 − (0.95•Defoliation) − (2.29•Tannin)

Neither canopy-wide defoliation level outside bags nor any of the other chemistry measures were correlated with mortality from virus. A summary of foliage characteristics is given in Table 2.

Despite the inhibition of the virus by leaf damage in bags on the 5 bioassay trees (Fig. 2), defoliation levels inside bags were not correlated with any of our measures of chemistry from the group of 17 treatment trees. In other words, there were no measurable increases in the phenolic compounds generally associated with induction in oaks. Measurements of phenolic and protein chemistry for all 17 trees are summarized in Table 3.

Table 2. Foliage characteristics (chemistry and defoliation) from 5 trees used in laboratory bioassays with gypsy moth and NPV. KIO3 = gallotannins (% tannic acid equivalents); Folin-Denis = total phenolics (% tannic acid equivalents); Radial/BSA = protein binding assay (cm²); PCs = proanthocyanidins (% quebracho tannin equivalents); Protein = mg%BSA equivalents; Canopy Defol. = defoliation estimated outside bags (%); Bag Defol. = defoliation estimate inside bags (%). N = sample size and SD = standard deviation. Defoliation estimates were arcsine square-root transformed before analysis. N = 5 for all means

Measurement	Mean	SD
Chemistry		
KIO3	14.11	0.59
Folin-Denis	9.31	1.47
Radial/BSA	4.79	0.11
PCs	5.04	1.74
Protein	6.64	0.27
Defolation		
Bag Defol.	36.64	2.59
Canopy Defol.	26.58	0.44

Table 3. Measurements of foliage chemistry from red oak trees. Leaves were sampled from inside (in) and outside (out) bags on each tree during May 1990 and 1991. KIO3 = gallotannins (% tannic acid equivalents); Folin-Denis = total phenolics (% tannic acid equivalents); Radial/BSA = protein binding assay (cm²); PCs = proanthocyanidins (% quebracho tannin equivalents); Protein = mg%BSA equivalents. N = sample size and SD = standard deviation. N = 17 for 1990 and N = 10 for 1991 for all chemical analyses

Measurement	Position	1990	1991
		Mean (SD)	Mean (SD)
KIO3	(in)	14.74 (6.82)	14.32 (3.04)
KIO3	(out)	14.88 (8.63)	14.76 (4.04)
Folin-Denis	(in)	9.57 (4.07)	8.33 (1.64)
Folin-Denis	(out)	9.99 (4.62)	8.95 (1.83)
Radial/BSA	(in)	5.32 (2.78)	2.42 (0.87)
Radial/BSA	(out)	4.99 (2.64)	2.22 (0.78)
PCs	(in)	6.46 (3.39)	11.11 (6.81)
PCs	(out)	9.41 (6.66)	16.81 (9.99)
Protein	(in)	7.12 (0.69)	8.25 (0.64)
Protein	(out)	7.47 (1.13)	7.86 (1.13)

Bioassay of viral efficacy on foliage damaged in the previous year

Gypsy moth mortality from virus in the second year was correlated with both foliage hydrolysable tannin concentrations, and concurrent year defoliation generated inside bags. Hydrolysable tannin concentration was the first variable selected by stepwise multiple regression, with increasing tannin concentrations related to higher LD50s, and therefore greater inhibition of the virus (r-sqd = 0.54, d.f. = 1,8, $p=0.015$, Fig. 3). Defoliation generated inside bags was the second (and last) variable selected by multiple regression, with higher defoliation

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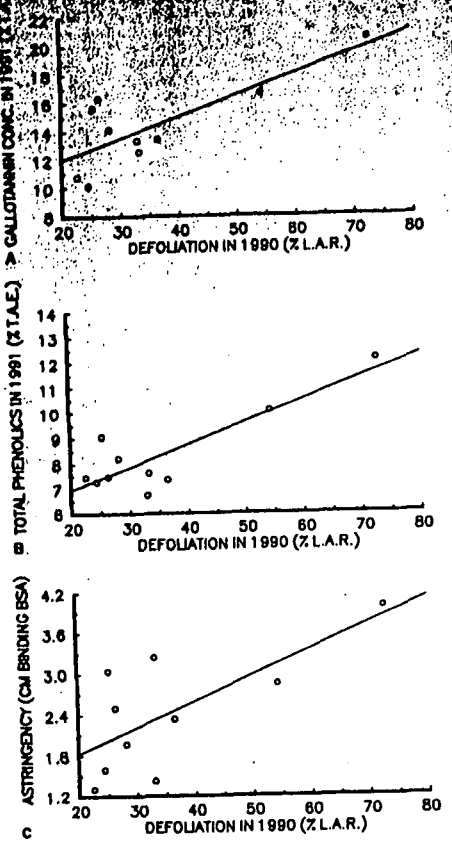

Fig. 4A–C. The relationships between unmanipulated canopy-wide defoliation (per cent leaf area removed) of 10 red oak trees in 1990 and A gallotannin content, B total phenolic content and C astringency of the foliage from the same trees in 1991. Tannin concentrations are reported as tannic acid equivalents, and astringency as cm binding of BSA protein. Data were transformed before analysis (see methods)

resulting in higher LD50s ($p = 0.017$). The combined regression suggests that, as in 1990, high foliar hydrolysable tannin concentrations and higher defoliation levels are related to increasing inhibition of LdNPV (r-sqd = 0.81, d.f. = 2,7, $p = 0.003$). The equation of the line is:

$$LD50 = 3.80 + (1.16 \cdot \text{tannin}) + (0.14 \cdot \text{defoliation})$$

A summary of 1991 foliage characteristics is given in Table 3. No other chemistry measures were correlated with gypsy moth mortality in the laboratory bioassay in 1991, and neither was current year defoliation outside bags. As in 1990, the defoliation generated within bags in 1991 was not correlated with any measures of chemistry taken in 1991.

There is some evidence, however, that the phenolic chemistry of the oak foliage of the 10 bioassay trees in 1991 may have been determined, in part, by defoliation levels in 1990. Trees which suffered high levels of canopy-wide defoliation in 1990 had the highest levels of three of our measures of phenolic chemistry in 1991: potassium iodate-reactive phenolics, total phenolics, and the radial diffusion protein binding assay (r-sqd = 0.60, d.f. = 9, $p < 0.01$); r-sqd = 0.72, d.f. = 9, $p < 0.01$; r-sqd = 0.48, d.f. = 9, $p < 0.03$ respectively, Fig. 4). Although all three relationships are strengthened by the presence of two high-defoliation trees, and are correlative rather than experimental, they provide the first evidence of across-year phenolic induction in red oak. Moreover, since potassium iodate-reactive phenolics were negatively correlated with gypsy moth mortality from virus in 1991 (Fig. 3), canopy-wide defoliation in 1990 may have inhibited infection by virus in 1991.

However, potassium iodate-reactive phenolics were not higher overall in the population of oaks sampled in 1991 (Table 3). Gypsy moth defoliation in 1990 did not, therefore, induce general, population-wide increases in oak gallotannins in our study plot. Nonetheless, the tannin content of individual trees in 1991 was positively correlated with the previous year's defoliation (Fig. 4).

Field evaluation of wound-induced inhibition of LdNPV

The mortality of feral gypsy moth larvae infected under field conditions in 1990 was correlated with the natural defoliation levels on 14 sample trees in the same year. Fewer larvae died from viral infection as defoliation levels on trees increased (weighted r-sqd = 0.35, d.f. = 1,13, $p = 0.026$, Fig. 5). No other variables were selected by the stepwise multiple regression analysis. The relative weakness of the field relationship between defoliation and viral inhibition, compared with the laboratory trials, probably reflects the unknown (unmanipulated) variation in virus inoculum among trees. The subset of dead larvae stained and examined for PIBs all showed evidence of viral infection although, since the field sampling lacks a zero-infection control, we cannot exclude the possibility that other sources of mortality were involved. None of our chemistry measures was associated with natural larval mortality of feral gypsy moth on the 14 sample trees in 1990, nor with the defoliation estimates. A summary of the foliage characteristics of the 14 sample trees is given in Table 4.

Discussion

We present the first evidence that wound-induced responses in plants can influence the pathogens of insect herbivores. Induction is known to have deleterious ef-

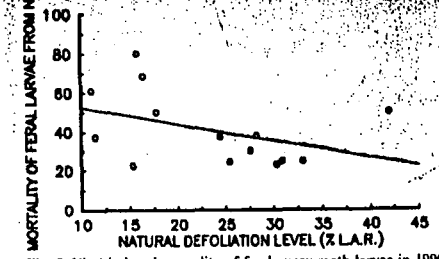

Fig. 5. Viral-induced mortality of feral gypsy moth larvae in 1990 and the concurrent year's defoliation from the 14 trees from which the larvae were collected. Data were transformed before analysis (see methods)

Table 4. Foliage characteristics (chemistry and defoliation) from 14 unmanipulated red oak trees in 1990. KIO3 = gallotannins (% tannic acid equivalents); Folin-Denis = total phenolics (% tannic acid equivalents); Radial/BSA = protein binding assay (cm²); PCs = proanthocyanidins (% quebracho tannin equivalents); Protein = mg% BSA equivalents; Canopy Defol. = defoliation estimated from the oak canopy. N = sample size and SD = standard deviation. $N = 14$ for all means

Measurement	Mean	SD
KIO3	13.60	7.47
Folin-Denis	8.17	5.15
Radial/BSA	4.94	3.65
PCs	10.88	8.54
Protein	7.68	4.47
Canopy Defol.	29.78	7.48

fects on some herbivores (Karban and Myers 1989) and plant pathogens (Bell 1981; Kuc 1981, 1987; Agrios 1988). Our data suggest, however, that the gypsy moth can alter the leaf quality of a major host, and gain protection from its own nuclear polyhedrosis virus. This result contrasts with previous studies demonstrating deleterious effects of oak induction for gypsy moths (Schultz and Baldwin 1982; Rossiter et al. 1988).

In three separate experiments, current year defoliation was related to inhibition of LdNPV. Since defoliation levels on oak are related to larval density (Fig. 1), there is the potential for positive feedback in the system – higher larval densities result in higher leaf damage levels which may protect gypsy moth larvae from virus.

We could find no chemical mechanism to explain the impact of defoliation on LdNPV. None of our measures of phenolic chemistry was related to leaf damage levels within a year, contrary to the results of Rossiter et al. (1988) in which gypsy moth defoliation caused increases in red oak phenolics. However, our measurements of phenolic chemistry were made during the third larval instar, when larvae naturally consume virus on foliage (Woods and Elkinton 1987), and therefore when leaf quality might influence infection. The within-year induc-

[illegible] Kaplan et al. (1992) was measured over the entire larval feeding period (approximately 8 weeks) and measurements of changes in polyphenolic compounds may require this extended period to develop.

Nonetheless, we did find a possible role for foliar gallotannin concentration in the inhibition of LdNPV. In two laboratory bioassays, gallotannin concentrations were negatively correlated with larval mortality from virus. The effect was weak in 1990, but stronger than that of current year defoliation in 1991 (Fig. 3). Why the putative effect of gallotannin should vary among years is unclear. One possibility is that gallotannin concentrations may be related to defoliation levels in the previous year, and there is some evidence for that in our study. Three related measurements of foliar tannins in 1991, including gallotannin concentration, were correlated with canopy-wide defoliation levels in 1990 (Fig. 4). A moderate gypsy moth outbreak peaked in 1990 at our field site, and across-year induction may have had an influence on gallotannin concentrations in 1991.

We stress, however, that the suggested role of gallotannins, and across-year induction, in the inhibition of LdNPV are the results of correlation analyses and (unlike our defoliation treatments for laboratory bioassays) not the result of manipulation. Gallotannins may be correlated with some other factor that influences the pathogenicity of the virus. Moreover, since the canopy-wide defoliation in 1990 was unmanipulated, the correlation between it and tannin chemistry the following year may be related to larval choice among foliage varying in quality rather than to across-year systemic induction. Nonetheless, across-year phytochemical induction has been demonstrated in other systems (Baltensweiler et al. 1977; Bryant et al. 1983; Haukioja and Neuvonen 1985), and may influence the variation in foliar tannin concentrations in red oak.

Phenolics are likely candidates for the induced viral inhibitor in oak since constitutive variation in phenolic-based allelochemicals can influence infection by insect pathogens (David and Taylor 1977; Felton and Dahlman 1984; Felton et al. 1987; Keating and Yendol 1987; Felton and Duffy 1990). Both experimental manipulation of diet (Felton et al. 1987; Keating et al. 1989) and correlations with leaf chemical components (Keating and Yendol 1987; Keating et al. 1990) implicate phenolics and polyphenolics as major pathogen inhibitors.

Whether induction is ultimately beneficial or deleterious for the gypsy moth will depend upon a balance between positive and negative forces. Wound-induced increases in gallotannins in oak reduce the pupal weight and fecundity of the gypsy moth (Rossiter et al. 1988), and declining food quality during outbreaks (Bess et al. 1947; Wallner and Walton 1979; Campbell 1981) may influence herbivore population dynamics more than inhibition of the virus. However, a modified Anderson and May (1980) epizootiology model, with both gypsy moth fecundity and susceptibility to virus related to foliar gallotannin concentrations, predicts that population dynamics are much more sensitive to viral inhibition than phenolic-induced changes in fecundity (Foster et al. 1992). Variation in phenolics can influence mortality by

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[illegible] 1990) [illegible] [illegible] 30X [illegible] [illegible] lower [illegible] that [illegible] in the present study) will re[illegible] [illegible] the positive influence of [illegible] [illegible] viral infection (Foster et al. 1992).

Negative impacts of phytochemical induction on herbivore pathogens could be common since induction is considered a general phenomenon in plants (Schultz 1988; Karban and Myers 1989; Tallamy and Raupp 1991) often involving increases in phenolic compounds. Moreover, the medical and plant pathology literatures describe the antimicrobial properties of phenolics, active against pathogens as diverse as HIV, herpes virus, plant mosaic viruses and plant bacteria and fungi (e.g. Cadman 1960; Friend 1979; Harborne 1988; reviewed in Schultz et al. 1992). If compounds induced by defoliation in red oak can inhibit the virus of a nonnative herbivore such as the gypsy moth, it suggests that responses of plants to damage may represent generalized wound repair or antimicrobial activity (Hartley and Lawton 1990), rather than adaptive defenses against herbivores. We suggest adding insect pathogens to the list of natural enemies of herbivores influenced by induction (Price et al. 1980; Faeth 1987, 1991; Raupp and Sadof 1991), and that many of the supposed direct effects of induction on herbivores may be indirect effects, mediated by pathogenic organisms.

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PATTERNS OF LEAF DEVELOPMENT AND HERBIVORY IN A TROPICAL UNDERSTORY COMMUNITY[1]

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Abstract. Most plant–herbivore studies have demonstrated that young leaves are preferred over mature leaves, and that the majority of lifetime damage occurs during the 1st mo. In spite of this, we know little about how young leaves are defended. Young leaves are an ephemeral resource, and herbivore damage may be reduced by (1) producing leaves at times of low herbivore abundance, (2) synchronous leaf production, or (3) rapid leaf expansion. To address these hypotheses I examined patterns of leaf phenology, leaf expansion, and herbivory in saplings of 32 species in a Panamanian lowland moist forest.

Leaf phenology ranged from continuous to highly synchronous, and mean monthly damage rates varied from 6 to 60%. Within species, leaves produced during the dry season, a period of relatively low insect abundance, received less damage than leaves produced during the wet season. Leaves produced during synchronous flushes received less damage than leaves produced out of synchrony. Species with continuous or synchronous leaf production had lower damage rates than intermediate species, but growth rates and survivorship were not correlated with leaf production. It appears that higher damage rates in intermediate species may be compensated by reduced investment in chemical defenses compared with continuous species, and a less restricted growing season and reduced storage costs compared with synchronous species. Previous studies have identified leaf expansion rate as an important young leaf defense, but in this study there was no correlation between expansion rate and herbivory.

Key words: herbivory; leaf expansion; leaf phenology; Panama; seasonality; synchrony; tropics.

INTRODUCTION

In general, herbivores prefer young leaves over mature leaves (Coley 1980, 1983, Crawley 1983, Raupp and Denno 1983, Lowman 1985). The preference for young leaves is supported by the observation that in 29 tropical species, with a mean leaf lifetime of 2.5 yr, >70% of the lifetime damage occurs in the 1st mo when a leaf is expanding (Coley and Aide 1991). Partial defoliation (Marquis 1984) and natural herbivory (Louda 1984, Crawley 1985) can negatively affect plant growth and reproduction. Defoliation experiments also have demonstrated that young leaves make a greater contribution to plant fitness than do mature leaves (Krischik and Denno 1983, Jurik and Chabot 1986, Mendoza et al. 1987).

If most herbivore damage occurs when a leaf is young, and if this damage affects plant fitness, then it is important to understand how young leaves are defended. Most studies of antiherbivore defenses have focused on mature leaves and have demonstrated that chemical and physical defenses reduce damage (Bryant and Kuropat 1980). Defense type and quantity are thought to be determined by the resource availability of the environment, and species with slow growth rates are predicted to invest in more defenses than fast growing species (Coley et al. 1985). Pioneering studies of plant–herbivore interactions suggested that young leaves are unlikely to be defended to be the same extent as mature leaves (Feeny 1970, 1976, Rhoades and Cates 1976), but recent reviews show that young leaves contain diverse secondary chemicals and, in some cases, at higher concentrations than mature leaves (McKey 1979, Coley and Aide 1991). Nonetheless, the importance of secondary chemicals in the defense of young leaves is still poorly understood. Leaf toughness is a major determinant of herbivory to mature leaves (Coley 1983), but it is unlikely that leaf toughness can be an important defense for young leaves because fiber, lignin, and cuticular thickening, materials that contribute to leaf toughness, would constrain leaf expansion for developing leaves. Young leaves of some species produce extrafloral nectaries that attract ants that may defend young leaves (McKey 1988). Although species that produce extrafloral nectaries are more common in the tropics (Coley and Aide 1991), they are relatively rare among slow growing species (Schupp and Feener 1991) and these species are expected to have evolved alternative mechanisms to defend young leaves.

In summary, the physical, chemical, and biotic defenses available to young leaves are not as effective in reducing herbivory as the defenses employed by mature leaves. However, because young leaves are an ephemeral stage in the life of a leaf, characteristics of leaf development may influence the degree of vulnerability to herbivores (Aide 1988, Clark and Clark 1991).

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To address this idea, I studied the relationship between herbivore damage to young leaves and two developmental characteristics: leaf phenology, the timing of leaf production, and leaf expansion rate, the rate of development from a bud to a completely expanded leaf.

Leaf phenology may reduce herbivore damage either by the seasonality or the synchrony of leaf production. In some tropical forests, insect abundance is lowest during the dry season (Wolda 1978, Lowman 1982); therefore, leaves produced at this time should receive less damage. Synchronous leaf production also may reduce damage to young leaves by satiating herbivores (Feeny 1976, McKey 1979, Leigh and Windsor 1982, Coley 1983, Crawley 1986, Aide 1988, McKey 1989, Clark and Clark 1991). Although few studies have demonstrated an effect of satiation on herbivores, synchronous fruit production, at the species (Janzen 1976, Augspurger 1981) and community (Ashton et al. 1988, Schupp 1990) levels, has been shown to reduce seed predator damage, and this has been attributed to predator satiation.

Leaves are most vulnerable to herbivores during the period of leaf expansion. Therefore, rapid leaf expansion could reduce herbivore damage to young leaves by shortening the developmental period and by more quickly employing the effective defenses of mature leaves (Hay et al. 1988, Aide and Londoño 1989, Kursar and Coley 1991).

These hypotheses were tested by studying the patterns of leaf production, leaf expansion, and herbivory of saplings of 32 common woody species on Barro Colorado Island, Panama.

METHODS

Study site

The study was conducted on Barro Colorado Island (BCI) (9°09′ N, 79°51′ W), in the Republic of Panama. BCI (15.6 km²) is the largest island in Gatun Lake (Panama Canal) and was isolated when the Chagres River was dammed in 1911 (Croat 1978). The vegetation is classified as tropical moist forest (Holdridge et al. 1971) or semideciduous lowland forest (Foster and Brokaw 1982).

There are two distinct seasons on BCI: wet (mid-April to mid-December) and dry (mid-December to mid-April) (Rand and Rand 1982). The annual rainfall for the 10 yr previous to the study was 2566 ± 745 mm (mean ± 1 SD), and the rainfall totals for the 2 yr of this study (1986: 2221 mm, 1987: 2953 mm) were within 1 SD of the 10-yr mean (Windsor 1988). Although maximum daytime temperatures are slightly higher during the dry season, rainfall is the most seasonal climatic factor. As the dry season proceeds, soil water content drops (Wright and Cornejo 1990a, b), but occasional storms during the dry season appear to be important cues for the flowering of some canopy trees (Gentry 1974) and understory shrubs (Augspurger 1982). Litterfall peaks during the transition between the wet and dry season (December to January) (Foster 1982, Wright and Cornejo 1990a). The partially deciduous canopy and the lack of cloud cover during the dry season significantly increase the light levels in the forest understory (A. P. Smith et al., *unpublished manuscript*). A brief dry period (1–2 wk) within the wet season, the veranillo, usually occurs during August. Associated with the veranillo are small peaks in litterfall (Wright and Cornejo 1990a), leaf production (Coley 1983), and flowering (Foster 1982).

Study species

Patterns of leaf phenology and herbivory of juvenile plants (1–2 m tall) were studied in 32 woody species representing 21 families (Table 1). The species include nine shrubs, five understory treelets, nine midstory trees, and nine canopy trees (Table 1). Nomenclature follows Croat (1978). All species, except *Ouratea lucens* and *Talisia princeps*, are among the 40 most abundant species in the mature forest (S. P. Hubbell and R. B. Foster, *unpublished manuscript*).

Leaf phenology and herbivory census

Measurements.—In November 1985, 15 individuals of four species (*Faramea occidentalis, Ouratea lucens, Quararibea asterolepis, Talisia princeps*) and 30 individuals of two species (*Hirtella triandra* and *Rheedia edulis*) were selected. In September 1986, 20 individuals of each of 26 additional species were added to the study. All plants occurred in the shaded understory of the old forest (Foster and Brokaw 1982). If the light environment of a plant changed drastically due to the creation of a light gap, the plant was dropped from the census.

Plants were censused on days 1–4 of each month. For each plant, I counted the number of leaves produced since the previous census and haphazardly marked up to 10 of these new leaves with colored wire. If 10 or fewer leaves were produced, all were marked. The following month when leaves were fully expanded I estimated the potential leaf area (total area of a leaf if no damage had occurred) and the area damaged, on all marked leaves. Measurements were made using a plastic grid. Leaf areas were estimated to 1 cm² and damaged area to 0.1 cm².

Analysis.—All species were censused for 17 mo (September 1986–January 1988), and results are presented for 1987. For each individual, I calculated the proportion of its annual leaf production that was produced in each month. For each species, the monthly proportions for individuals were averaged to determine the species pattern. If leaf production were continuous, then an average of ≈8.33% of the annual leaf production would occur each month. The coefficient of variation (CV) in monthly proportions of annual leaf production was used as an index of leafing synchrony. A

TABLE 1. Species characteristics. A—life-form (S, shrub, U, understory treelet, M, midstory tree, T, canopy tree) (following categories of Welden et al. 1991), B—CV of leaf production, an index of phenological synchrony, C—CV of percent herbivory during the 1st mo, D—mean percent herbivory (the average of herbivore damage on each individual cohort produced during 1987), E—leaf expansion rate (% increase in final leaf area/d).

Species	Family	A	B	C	D	E
Acalypha diversifolia Jacq.	Euphorbiaceae	S	0.58	0.32	16.6	5.0
Alseis blackiana Hemsl.	Rubiaceae	T	1.40	0.88	12.1	4.6
Beilschmiedia pendula (Sw.) Hemsl.	Lauraceae	T	1.41	0.79	8.4	4.7
Capparis frondosa Jacq.	Capparidaceae	S	1.06	0.29	45.5	7.0
Coussarea curvigemmia Dwyer	Rubiaceae	U	1.23	0.39	24.5	4.8
Desmopis panamensis (Rob.) Saff.	Annonaceae	U	1.10	0.40	21.2	3.3
Eugenia oerstedeana Berg	Myrtaceae	M	0.85	0.18	27.9	24.3
Faramea occidentalis (L.) A. Rich.	Rubiaceae	U	1.12	0.45	14.6	5.7
Guarea guidonia (L.) Sleumer	Meliaceae	M	0.49	0.42	6.0	9.3
Guarea sp. nov.	Meliaceae	M	1.13	0.09	12.4	7.3
Hirtella triandra Sw.	Chrysobalanaceae	M	0.46	0.17	18.5	4.4
Hybanthus prunifolius (Schult.) Schulze	Violaceae	S	2.23	0.33	16.4	5.5
Lacistema aggregatum (Berg) Rusby	Lacistemaceae	U	0.43	0.30	14.6	6.0
Mouriri myrtilloides (Sw.) Poir. subsp. *parvifolia* (Benth.) Morley	Melastomataceae	S	0.42	0.18	35.5	1.9
Ouratea lucens (H.B.K.) Engler in Mart.	Ochnaceae	S	0.53	0.34	20.9	13.0
Poulsenia armata (Miq.) Standl.	Moraceae	T	0.39	0.46	9.5	16.4
Pouteria unilocularis (Donn. Sm.) Baehni	Sapotaceae	T	0.85	0.77	21.8	7.8
Piper cordulatum C. DC.	Piperaceae	S	0.54	0.36	9.0	3.1
Prioria copaifera Griseb.	Leguminosae	T	0.54	0.37	33.4	14.0
Protium panamense (Rose) I. M. Johnston	Burseraceae	M	0.35	0.35	30.1	10.6
Protium tenuifolium Engler subsp. *sessiliflorum* (Rose) Porter	Burseraceae	M	0.61	0.39	61.0	7.9
Psychotria horizontalis Sw.	Rubiaceae	S	0.84	0.29	29.2	3.9
Quararibea asterolepis Pitt.	Bombacaceae	T	0.69	0.28	22.2	11.3
Rheedia edulis (Seem.) Planch. & Tr.	Guttiferae	M	0.77	0.33	21.2	6.6
Rinorea sylvatica (Seem.) O. Kuntze	Violaceae	S	2.06	0.39	31.5	16.1
Sorocea affinis Hemsl.	Moraceae	S	1.34	0.64	20.9	8.1
Swartzia simplex (Sw.) Spreng. var *ochnacea* (A. DC.) Cowan	Leguminosae	U	0.79	0.49	51.5	8.6
Tachigalia versicolor Standl. & L. O. Wms.	Leguminosae	T	0.46	0.35	29.1	9.5
Talisia princeps Oliv.	Sapindaceae	M	1.52	0.54	15.3	23.9
Tetragastris panamensis (Engler) O. Kuntze	Burseraceae	T	0.73	0.37	55.7	7.7
Trichilia tuberculata (Planch. & Tr.) C. DC.	Meliaceae	T	0.82	0.41	19.4	5.2
Virola sebifera Aubl.	Myristicaceae	M	0.30	0.31	13.2	5.1

CV near zero indicates continuous leaf production, and a high CV indicates highly synchronous leaf production.

Herbivore damage to young leaves was estimated when leaves were ≈1 mo old. Damage was calculated by dividing the total area damaged by the estimated total potential leaf area. If a marked leaf was missing, its area was assumed to be the average of the potential leaf area of the surviving leaves, and this area was added to the total of herbivore damage and the total potential leaf area.

Past studies have underestimated herbivory because measurements do not include leaves that were completely eaten or whole flushes that were aborted due to stem-boring insects. The inclusion of lost leaves can increase estimates of young leaf herbivory by 2.4 times (this study) and mature leaf herbivory by 1.6 times (Coley 1982) to 2.3 times (Lowman 1984). If leaves have not completely expanded, including missing leaves will overestimate the dry mass lost to herbivores. On the other hand, because herbivory during development has the largest negative effect on lifetime leaf profitability (Jurik and Chabot 1986), these values may underestimate the opportunity costs.

Within-species comparison of damage was made by considering each leaf cohort (leaves produced by an individual in a single month) as an independent event. To determine the effect of season on herbivore damage, I compared the mean damage of leaf cohorts produced in the 4-mo dry season to that of cohorts produced in the 8-mo wet season. To determine the effect of synchronous leaf production in the 10 most synchronous species, I compared the mean damage on leaf cohorts produced in the month of peak leaf production to the mean damage on all other leaf cohorts.

Community patterns of annual leaf production were calculated as the means of the monthly estimates of all species. Community herbivory levels on 1-mo old leaves were calculated as the average of mean values for all species that produced leaves in a given month.

The relationship of the CV of herbivory and mean herbivory to the CV of leaf phenology was determined by using a technique for nonlinear analysis (Feener et al. 1988). The herbivory data were arcsine transformed, and phenology data were centered by subtracting the mean. *Hybanthus prunifolius* and *Rinorea sylvatica* were excluded from the analysis because the

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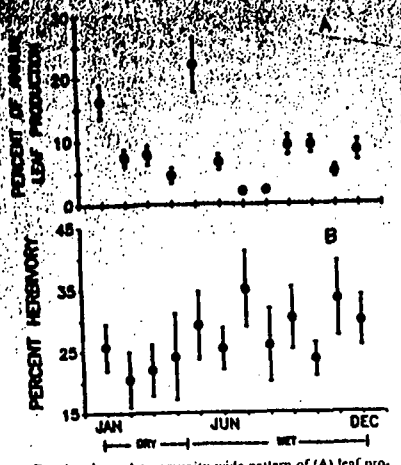

FIG. 1. Annual community-wide pattern of (A) leaf production and (B) leaf herbivory of saplings for a group of 32 canopy and understory species on Barro Colorado Island, Panama. Leaf production values are the means of the monthly estimates for all species. Monthly damage values are the means of percent damage values (% area lost) for all species that produced leaves that month. Error bars are ±1 SE. Data are from 1987.

values for the cv of leaf production are greater than the upper quartile plus 1.5 times the interquartile range (Wilkerson 1987). The quadratic term was used in the regression only if it significantly improved the fit of the model.

Leaf expansion rate

Leaf expansion rate was determined by taking serial measurements (1–3 d intervals) of leaf area on individual leaves (3–5 leaves/species) as they expanded from 20% full size to full size. The slope of the relationship between percent expanded and time was used as an index of leaf expansion rate. A slope of 5.0% would mean that a leaf would take 20 d to expand from 20 to 100% full size.

Sapling growth and survivorship

Data on sapling growth and survival are from Welden et al. (1991) for plants (1–4 cm dbh [diameter at breast height] for trees and 1–2 cm dbh for shrubs) in the understory (canopy height > 10 m). The measurement interval was 1982–1985. Growth is the median annualized percentage increment in dbh among surviving saplings. Survivorship is the annualized percentage of saplings surviving the intercensus period.

RESULTS

Community leaf phenology

During 1987, the community pattern of leaf phenology (32 species) showed distinct peaks in January, the beginning of the dry season, and in May, the beginning of the wet season (Fig. 1A). Approximately 20% of the annual leaf production occurred during the three driest months (February, March, April). Leaf production was lowest during two wet season months (July, August). Although there are distinct seasons on BCI, monthly leaf production did not differ significantly between dry and wet season months (dry: $\bar{X}$ = 9.0% (N = 4 mo); wet: $\bar{X}$ = 8.1 (N = 8 mo); Student's t test, t = 0.24, P = .8).

The synchrony of leaf production varied markedly among understory individuals of the 32 species (Appendix 1). *Hybanthus prunifolius* and *Rinorea sylvatica* produced 90% of their leaves in only a single month, but other species (e.g., *Virola sebifera*, *Protium panamense*) produced leaves throughout the year (Appendix 1). The most synchronous species produced leaves, at the beginning of the wet season (e.g., *H. prunifolius*, *R. sylvatica*, *Alseis blackiana*), or during the wet-to-dry season transition (e.g., *Beilschmiedia pendula*, *Sorocea affinis*). Some species produced leaves in both of these periods (e.g., *Pouteria unilocularis*, *Trichilia tuberculata*). Others also produced a flush following the veranillo (e.g., *Capparis frondosa*, *Tachigalia versicolor*). The community pattern of leaf production showed two distinct peaks (Fig. 1A), but some species produced leaves over a 6–12 mo period (Appendix 1).

Herbivory on new leaves

The community pattern of herbivory in 1987 showed that, on average, 27% of the potential leaf area was lost during the 1st mo, when a leaf is expanding (Fig. 1B). Damage to new leaves was highest in July (35%), the month of lowest leaf production, and lowest (20.5%) in February, a dry season month (Fig. 1B). At the community level, leaves produced during the dry season (January through April) received significantly less damage (23.1%) than leaves produced during the wet season (May through December; 29.1%) (Student's t test, t = 2.76, P = .02).

A within-species comparison of early herbivory damage between wet season and dry season leaf cohorts showed that 23 of the 32 species received higher levels of damage during the wet season (Fig. 2, Wilcoxon signed-ranks test, P = .003). Across species, the positive relationship between damage during the wet and dry seasons (Spearman r_s = 0.78, P < .001, N = 32) indicates that regardless of the seasonal effect, some species experience consistently higher levels of damage than others (Fig. 2).

Along with a seasonal effect on herbivore damage, there is also an effect of relative degree of synchrony. The coefficient of variation of monthly herbivory is

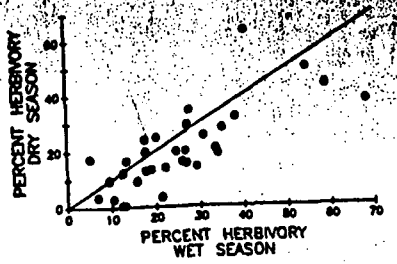

FIG. 2. Comparison of damage (area loss) rates to new leaves (≈1 mo old) between leaves produced during the dry and wet seasons for each of 32 species. The regression line (slope = 1) represents the relationship of equal damage rates in each season.

positively correlated with the cv of monthly leaf production, an index of the degree of synchrony (Fig. 3A; Appendix 2). On average, therefore, the more synchronous species have higher monthly variation in herbivory than species that produce leaves more continuously. A possible cause of high variation in herbivory for the more synchronous species is that damage is low during the peak month, but leaves produced during nonpeak months have higher damage rates. Intraspecific comparisons of herbivore damage between leaf cohorts produced during the peak month and nonpeak months for the 10 most synchronous species support this hypothesis. All 10 species had lower damage rates during the month of peak leaf production than in nonpeak months (Table 2, Wilcoxon signed-ranks test, P = .005).

In addition, leaf phenology had an effect on mean herbivory damage (Fig. 3B). An analysis of variance showed that a linear model explained only 1.5% of the variance, while the addition of a quadratic term significantly increased the variance explained (18.2%) (Appendix 2). These data suggest that there is a trend for species with intermediate leaf production to have higher herbivory rates compared with species with relatively more synchronous or continuous leaf production.

Sapling growth and survivorship

The annualized percent dbh growth of only 5 of the 32 species was >0 (Welden et al. 1991). The annualized survivorship was >96% for all species except *Acalypha diversifolia* (89%) and *Poulsenia armata* (86%) (Welden et al. 1991). Although patterns of leaf production varied among the 32 species, there was no relationship between the cv of leaf synchrony and sapling growth (Spearman r_s = 0.21, NS, N = 32) or sapling survivorship (Spearman r_s = 0.26, NS, N = 32).

Leaf expansion rate

For the 32 species, mean leaf expansion rate (percent increase of final leaf area per day) was 8.5% and ranged from 2% in *Mouriri myrtilloides* to 24% in *Eugenia oerstedeana* (Table 1). The majority of species expanded from 20% full size to 100% full size in 10–20 d, but some species expanded in 4–5 d and a few took > 30 d. This variation in leaf expansion rate caused the expanding leaves of different species to be differentially exposed to herbivores. However, leaf expansion rate was not significantly related to herbivore damage for the 32 species examined (Fig. 4, Spearman r_s = 0.22, P > .1).

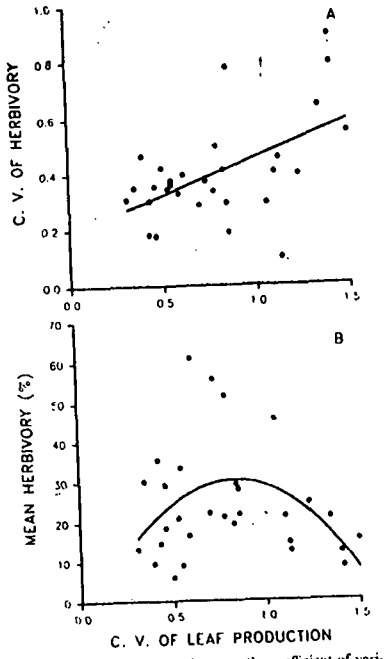

FIG. 3. The relationship between the coefficient of variation (cv) of leaf production and (A) cv of herbivory and (B) mean percent herbivory. *Hybanthus prunifolius* and *Rinorea sylvatica* were excluded from the analysis (Appendix 2) because their values for the cv of leaf production are greater than the upper quartile plus 1.5 times the interquartile range for the 32 species examined (Wilkerson 1987). The regression lines were determined using a technique for nonlinear analysis (Appendix 2; see *Methods*).

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Table 2. A comparison of mean percent herbivory damage (loss of leaf area) on cohorts of leaves produced in peak and nonpeak months for the 10 species with the most synchronous leaf phenologies.* *n* is the number of individuals that produced leaves in the peak month or nonpeak months.

Species	Herbivory level: Peak %	Peak *n*	Nonpeak %	Nonpeak *n*	Diff.
Hybanthus prunifolius	9.4	21	22.5	24	13.1
Rinorea sylvatica	13.0	20	42.9	32	29.9
Talisia princeps	9.9	4	26.1	2	16.2
Bellschmiedia pendula	7.9	15	9.1	9	1.2
Alseis blackiana	4.0	15	17.9	21	13.9
Sorocea affinis	11.3	14	29.9	15	18.6
Coussarea curvigemmia	24.4	18	24.6	35	0.2
Guarea sp. nov.	12.0	13	12.6	29	0.6
Faramea occidentalis	12.2	23	20.7	9	8.5
Desmopsis panamensis	14.7	18	24.1	40	9.4
Mean ± SD	11.9 ± 5.3		23.0 ± 9.7		11.2 ± 9.3

* Damage was measured ≈ 1 mo after leaves were produced. Species are ranked in descending order by their coefficient of variation of leaf area production.

Discussion

In this study, 27% of the new leaf area was lost during the 1st mo of a leaf's lifetime. Although studies to date (see studies reviewed in Coley and Aide 1991) indicate that young leaves are generally preferred over mature leaves, the extent of the damage and the consequences may have been underestimated. Photosynthetic capacity, leaf nitrogen, and stomatal conductance decrease with leaf age (Chabot and Hicks 1982, Field and Mooney 1983); therefore, herbivore damage to young leaves will have a greater effect on whole-plant productivity than damage to mature leaves (Krisckik and Denno 1983, Jurik and Chabot 1986, Mendoza et al. 1987). Despite the consequences of herbivory to young leaves, little is known about the defenses of this vulnerable stage (Kursar and Coley 1992).

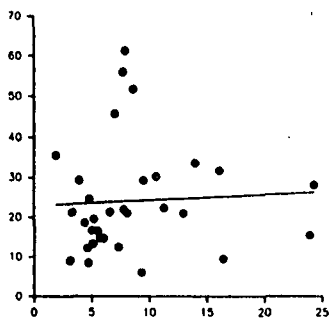

Fig. 4. The relationship between mean percent herbivory during the 1st mo and leaf expansion rate for 32 species. The herbivory value is the mean value of all monthly values in which a species produced leaves. Expansion rate is the slope of the relationship between age and percent full size for leaves between 20% and full size.

Young leaf herbivore defenses

Seasonality of leaf phenology.—The present study suggests two ways that leaf phenology can affect herbivory on young leaves. First, leaves produced during the dry season, the period of lowest insect abundance on BCI (Wolda 1978), received less damage than leaves produced during the wet season. In 1987 most dry season leaf production occurred in January, when soil moisture was still high (Wright and Cornejo 1990*a*, *b*) and light levels in the understory were increasing (A. P. Smith et al., *unpublished manuscript*) due to leaf loss by canopy trees (Wright and Cornejo 1990*a*, *b*). Both the increased irradiance, which could serve as proximal cue and provide extra energy, and the high soil moisture content may have contributed to the January peak. Even though understory plants can be water stressed during the following three dry season months (Rundel and Becker 1987), these months accounted for 20% of the annual leaf production.

For many plants, leaf buds are formed months before they expand. Once conditions or environmental cues are appropriate, the leaves expand rapidly (Kozlowski 1971). Even if herbivores respond to the same environmental cue as their host plants, several life stages (e.g., pupa, egg, and larva) may have to develop before feeding begins. Such a lag-time may allow many young leaves to escape damage. This suggests that differences between plants and herbivores in drought tolerance and response time to environmental cues may be important determinants of damage rates to young leaves.

Synchronous leaf phenology.—A second phenological factor associated with lower herbivore damage was

synchronous leaf production. For the 10 most synchronous species, leaves produced in nonpeak months received 2 times more damage than leaves produced during peak months (Table 2). [illegible] had also been identified in another [illegible] *Gustavia superba* (Lecythidaceae) (Aide 1991). In a 2-yr study of two populations of *G. superba*, leaves produced out of synchrony received 3–4 times more damage than leaves produced in synchrony (Aide 1991).

Herbivores may be an important selective pressure on the timing of leaf production (Aide 1918), and environmental factors may constrain leaf production to synchronous leaf flushes. In this lowland moist forest, the combined effects of greater herbivore pressure during the wet season, and water deficits during the dry season, could lead to synchronous leaf production at the beginning or end of the wet season. Regardless of the evolutionary pressures that have selected for synchronous phenologies, they appear to be cued by a proximal abiotic event.

Although herbivore pressure is thought to be greater in tropical forests than temperate forests (Coley and Aide 1991, but see Landsberg and Ohmart 1989), synchronous leaf production may also influence herbivore pressure in temperate communities (Feeny 1976). Many umbelliferae species are acceptable food plants for swallowtail butterfly larvae, but a few species with early leaf phenology escape herbivore damage (Finke and Scriber 1988). In oaks, damage due to herbivores, physical damage, or fire can result in leaf production later in the season; these delayed leaf cohorts receive high damage rates (Washburn and Cornell 1981, Auerbach and Simberloff 1984). Even in the extreme abiotic conditions of deserts, herbivores have influenced leaf phenology of the common shrub *Prosopis glandulosa* (Nilsen et al. 1987). In all these examples, synchronous leaf production is associated with reduced herbivory.

Continuous leaf phenology.—Although synchronous leaf production may reduce herbivory, many species in this study produce leaves throughout the year and are unlikely to escape herbivores in time. For these species, chemical defenses (Macauley and Fox 1980), parasitoids (Price et al. 1980), or ants at extrafloral nectaries (McKey 1988, 1989) may be more effective defenses. Only 4 of the 32 species had extrafloral nectaries (Schupp and Feener 1991), and only *Hirtella triandra* had both continuous leaf production and extrafloral nectaries. This suggests that although continuous leaf production may favor extrafloral nectaries (McKey 1988, 1989), carbon limitation reduces the suitability of this defense in the understory (Schupp and Feener 1991).

Costs of defense.—Although the species with intermediate patterns of leaf production tended to have the highest herbivore damage (Fig. 3B), there was no relationship between the degree of leaf synchrony and growth or survivorship. This suggests that although the relatively more continuous and synchronous flushing species experienced lower damage rates (Fig. 3B), this benefit was balanced by a cost. If continuously flushing species do not escape herbivores in time, they may defend young leaves with high concentrations of chemical defenses that can have a negative effect on growth rate (Coley 1986). Synchronous flushing species may escape or satiate herbivores, but growth is restricted to one or two major flushes per year. The asynchrony between assimilation and growth will lead to an increased investment in storage capacity (Chapin et al. 1990) and an increase in opportunity costs.

Leaf expansion rate.—Across species, leaf expansion, from 20% full size to full size took 4–50 d. Previous work has suggested that rapid leaf expansion decreases the time young leaves are vulnerable to herbivores (Aide and Londoño 1989, Kursar and Coley 1991). Results from this study showed no relationship between expansion rate and damage and do not support this observation. Although leaf expansion does not explain variation in herbivory across species, more detailed studies (Hay et al. 1988, Aide and Londoño 1989) suggest that for some species leaf expansion can be an important defense for young leaves.

Conclusions

The period of expansion is the most vulnerable stage during the lifetime of a leaf. Many of the defenses of mature leaves are not available to developing leaves, but it appears that a diversity of defenses, some chemical or symbiotic, have evolved to reduce damage to young leaves. This study emphasizes that young leaves are an ephemeral stage, and aspects of leaf phenology can serve as defense mechanisms. Species may produce leaves during periods (e.g., dry season) when insect abundances are low or leaves may be produced in synchronous flushes, possibly satiating herbivores.

Studies of flower and fruit phenology have recognized the importance of biotic selective pressures (Rathcke and Lacey 1985), but the relevance of biotic selective pressures has received little attention with regard to leaf phenology. Given the high levels of herbivory on young leaves, it is likely that herbivores have influenced patterns of leaf phenology.

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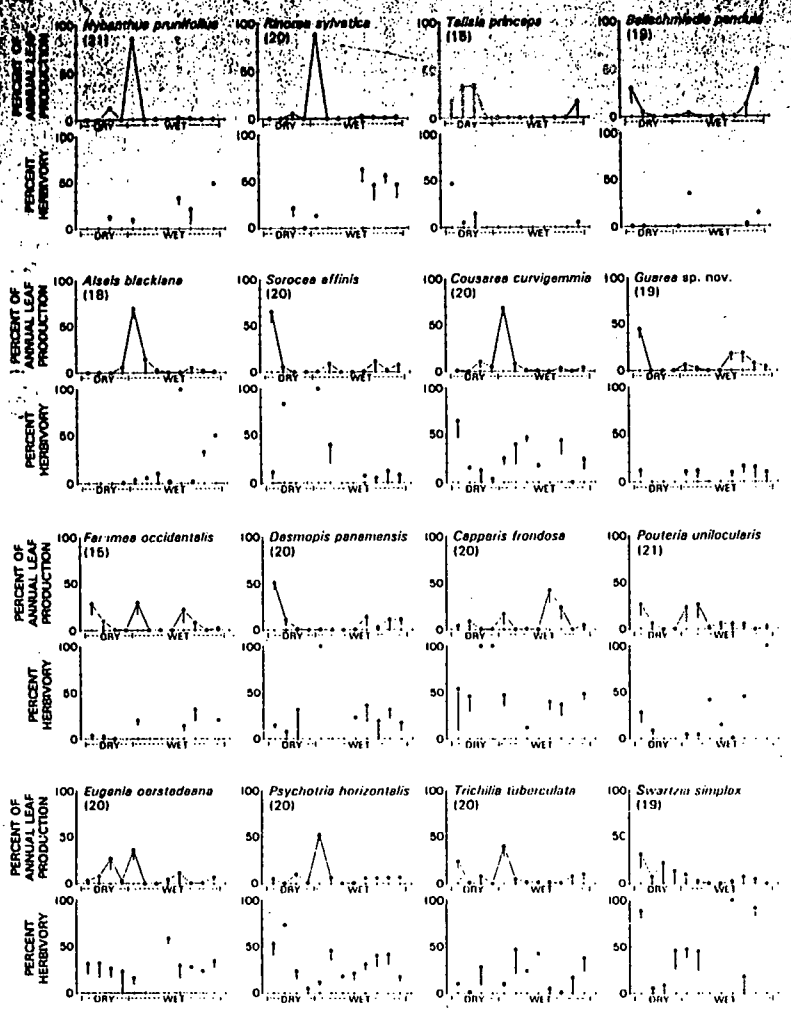
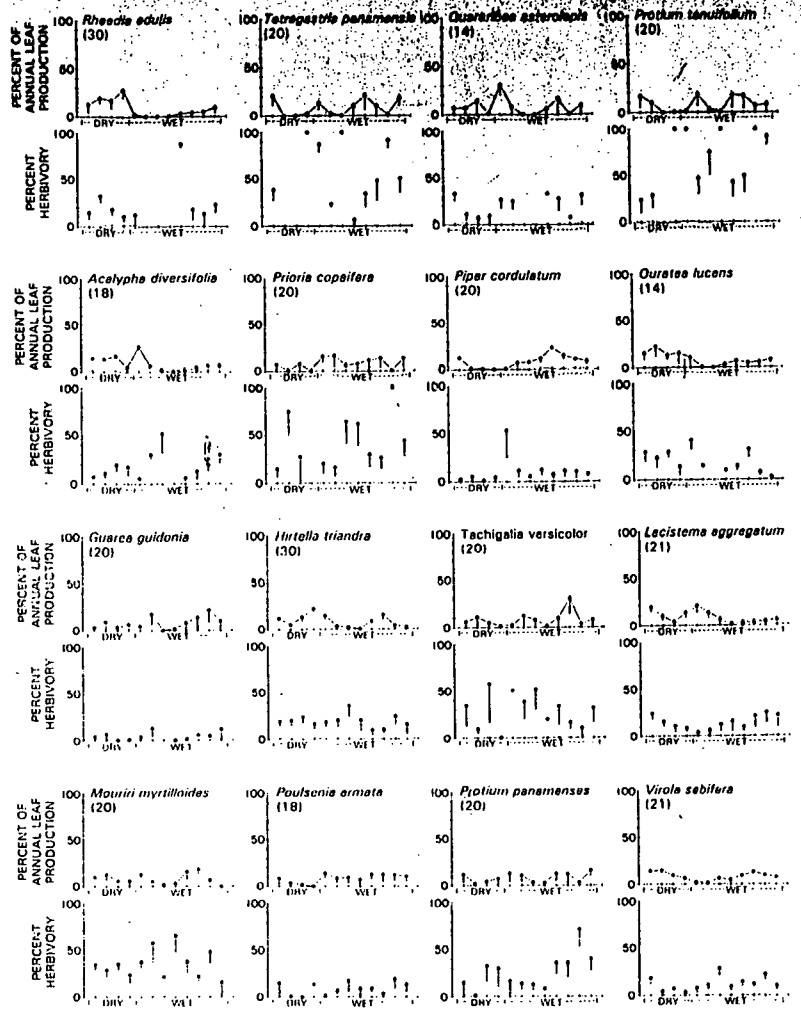


APPENDIX I

Annual pattern of leaf production and herbivory for each of 32 species. Leaf production is the mean monthly percentage of annual leaf production of all individuals (number in parentheses) of each species. Percent herbivory is the mean value of individuals that produced leaves in each month. Error bars are 1 se. Data are presented for January to December 1987.



APPENDIX I. Continued.

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APPENDIX 2

Analysis of variance tables for linear and quadratic regressions of the coefficient of variation (cv) in herbivory and mean herbivory against the cv of leaf production (an index of the degree of leaf synchrony). Herbivory data were arcsine transformed, and the cvs of leaf production were centered by subtracting the mean.

A) cv in herbivory

Source	SS	df	MS	F	P
Explained	0.361	2	0.181	6.464	<.01
Linear	0.285	1	0.285	10.179	<.005
Quadratic	0.076	1	0.076	2.714	NS
Residual error	0.753	27	0.028		
Total	1.114	29			

B) Mean herbivory

Source	SS	df	MS	F	P
Explained	0.138	2	0.069	3.000	<.1
Linear	0.011	1	0.011	0.478	NS
Quadratic	0.127	1	0.127	5.522	<.05
Residual error	0.620	27	0.023		
Total	0.758	29			

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MOOSE BROWSING AND SOIL FERTILITY IN THE BOREAL FORESTS OF ISLE ROYALE NATIONAL PARK[1]

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Abstract. Selective foraging by moose on hardwoods and avoidance of conifers alters community composition and structure, which in turn can affect nutrient cycles and productivity. The effect of moose browsing on the nutrient cycles of boreal forests was studied using three 40-yr-old exclosures on Isle Royale, Michigan. Two alternative mechanisms by which moose affect ecosystems were tested: (1) moose depress both the quantity and quality of litter return to the soil, and hence N mineralization and net primary productivity, by browsing on hardwoods and avoiding conifers; (2) moose stimulate N mineralization, and hence net primary productivity, by opening the canopy and by dropping fecal pellets. Soil nutrient availability and microbial activity, including exchangeable cations, total carbon and nitrogen, nitrogen mineralization rates, and microbial respiration rates, were uniformly higher in exclosures than outside. These differences were more significant where browsing intensity was high and less often significant where browsing intensity was low. N mineralization in browsed plots declined with increasing moose consumption rates. Net primary production in exclosures and browsed plots was strongly correlated with N mineralization. N mineralization in turn was positively correlated with litter N return and negatively correlated with litter cellulose content. These differences in litter quantity and quality were caused by an increased abundance of unbrowsed spruce outside the exclosures. Moose pellets alone mineralized less N but more C than soil alone, but pellets combined with soil stimulated N and C mineralization more than the sum of the two separately. However, this did not appear to be sufficient to offset the depression in nitrogen and carbon mineralization in soil resulting from the increased abundance of unbrowsed spruce. We conclude that, in the long term, high rates of moose browsing depress N mineralization and net primary production through the indirect effects on recruitment into the tree stratum, and subsequent depression of litter N return and litter quality. These results suggest that the effects of herbivores on ecosystems may be amplified by positive feedbacks between plant litter and soil nutrient availability.

Key words: Alces; *boreal forests; exclosures; food webs; herbivory; Isle Royale, Michigan; moose; nitrogen cycling; nitrogen mineralization.*

INTRODUCTION

The effects of herbivores on boreal forests are potentially large and long lasting (Krefting 1974, Snyder and Janke 1976, Wolff and Zasada 1979, Bryant and Chapin 1986, Bryant 1987, Naiman et al. 1988, Pastor et al. 1988, McInnes et al. 1992). How herbivores affect nutrient cycles in these forests is particularly important because nutrient availability is generally low (Flanagan and Van Cleve 1983, Pastor et al. 1987*a*, Bonan and Shugart 1989), and changes in nutrient availability are major factors driving succession (Van Cleve and Viereck 1981). Furthermore, populations of boreal herbivores fluctuate drastically between years and decades (Haukioja et al. 1983 and references therein), and these fluctuations may in turn be related to changes in nutrient cycles and inherent lag times imposed by herbivory (Schultz 1964, Bryant and Chapin 1986).

There are several important links between foraging behavior of boreal mammals, the responses of boreal plants to browsing, and the way these plants cycle nutrients. Coley et al. (1985) hypothesize that the slow growth and low nutrient uptake by plants adapted to soils of low N availability, particularly conifers, requires continuous production of secondary defensive compounds to protect their tissues; in contrast, plants adapted to high nutrient availability, particularly early successional hardwoods, do not invest highly in secondary compounds but rather have high nutrient up-

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PLANT RESISTANCE TO INSECT HERBIVORES: A FIELD TEST OF THE ENVIRONMENTAL STRESS HYPOTHESIS[1]

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Abstract. We tested the hypothesis that environmental stresses decrease overall plant resistance to insect herbivory in the field and evaluated biochemical mechanisms proposed to explain insect response to stressed plants. To impose a stress treatment, we severed lateral roots and rhizomes of a native crucifer (bittercress, *Cardamine cordifolia*) and quantified plant and herbivore responses for treatment and control clones. Severing roots and rhizomes once, early in the growing season: (1) produced moderate, but detectable, changes in plant physiological traits, specifically greater transient leaf water deficits at midday ($P < .05$) and elevated nitrate-nitrogen concentrations ($P < .05$); (2) altered plant quality, by causing an increase in soluble carbohydrates ($P < .003$), isoleucine concentrations in leaves ($P < .01$), and possibly glucosinolate concentration ($P < .10$), but made no differences in most primary nutrient concentrations, including total nitrogen, total free amino nitrogen, total amino acids, proline, and leaf water content; and (3) led to increased herbivory by chewing and leaf-mining ($P < .001$), but not by sap-feeding, insect herbivores. Trends toward decreased plant stature and fruit reproduction were not significant after 1 mo. In addition to the significant effect of our treatment, we found extensive variation in the magnitude of response to stress and herbivory among replicates. We hypothesize that environmentally induced physiological variation among plants within a plant population commonly distributes insect herbivory disproportionately onto a subset of the individuals, and in so doing influences the demography, distribution, and evolution of that plant population.

Key words: Cardamine cordifolia; *environmental stress; herbivore–plant interaction; insect herbivory; insect-plant; plant-animal interactions; stress.*

INTRODUCTION

Variation in herbivore damage among plants within a population is one of the most striking, consistent, and yet relatively unexplored, features of plant–insect interactions (Harper 1977, Crawley 1983, Denno and McClure 1983, Louda et al. 1990). Such individual variation may be one of the most critical aspects in both the population dynamics (Louda 1982, 1983) and evolution (Thompson 1988) of plant–insect systems.

Many factors could account for such variation. Among those factors, the potential stresses imposed by water deficits, nutrient imbalances, or pollutants in the environment have been hypothesized to improve plant quality and, thus, decrease individual plant resistance to insect herbivory (see White 1969–1984, Tingey and Singh 1980, Hughes et al. 1982*a*, *b*, Cates et al. 1983, Louda 1986, 1988, Mattson and Haack 1987*a*, *b*, Heinrichs 1988, Hughes 1988, Jones and Coleman 1991). However, some observations contradict this generalization (e.g., Miles 1982*b*, Myers 1985, Waring and Price 1988). Since few tests of this hypothesis have been done for native plants in the field, especially for nonwoody species, we designed this study to do so.

By "stress" we mean environmental conditions or changes that have measurable negative effects on plant traits or performance (e.g., Hsiao 1973, Boyer 1982). Water deficit stress, for example, has been defined as the induction of turgor pressure below the maximal potential pressure (Fitter and Hay 1981, Osmond et al. 1987). The magnitude of such stress is determined by the extent and the duration of deviation or deprivation. Hsiao (1973) proposed three functional levels for water stress: *mild* = deficit of < 0.5 MPa, *moderate* = deficit of 0.5 to 1.5 MPa, and *severe* = deficit of > 1.5 MPa. Here we estimate stress as the deviation in plant performance, compared to that of controls, in response to a specific experimental manipulation of growing conditions. In addition, we use other changes generally associated with stress, such as increased concentrations of nitrate-nitrogen and soluble carbohydrates in leaf tissues (Hsiao 1973, Mattson and Haack 1987*a*, *b*), to detect plant response and to index the degree of deviation compared to the performance of control plants.

Stresses on plant growth, such as reductions in the availability of soil water, could cause decreased plant resistance. Stress can increase the availability of nutrients (White 1969–1984, McNeill 1973, McNeill and Southwood 1978, Mattson 1980, Mattson and Haack

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1987*a*, *b*), decrease the concentrations of defensive compounds in leaves (Rhoades 1983, 1985, Gershenzon 1984, Mattson and Haack 1987*a*, *b*), or alter the ratio of nutrients to chemical defenses (Bazzaz et al. 1987). Alternately, however, stress can lead to increased plant resistance to insects. For example, higher concentrations of allelochemics are reported for some plants in harsh or stressful environments than in ones considered more benign for plant growth (e.g., Janzen 1974, McKey 1979, Edwards and Wratten 1983, Gershenzon 1984, Coley et al. 1985). Either response, however, would affect predictions of herbivore use and impact. Yet, little direct experimental evidence exists on the response of native plants to environmental variation and on insect herbivore response to environmentally induced physiological variation of native plants under field conditions.

The information available suggests a positive relationship, in general, between insect feeding damage and plant stress, i.e., for trees (e.g., Cates and Alexander 1982, Cates et al. 1983, Redak and Cates 1984, Mattson and Haack 1987*a*, *b*, Heinrichs 1988), for crops (see Mattson and Haack 1987*a*, *b*, Heinrichs 1988), and for the few indigenous herbaceous species studied to date (Lewis 1979, 1984, Louda et al. 1987*a*, *b*, *c*, Collinge and Louda 1988*b*, Louda 1988). Interestingly, much more evidence exists for such a relationship for trees and crops than for native herbaceous plants. This discrepancy could represent either a fundamental difference in insect–plant interactions caused by alternate plant life histories or by a lack of sufficient information on such interactions for herbaceous species in nature.

The purpose of our study was to test the stress hypothesis in the field, by experimentally evaluating a sequence of four essential assumptions that underlie it. As a model system, we used the interaction between a native, herbaceous crucifer, *Cardamine cordifolia* A. Gray (bittercress), and its three main insect herbivore guilds. The underlying predictions are as follows. First, imposition of moderate stress under field conditions should modify plant physiological status, as it does in laboratory studies, by decreasing plant water potential, transpiration or nutrient uptake and increasing leaf temperatures, stomatal resistances, or leaf nitrate-nitrogen concentrations. Second, associated changes in leaf tissues should improve the quality of those tissues for insect herbivores, either increasing the availability of primary nutrients or decreasing concentrations of potentially defensive compounds, such as the mustard oil precursors or glucosinolates. Third, altered leaf quality should lead to higher use and damage by insect herbivores. Consequently, fourth, damage should decrease plant growth and reproduction relative to that of less stressed control plants.

The evidence supporting the first prediction, that various environmental stresses generally cause several predictable physiological changes, is voluminous (e.g., Kozlowski 1968, 1984, Levitt 1972, Hsiao 1973, Hsiao et al. 1976, Oka and Pimentel 1976, Gershenzon et al. 1978, Tingey and Singh 1980, Turner and Kramer 1980, Bradford and Hsiao 1982, Hanson and Hitz 1983, Hsiao and Bradford 1983, Kramer 1983, Mattson and Haack 1987*b*, Cates and Redak 1988, Heinrichs 1988). The changes associated with moderate water, nutrient, mineral, temperature, and pollutant stresses include: (a) altered gene expression; (b) reduced cell expansion, cell wall synthesis, protochlorophyll formation, and protein synthesis; (c) lowered levels of nitrate reductase; (d) decreased stomatal opening and CO_2 assimilation, usually causing increased leaf temperatures; (e) decreased osmotic potential via the accumulation of osmolytes, such as inorganic ions, amino acids and especially proline, sugars and sugar alcohols, and organic acids; and (f) increased concentrations of some plant natural products, including mustard oil glycosides (see Hsiao 1973, McNeill 1973, Mattson 1980, Gershenzon 1984, Mattson and Haack 1987*a*, *b*, Heinrichs 1988).

Evidence underlying the second prediction, that changes associated with moderate stress often modify plant tissues in ways that improve their quality for insects, is also abundant (e.g., Kennedy 1958, Kennedy et al. 1958, Wearing and van Emden 1967, van Emden and Bashford 1968, 1971, Wearing 1972*a*, *b*, Lewis 1979, 1984, Haglund 1980, McClure 1980, Wolfson 1980, 1982, Hughes et al. 1982*a*, *b*, 1983, Miles et al. 1982*b*, Mattson and Haack 1987*a*, *b*, Collinge and Louda 1988*b*, Holtzer et al. 1988, Hughes 1988). For example, increases in soluble nitrogenous compounds (amino acids, amides) and in free sugars (nonstructural carbohydrates) generally improve the nutritive potential of plant tissues for insects (McNeill 1973, Baskin and Baskin 1974, Fox and Macauley 1977, Mattson 1980, McClure 1980, Scriber and Slansky 1981, Scriber 1984, Slansky and Scriber 1985, Slansky and Rodriguez 1987). Moderate levels of stress appear essential to this response since severely stressed plants are not used by most insects and mites (Mattson and Haack 1987*a*, Dale 1988, English-Loeb 1989).

Finally, evidence for the first two predictions leads logically to the third one, of greater damage to moderately stressed plants, and the fourth one, of decreased plant growth and reproduction in response to increased herbivory (e.g., White 1969, 1984, Mattson and Haack 1987*a*, *b*, Heinrichs 1988). Tests of these predictions are rare.

This set of predictions may be particularly relevant for explaining patterns of damage in crucifer–insect interactions. For example, *Dentaria diphylla* was heavily damaged by insects when transplanted from forest to old field (Hicks and Tahvanainan 1974). *Brassica oleracea* grown in the laboratory with lower soil water availabilities was preferentially used by *Pieris rapae* (Wolfson 1980, 1982). And, in our study system, greater insect damage occurs on bittercress plants: (1) growing naturally or experimentally in the sun vs. in the adjacent willow shade (Chew 1977, Louda and Rodman 1983*a*, *b*, Collinge and Louda 1988*a*, *b*; S. M. Louda, *unpublished manuscript*); (2) on dry vs. on wet, portions of short soil moisture gradients (Louda and Rodman 1983*b*, Louda 1988); (3) on experimentally potted + flooded ramets (Louda 1986); and (4) on chemically stressed treatments (Louda 1988). In addition, evidence on specific mechanisms has shown that total insect damage generally increases in our crucifer–crucivore system as: (1) glucosinolate concentrations decrease (Louda and Rodman 1983*a*, *b*, and in Bowers 1988), (2) nitrate-nitrogen concentrations increase (Louda 1988; S. M. Louda and J. E. Rodman, *unpublished data*), and (3) soluble carbohydrate concentrations increase (Collinge and Louda 1988*b*, Louda 1988).

Additionally, there is conflicting evidence on the role of water stress in crucifer–crucivore interactions. In contrast to the laboratory results (Wolfson 1982), oviposition and feeding by *Pieris rapae* were not greater on cabbages that were grown in pots at lower water availabilities (Miles et al. 1982*b*, Myers 1985). The next obvious step, which we take here, is to experimentally evaluate both the response of the plant and of the insect herbivores to the imposition of moderate stress under natural field conditions.

METHODS

Study system

We conducted the study at the Rocky Mountain Biological Laboratory, in the Elk Mountains of the central Rocky Mountains, Colorado (38°57′56″ N, 106°59′12″ W). The vegetation consists of stands of willows, aspen, and spruce, interspersed with bunchgrass (*Festuca thurberi* Vasey) meadows (Langenheim 1955, 1962). The growing season in this area normally extends from late May to early September (Langenheim 1962, Chew 1975, Louda and Rodman 1983*a*). Our study was done at the "Main Site" (Site 1) of previous work (see Louda and Rodman 1983*a*, *b*, Rodman and Louda 1984, 1985, Collinge and Louda 1988*a*, *b*), where bittercress occurs in a small, partly shaded ravine that receives run-off from a continuous snowmelt seep (Fig. 1).

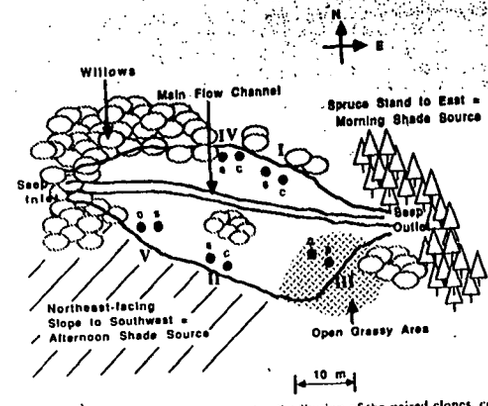

FIG. 1. Schematic map of the site (Main site), showing the distribution of the paired clones, comprising each replicate, within the population.

Bittercress is a medium-tall (30–75 cm), clonal perennial crucifer that occurs throughout the Rocky Mountains from Idaho and Wyoming, south to Arizona and New Mexico (Harrington 1954). Plants are locally abundant in moist soil, typically in the light shade of willows (Barrell 1969, Louda and Rodman 1983*a*). Growth begins immediately after snow melt, with additional vegetative growth occurring basally after flowering and fruiting are complete (S. M. Louda, *unpublished data*). Flowering occurs in July and fruits mature in August.

Over 28 species of phytophagous insects utilize bittercress in the study region (S. M. Louda, *unpublished data*). At our study site the ones inflicting the majority of the damage observed included: a native psyllid (*Aphalara* sp. nov., near *A. nubifera* Patch and *A. confusa* Caldwell); several curculionid weevils (*Ceutorhynchus* sp. nr. *moznettei* Fall, *C. pusio* Mannerheim, *C. americanus* Boheman, *C. subpubescens* LeConte, *C.* sp. nr. *neglectus* Blatchley, *C.* sp. nr. *pusillus* LeConte); a drosophilid leaf miner (*Scaptomyza nigrita* Wheeler); several chrysomelid leaf beetles (*Phyllotreta* sp. nr. *ramosa*, *P.* sp. nr. *viridicyanea* Chitt., *Phaedon* sp. nr. *oviformis*); and, the diamondback moth (*Plutella xylo-*

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stella (L.). All of these species are members of crucifer-feeding guilds (Bonnemaison 1965, Root 1973). One advantage of this system is that the diamondback moth is the only cosmopolitan pest species present. Our field observations and preliminary feeding trials (S. M. Louda, *unpublished data*) suggest little use of the other common crucifers in the area by most of these *Cardamine*-feeding insects. Thus, the primary consumers of this crucifer are "adapted" natural enemies (sensu Pimentel 1961, Root 1973, Feeny 1977).

Experimental protocol

We paired clones of bittercress distributed around the large naturally occurring stand. Replicates varied in exposure (Fig. 1). We randomly assigned one of two treatments to each member of the pair: control or stress ($N = 5$ pairs), in a randomized complete block design, with replicate pairs as blocks. Stress was imposed only at the beginning of the experiment (19 June 1985) by cutting rhizomes and lateral roots between ramets, 4–6 cm from root crowns, using a sharp knife. We disturbed the control clones (separated ramets and ran a blunt instrument along the soil surface) but did not actually cut roots. Severing peripheral roots has been used previously to study clonal integration (e.g., Hartnett and Bazzaz 1983) and ecological aspects of environmental stresses for trees (e.g., Cates and Alexander 1982, Cates and Redak 1988). We followed treatment response for 1 mo (18 July 1985). This interval was chosen as a compromise, to allow detection of chemical differences as well as herbivore responses. Most oviposition by insects occurs in June, and differential levels of damage have usually accumulated by mid-July (Louda 1984, Collinge and Louda 1988*a*, *b*, 1989). Concentrations of leaf chemicals decline throughout the season (Rodman and Louda 1984, 1985). Insect activity occurs early, but fruit set is generally not completed until late August.

We sampled characteristics and insect damage in the field: initially, after 2 wk, and after 1 mo. The plant characteristics measured were: ramet height; number of basal leaves; number of cauline leaves, including notation of missing and dead ones; length and condition of all leaves present; and, the number of flower buds, flowers and fruits. We use the sum of flower buds, flowers, and siliques (fruits) as an estimate of reproductive potential. We assessed insect use and damage by measuring total leaf area damaged (LAD), including leaf area mined (LAM), counting the number of mines (NOM), and recording the presence/absence of psyllid eggs and pitting damage for each leaf. Leaf area damaged (LAD) was caused by the chewing of weevils, leaf beetles, and moth larvae, and by the mining of the drosophilid flies. Feeding by the larvae of the fly *Scaptomyza nigrita* can be partitioned out as leaf area mined (LAM), and we did so since these larvae often cause the majority of feeding damage at wet sites (Collinge and Louda 1988*a*, *b*). Since we did not measure the size of individual mines, we estimated the average mine size on a leaf by dividing the area minded per leaf by the number of mines on each leaf (LAM/NOM; see Fig. 3C). Feeding and oviposition by sap-feeding insects, primarily the psyllid *Aphalara* sp. nov., caused aberrant cell development and damage to leaves and stems that we refer to as "pitting" (J. R. Fleming and S. M. Louda, *personal observations* and *unpublished manuscript*). By recording all information by leaf position on each ramet, we could examine the distribution of damage among leaves within ramets as well as compare the distribution of damage between treatments.

To evaluate plant physiological response to our treatment, we measured: dawn and midday leaf water potentials, as well as midday stomatal resistances and leaf temperatures. We measured leaf water potentials using a Scholander Pressure Chamber (Scholander et al. 1965), and the other leaf parameters with a steady-state, null balance porometer (LI-COR 6000). Leaves used for physiological measurements were on ramets of the clone that were not used for measurements of insect damage and plant growth. Data on physical parameters include published climatological information for Crested Butte, Colorado (NOAA 1985) and measurements taken every 2 wk of photosynthetically active radiation (PAR), relative humidity, and air temperature. We estimated soil moisture content gravimetrically for replicate soil samples in each treatment.

At the end of the experiment (19 July 1985), we also measured plant chemical response by analyzing leaf samples for: leaf water content; total Kjeldahl nitrogen; free amino (ninhydrin) nitrogen, including the proportion of beta-amino nitrogen estimated as proline equivalents; individual amino acid concentrations; water-soluble nitrate-nitrogen; total nonstructural carbohydrates; and, isothiocyanate-yielding glucosinolate concentrations. Ratios of primary to secondary compound concentrations were calculated from these data. Foliage samples were collected for each replicate ($N = 5$ ramets/treatment), placed into plastic bags containing cold water, returned to the laboratory, measured, and preserved within 2 h. We boiled leaves to be analyzed for glucosinolates for 5–10 min in 70% methanol (Rodman 1978). Leaves for nitrogen and carbohydrate analyses were weighed, frozen in liquid nitrogen, lyophilized, and stored over desiccant until they were ground for analyses (425 μm mesh sieve).

Standard analytical methods were used for: (1) total Kjeldahl nitrogen (Plant and Soils Analytical Lab, Agronomy Department, University of Nebraska–Lincoln; Bremner 1966, Isaac and Johnson 1976); (2) ninhydrin-detectable free amino nitrogen, as milligrams per gram dry mass of leucine and proline equivalents (Moore and Stein 1954); (3) high-pressure liquid chromatographic (HPLC, pico-tag) estimates of the concentration of 18 amino acids, (4) nitrate-nitrogen (Harris Laboratories, Lincoln, Nebraska; Cataldo et al. 1975); (5) total nonstructural carbohydrates (Palmer Laboratories, Agricultural Experiment Station, University of Alaska, Palmer, Alaska; Smith 1969); and (6) gas chromotographic estimates of the concentrations of the five isothiocyanate-yielding glucosinolates (IYG) common in bittercress (M. A. Blua, San Diego State University, 1984 and *personal communication*; Rodman 1978, Blua and Hanscom 1986).

We used multivariate analysis of variance to analyze overall insect and plant responses to the treatment, since many of the dependent variables of plant response and herbivore response were interrelated. All except one of the MANOVA models for insect and for plant responses were significant, but the model for overall chemical response was not ($P < .12$). We examined the data for insect and plant response further using two-way ANOVA of treatment, replicate pair, and interaction effects in the component variables of plant and insect response on each date. We used error mean square for all variance ratios (SAS Type III sum of squares; Sokal and Rohlf 1981, Wilkinson 1986). Chemical differences at the end of the 1-mo experiment (18 July) were analyzed further using one-way ANOVA by treatment. Physical variation was analyzed using two-way ANOVA by treatment and date (1 July and 18 July). In all analyses we used square root transformed values ($Y + \frac{3}{8}$) of counts, log ($Y + 1$) values of linear and area measurements, and arcsine-transformed values for proportions (Sokal and Rohlf 1981).

Insect damage response variables for each leaf, averaged for all leaves on each ramet ($N = 5$ ramets per treatment per date) were: leaf area damaged (LAD) per leaf, leaf area mined (LAM) per leaf, and number of mines (NOM) per leaf. Cumulative damage estimates were: the sum over all leaves on a ramet (LAD, LAM), or the proportion of leaves on the ramet with psyllid pitting or eggs, or drosophilid mines. The cumulative measures are most relevant for evaluation of insect effect on plant performance, but selected measures are presented on a per leaf basis to allow comparison with previously published work. Plant response variables analyzed were: ramet height, number of basal leaves, number and length of cauline leaves, number of leaves missing or dead, and fruit (=silique, =pod) production per ramet. As an estimate of potential fruit and seed reproduction we summed the number of flower buds, flowers, and fruits observed. Chemical response variables were concentrations of: total Kjeldahl nitrogen, total amino acids (high-pressure liquid chromatography, HPLC), nitrate-nitrogen, total nonstructural carbohydrates, and isothiocyanate-yielding glucosinolates.

Results

Overall, our results are consistent with the first three predictions of the stress hypothesis for variation in plant resistance to adapted insect herbivores, but not with the fourth. We found that cutting rhizomes and roots: (a) produced a moderate, but detectable, change in plant physiological condition (prediction 1); (b) altered plant quality by causing elevated levels of isoleucine, sugars, and possibly glucosinolates in treated plants (prediction 2); and (c) led to increased herbivory by chewing and mining insects (prediction 3). However, leaf production increased in the stress treatment. So, the predicted decreases in plant performance (prediction 4), which were observed as trends in leaf survival and fruit production, were not statisically significant after 1 mo.

Environment

Physical environmental conditions were similar for the two treatments (Table 1), as expected for adjacent clones. Light intensities were typical for a partly shaded habitat on a clear day at 2 wk and for a cloudy day at the end of a month. Relative humidity at leaf level was high, especially on the final sampling date, and comparable between treatments on both dates. Measured midday air temperatures for both treatments were moderate (20.7°–23.3°C). Rainfall was higher in the final 2 wk of the experiment than in the first 2 wk: 17.8 mm compared to 12.4 mm (NOAA 1985). Soil moistures were similar between treatments and the differences between dates paralleled rainfall variation.

Plant physiological response

The differences in the physiological parameters between our treatments suggest that we imposed moderate, but transient, midday water deficit stress by severing rhizomes and peripheral roots (Table 2). Deficits in dawn leaf water potentials were small and similar between treatments on both sampling dates. However, at midday the transient leaf water deficits were moderately high (sensu Hsiao 1973) and greater for the stress treatment than for the control ($P < .05$). At midday, leaf temperatures and stomatal resistances were similar between treatments on both dates (Table 2). Both of these variables were higher on 1 July than on 18 July, possibly reflecting the lower rainfall in the first 2 wk of the experiment. Higher relative humidity at the end of the experiment (Table 1) may also have contributed. The results thus indicate that severing rhizomes early in the growing season inflicted moderate water deficit stress, and that the extent of response varied with replicate position (Fig. 1) within the local environment (see below, *Results: Intrapopulation variation*).

Plant chemical response

Analysis of plant chemical response to the cutting of rhizomes and lateral roots had six main results (Table 3). First, chemical responses overall were not consistent, leading to a nonsignificant, though suggestive, MANOVA model ($P < .12$).

Second, the amount and quality of nitrogen did not increase with stress overall. We found that total nitro-

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TABLE 1. Physical habitat characteristics during the experiment near stressed (root-cut) and control clones of bittercress (19 June–18 July 1985).†

	July 1985 (week 2)					18 July 1985 (week 4)				
	Stress		Control			Stress		Control		
	$\bar{X}$	SE	$\bar{X}$	SE	P	$\bar{X}$	SE	$\bar{X}$	SE	P
PAR (μmol·m⁻²·s⁻¹)	1076	96	1124	129	NS	649	136	678	146	NS
RH (%)	32.4	2.19	34.0	3.86	NS	45.1	5.36	45.5	6.15	NS
Air temperature (°C)	23.4	0.18	22.9	0.27	NS	20.7	1.01	21.1	0.93	NS
Soil moisture (%)	28.7	2.52	26.9	2.89	NS	35.6	3.55	36.0	3.37	NS

† Taken at upper leaf surface near midday (1100–1400 h) or near experimental plants.
‡ $N = 5$ paired replicates per treatment; two-way ANOVA for paired comparison by date and treatment, F test (1,1,4 df); NS = $P > .20$.

gen, free amino nitrogen, and total amino acid concentrations were similar between treatments, all $P > .20$). Also, the ninhydrin estimates of beta-amino nitrogen concentrations, which include primarily proline and hydroxyproline, appeared high (64–68%) but comparable between treatments ($P > .20$). HPLC estimates of individual amino acid concentrations both substantiated the absence of response in proline, an amino acid that often increases with stress (Mattson and Haack 1987*a*, *b*), and showed a significant difference only in isoleucine (Table 3).

Third, nitrate-nitrogen concentrations increased significantly in the stress treatment ($P < .05$). This result supports the interpretation that our treatment induced moderate stress. Reduction in nitrate reductase, and thus accumulation of nitrate, is often an initial response to stress (Hsiao 1973, Mattson and Haack 1987*a*, *b*).

Fourth, the sugar content of leaf tissues doubled. Total concentration of nonstructural carbohydrates, which includes all simple sugars and sugar alcohols but excludes starch and cellulose, was significantly higher for stressed plants than for control plants ($P < .003$). Hydrolysis of starch usually increases with stress (Gates 1964, Mattson and Haack 1987*a*, *b*).

Fifth, leaf water content was similar between treatments. Thus, any insect response could not be explained by treatment-induced differences in the availability of water in the foliage.

Sixth, the concentrations of characteristic secondary compounds, the isothiocyanate-yielding glucosinolates, appeared somewhat higher in stressed plants than in control plants, but the difference was not quite significant statistically ($P < .10$, Table 3). Absolute levels of glucosinolate observed were relatively low ($\bar{X} = 1.78$ mg/g). Since average glucosinolate concentrations normally decline throughout the growing season (Rodman and Louda 1984, 1985), the difference that we observed suggests that the usual decline was retarded by the stress treatment.

In sum, the chemical differences associated with the imposition of root-cutting stress in early season, when total leaf nitrogen concentrations were relatively high (>3.6%), were increases in: isoleucine (133%), sugars (105%), nitrate nitrogen (20%), and possibly glucosinolates (25%). As a consequence of the changes above, one ratio of nutrients-to-allelochemicals increased: the ratios actually declined: total nitrogen-to-glucosinolates (22%) and total amino acids-to-glucosinolates (32%, Table 3).

Herbivore response

Insect damage increased significantly on plants in the stress treatment (Fig. 2). The increase in leaf area damaged (LAD) on plants in the stress treatment was exponential (Fig. 2A, B). The time lag in the development of damage could reflect the lag between oviposition and accumulation of feeding damage, the relative rates of leaf expansion and consumption, or the greater differences in transient water deficits later in the experiment. The MANOVA models explained a significant portion of the variation in damage on all

TABLE 2. Physiological response of bittercress to root-cutting vs. the control treatment (1985) at the Main Site, Gothic, Colorado.†

	1 July 1985 (week 2)				18 July 1985 (week 4)			
	Stress		Control		Stress		Control	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
Dawn leaf water potential deficit (MPa)	−0.27	0.34	−0.29	0.33	−0.30	0.29	−0.25	0.53
Midday leaf water potential deficit (MPa)	−1.53	0.81	−1.39	0.72	−1.16	0.11	−0.89	0.12
Stomatal resistance (s/cm)	9.62	0.86	9.20	0.95	5.38	0.60	5.68	0.66
Leaf temperature (°C)	22.5	0.21	22.2	0.41	19.8	0.94	20.2	0.90

† $N = 5$ replicates per treatment; two-way mixed-model ANOVA of date and treatment, $F_{0,1,4}$, NS = $P > .20$.

TABLE 3. Chemical differences and insect damage 1 mo (18 July) after root-cutting treatment on bittercress early in the growing season (19 June 1985).†

Variables	Stress		Control		F	P
	$\bar{X}$	SE	$\bar{X}$	SE		
Primary compounds						
Total nitrogen (TN, %)	3.65	0.10	3.9	0.28	0.56	NS
Free amino nitrogen (mg/g)	18.5	2.45	20.4	2.31	0.28	NS
Beta-amino N (%)	64.7	2.46	67.9	3.65	0.58	NS
Total amino acids‡ (TAA, mg/g)	2.94	0.82	2.75	0.62	0.01	NS
Isoleucine (mg/g)	0.07	0.01	0.03	0.01	11.25	0.01
Proline (mg/g)	0.14	0.04	0.12	0.09	0.35	NS
Nitrate nitrogen (μg/g)	1260	69.6	1050	52.44	5.80	0.043
Soluble carbohydrates (TNC, %)	12.9	1.69	6.3	0.45	16.96	0.003
Leaf water content (%)	84.9	1.02	86.4	1.18	1.00	NS
Secondary compounds and nutrient-allelochemical ratios						
Glucosinolates (IYG, mg/g)	1.97	0.18	1.58	0.10	3.48	0.099
TN/IYG	1.91	0.17	2.46	0.12	6.92	0.03
TAA/IYG	1.54	0.45	1.70	0.35	0.08	NS
TNC/IYG	6.88	1.21	4.14	0.53	4.31	0.071
Associated insect damage						
Leaf area damaged (mm²/leaf)	89.7	11.29	53.0	5.92	47.01	0.001
Leaf area mined (mm²/leaf)	71.8	11.44	31.6	5.55	29.97	0.001
Pitting (%)	29.3	4.55	30.3	4.82	1.06	NS

† $N = 5$ replicates/treatment (treatment 19 June; samples collected 18 July 1985); overall MANOVA (df = 1,4), $F = 3.58$ ($P < .12$); one-way ANOVAs on chemical data (df = 1,4) and two-way ANOVAs on damage (see figures).
‡ HPLC (pico-tag) for 18 major amino acids: only isoleucine differed.

three dates, using Wilk's Criterion and Hotelling-Lawley Trace tests (Table 4; Wilkinson 1986).

Initially (19 June 1985), the herbivore loads were low and very similar for both treatments (Fig. 2A, B, C), except that more leaves of the controls had been pitted by the sap-feeding psyllids (Fig. 2D, Table 4). Even this early in the season, replicates around the stand (Fig. 1) differed significantly in all estimates of herbivore load except in pitting (Table 4). Replicate differences typically persisted, and led to an interaction between replicate and treatment in determining level of damage (Table 4).

Two weeks after cutting rhizomes (1 July), two differences between treatments occurred. The amount of pitting increased more on stressed plants than on controls (38.2 vs. 11.8%, $P < .05$; Fig. 2D). The cause cannot be inferred; it may have been a response to either the initial difference in herbivore load between the treatments or to the stress treatment. Second, the proportion of leaves with mines increased on control plants ($P < .02$; Fig. 2F, Table 4), suggesting a difference in the distribution of either egg deposition or early instar success between the two treatments. No differences in the total amount of leaf area chewed (Fig. 2B) or mined (Fig. 2C) were evident at 2 wk (Table 4).

One month after the treatment, significant variation in loss among the replicates persisted (Table 4). Four of the five variables used to estimate insect response to stressed plants were significantly higher for plants in the treatment with severed peripheral roots (Table 4). The one variable that was not was the proportion of leaves pitted (Fig. 2E), probably as a result of low oviposition rates by psyllids late in the season (J. R. Fleming and S. M. Louda, *unpublished data*). Overall, the results show that ramets in the stress treatment were generally and significantly more vulnerable to damage by chewing insect herbivores, particularly by the leaf miners, than were ramets in the control treatment. The opposite appeared true for sucking insects.

At the end of the experiment the area damaged by leaf miners was significantly higher on plants with severed roots (Fig. 2C, Table 4). Also, leaf-mining contributed a significantly higher proportion of total leaf area lost in the stress treatment than in the control treatment: 80.4 vs. 59.2% (paired t test, $P < .05$, Fig. 2A, C). The higher cumulative amount of leaf area mined in the stress treatment after 1 mo reflected at least four factors: (1) 42% more mines per leaf (Fig. 3A, $F_{0,1,4} = 4.27$, $P < .03$), (2) 127% greater area mined per leaf (Fig. 3B), (3) 45% higher proportion of leaves mined (Fig. 2F), and (4) 59% larger mines (Fig. 3C).

TABLE 4. Continued.

Date		Stress		Interaction	
F	P	F	P	F	P
0.03	NS	0.15	NS	0.91	NS
30.75	0.001	4.50	0.05	0.42	NS
24.64	0.001	0.01	NS	0.22	NS
11.54	0.004	0.01	NS	0.32	NS

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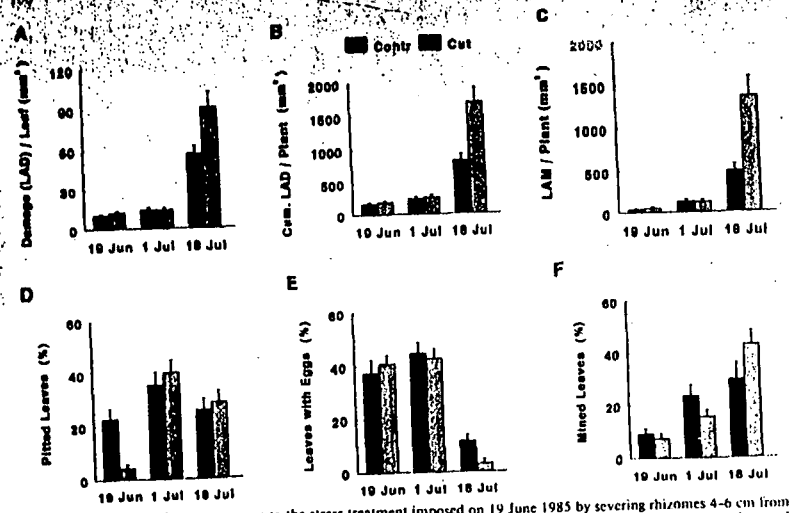

FIG. 2. Insect and damage response to the stress treatment imposed on 19 June 1985 by severing rhizomes 4-6 cm from the root crown of bittercress, *Cardamine cordifolia*, compared to the paired control treatment: (A) total leaf area damaged (LAD) per leaf, (B) average cumulative, total LAD for all leaves on a ramet, (C) leaf area mined (LAM) per ramet, (D) proportion of leaves pitted by psyllids per ramet (%), (E) proportion of leaves with psyllid eggs per ramet (%), and (F) proportion of leaves with leaf mines per ramet (%). Significant differences between treatments were identified using two-way ANOVA of the significant MANOVA model (Table 4). Data are means and 1SD.

TABLE 4. Multivariate and univariate analyses of variance in insect damage per bittercress ramet in response to root-cutting stress in June 1985.†

Variables‡	Treatment		Replicate		Interaction		
	F	*P*	*F*	*P*	*F*	*P*	R^2
19 June MANOVA (df 5,40)	4.21	0.004*					
Cumulative LAD/ramet	1.38	NS	17.38	0.001*	2.92	0.033	.674
Cumulative LAM/ramet	0.12	NS	24.87	0.001*	4.66	0.003	[illegible]
Pitting (% lvs/ramet)	22.39	0.001*	0.76	NS	2.99	0.030*	.483
Eggs (% lvs/ramet)	1.13	NS	6.39	0.001*	1.25	NS	.442
Mining (% lvs/ramet)	0.59	NS	12.05	0.001*	3.47	0.020*	.610
1 July MANOVA (df 5,39)	2.78	0.04					
Cumulative LAD/ramet	0.01	NS	16.02	0.001*	8.73	0.001*	.712
Cumulative LAM/ramet	0.68	NS	85.33	0.001*	4.19	0.006*	.900
Pitting (%)	1.03	NS	9.47	0.001*	1.76	0.003*	.593
Eggs (%)	0.32	NS	4.48	0.004*	1.31	NS	.370
Mining (%)	6.55	0.014*	36.82	0.001*	2.03	0.109	.802
18 July MANOVA (df 5,40)	4.53	0.003*					
Cumulative LAD/ramet	43.99	0.001*	38.65	0.001*	3.80	0.010*	.842
Cumulative LAM/ramet	23.14	0.001*	33.84	0.001*	2.18	0.089	.807
Pitting (%)	0.07	NS	2.55	0.054	5.65	0.001*	.451
Eggs (%)	12.66	0.001*	2.85	0.036	0.94	NS	.410
Mining (%)	9.48	0.004*	50.62	0.001*	11.02	0.001*	.865

* = significant at $P \leq .030$ using Bonferroni criterion for multiple comparisons; NS = $P > .200$.
† Test of MANOVA model for each data presented first; then, two-way ANOVA of treatment and replicate pair (df = 1,14) for each variable.
‡ LAD = leaf area damaged, LAM = leaf area mined.

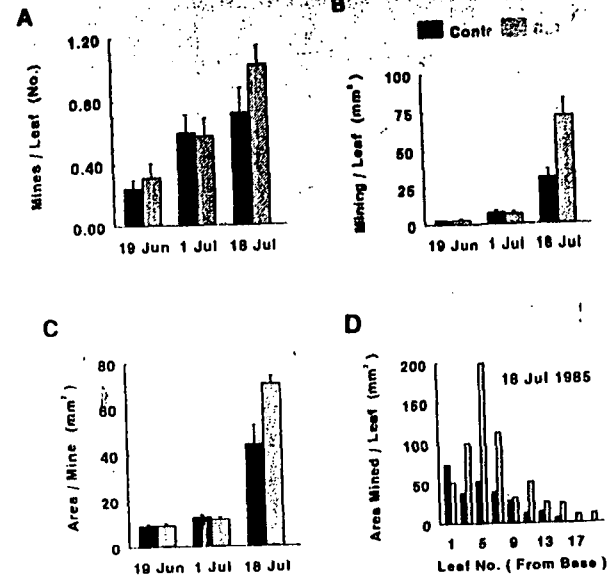

FIG. 3. Parameters of leaf mining in stress and control treatments on bittercress (*Cardamine cordifolia*), stress imposed in early season (1985): (A) number of mines per leaf, (B) average area mined per leaf, (C) estimated area per mine [leaf area mined]/[number of mines] on a per leaf basis, and (D) area mined per leaf in relation to leaf position from base to apex of ramet. Data are means and 1SD.

None of these four responses observed were caused by initial differences (Table 4). Finally, both the median and mode of the frequency distribution of leaf mining (LAM) shifted to the right, to younger leaves higher on the ramet, in the stress treatment (Fig. 3D).

Plant growth and reproductive response

Plant growth and reproductive responses to stress and the associated increase in herbivory were complicated. The MANOVA model included six variables: ramet height, number of basal leaves, number of cauline leaves, average length of cauline leaves, cumulative leaf mortality, and reproductive potential per ramet. Using Wilk's Criterion and the Hotelling-Lawley Trace tests, this model explained a significant portion of the observed variation, both initially and at the midpoint of the experiment, but not at the end of the experiment (Table 5).

Initially, plants in control clones were somewhat more advanced phenologically (Fig. 4). Control ramets were taller (Fig. 4A, $P < .001$), with fewer basal leaves (Fig. 4B, $P < .003$), and more reproductive investment in flower buds ($P < .001$). Replicates also differed among each other in ramet height, number of leaves, and flower buds present (Table 5).

Two weeks after cutting rhizomes, the initial differences between treatments in stem height (Fig. 4A) and in leaf length (Fig. 4E) had disappeared. The difference in the number of basal leaves reversed (Fig. 4B) and was not significant. And, a marginally significant increase in the number of cauline leaves (Table 5) occurred for the stressed plants (Fig. 4D). Cutting roots did not accelerate leaf mortality over the first 2-wk period (Fig. 4F). Reproductive potential, i.e., flower buds and flowers on this date, continued to be higher on control plants than on stressed ones (Table 5).

Four weeks after treatment, no significant differences remained between treatments in height (Fig. 4A), number of basal leaves (Fig. 4B), or length of cauline leaves (Fig. 4E). The earlier trend toward a greater number of cauline leaves on ramets in the stress treatment became larger (Fig. 4D) and significant (Table 5). And, in spite of greater leaf mortality (Fig. 4F) of the more heavily damaged leaves on stressed plants (Fig. 2A),

TABLE 5. Multivariate and two-way analyses of variance of growth and seed production by bittercress in response to stress imposed by severing rhizomes in early 1985.†

Variables	Treatment F	Treatment P	Replicate F	Replicate P	Interaction F	Interaction P	R^2
19 June MANOVA (df 6,39)	6.52	0.001*					
Ramet height (cm)	18.86	0.001*	10.75	0.001*	4.00	0.010	.661
Basal leaves (no.)	9.76	0.003*	3.49	0.020*	2.08	0.110	.445
Cauline leaves (no.)	0.00	NS	6.86	0.001*	1.15	NS	-
Leaf length (mm)	2.43	0.130	0.97	NS	0.49	NS	.172
Leaf mortality (no.)	3.19	0.080	1.67	NS	0.77	NS	.245
Reproductive potential	14.75	0.001*	5.65	0.002*	1.28	NS	.515
1 July MANOVA (df 6,39)	3.81	0.005*					
Ramet height (cm)	0.20	NS	2.76	0.041	2.18	0.089	.333
Basal leaves (no.)	1.84	NS	6.46	0.001*	2.10	0.099	.474
Cauline leaves (no.)	3.54	0.067	0.67	NS	1.24	NS	.218
Leaf length (mm)	0.18	NS	1.78	0.151	0.28	NS	.174
Leaf mortality (no.)	1.06	NS	1.14	NS	3.64	0.013*	.336
Reproductive potential	10.65	0.002*	0.08	NS	0.43	NS	.241
18 July MANOVA (df 6,39)	2.69	0.100					
Ramet height (cm)	1.91	0.174	4.46	0.005*	10.75	0.001*	.611
Basal leaves (no.)	0.03	NS	1.20	NS	0.60	NS	.153
Cauline leaves (no.)	8.85	0.004*	0.23	NS	0.74	NS	.241
Leaf length (mm)	0.44	NS	2.20	0.086	0.51	NS	.220
Leaf mortality (no.)	3.79	0.059	14.90	0.001*	6.44	0.001*	.690
Reproductive potential	1.80	0.188	3.11	0.026*	7.81	0.001*	.532
Fruit production	1.55	NS	5.19	0.002*	14.72	0.001*	.670

* = significant at $P \leq .030$ using Bonferroni criterion for multiple comparisons; NS = $P > .200$.
† Test of MANOVA model for each date presented first; then, two-way ANOVA of treatment and replicate pair (df = 1,14) for each variable.

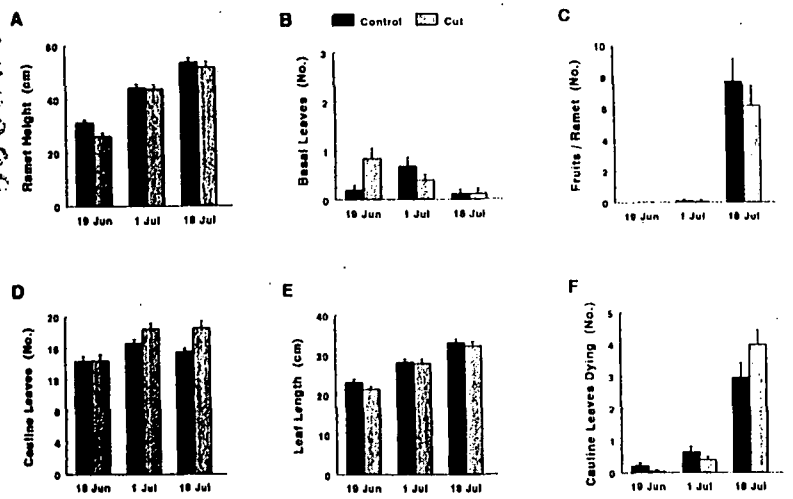

FIG. 4. Plant response to stress treatment imposed by severing rhizomes 4–6 cm from the root crown of bittercress, *Cardamine cordifolia*, compared to the controls: (A) ramet height (cm), (B) number of basal leaves, (C) number of siliques (fruits) per ramet, (D) number of cauline leaves per ramet, (E) average leaf length of the cauline leaves on a ramet, and (F) average number of yellow + dead + missing leaves on a ramet. Significant differences between treatments were identified using two-way ANOVA. Data are means and 1SD.

the *net* effect was a 16% increase in the number of living cauline leaves by 18 July (Fig. 4F). However, the plants in the stress treatment tended to form fewer fruits by 18 July (Fig. 4C). The observed increase in leaf mortality and decreasing trend in fruit production were consistent with findings from previous studies of herbivory on bittercress (Louda 1984, 1986).

Intrapopulation variation in plant and herbivore response

Herbivory increased on stressed plants; however, the magnitude of most plant and herbivore responses varied significantly among the replicates (Tables 4 and 5). Replicates were distributed around the 400 m^2 stand (Fig. 1). Initially, the replicates differed significantly in early season damage (Table 4); replicate V was most damaged and replicate III was least damaged ($P < .05$). The average level of herbivory by chewing, mining, and sap-feeding insect guilds continued to vary significantly among replicates throughout the experiment (Table 4). The least variation among replicates occurred in frequency of pitting by psyllids and of psyllid eggs (Table 4); the psyllids were the predominant sap-feeding insects. However, even the variation in psyllid damage among replicates was statistically significant at the midpoint of the experiment (Table 4).

By the end of the experiment, the replicates' stressed clones (Fig. 1) consistently ranked V, IV > > I > II > > > III for chewing and mining damage; and, control clones ranked V > > II, IV > I > > > III ($P < .05$). Thus, the extremes (V high, III low) were established early in the season and persisted. Replicate V was consistently the most damaged and replicate III was the least damaged, with or without the experimental imposition of stress. However, stress altered the relative ranking among the remaining replicates, damage increased on replicates IV and I relative to replicate II.

Early in the season, the level of chewing damage correlated only with ramet height ($P < .05$). This variation persisted, and interacted with treatment (Table 4), in determining the magnitude of observed herbivore response to stressed plants. Plant growth and reproduction also varied significantly among replicates in three, and marginally in a fourth, of the six factors measured to record plant response to stress and herbivory (Table 5). Initially these included plant height, number of basal and cauline leaves, and number of flower buds (Table 5). This variation among replicates persisted throughout the season and, for three of the six variables, interacted with treatment to affect the magnitude of plant response to stress and herbivory.

DISCUSSION

Stress in plant–insect herbivore interactions

Insect herbivory increased when we imposed moderate stress on bittercress relatively early in the growing season. The treatment effect was large and clearcut (Figs. 2 and 3, Table 4). And, our test shows that three of the four main assumptions underlying the stress hypothesis for variation in insect herbivory held.

First, the imposition of stress should alter plant physiological status, and it did, by increasing midday leaf water deficits (Table 2) and nitrate-nitrogen concentrations (Table 3).

Second, stress should induce chemical changes that improve leaf quality for adapted insects and it did, by causing higher levels of isoleucine and soluble carbohydrate, and possibly glucosinolates (Table 3). Increases in an amino acid and in sugars should increase palatability to insects generally (Slansky and Rodriguez 1987). Furthermore, if absolute levels of the characteristic compounds, the mustard-oil precursors or glucosinolates, are relatively low, as here, then an increase in their concentration could be expected to increase the use of crucifers by crucifer-feeding insects (Thorsteinson 1960, Chew 1988, Louda and Mole 1992).

Third, insects should respond to changes in plant quality of differentially stressed plants, and chewing and mining insects did (Figs. 2 and 3; Table 4). The increase in damage to foliage with stress is consistent with previous studies of bittercress (Louda and Rodman 1983*a*, *b*, Louda 1986, 1988, Collinge and Louda 1988*a*, *b*) and of many other plants (e.g., White 1969, 1974, 1976, 1978, Lewis 1979, 1984, Bernays and Lewis 1986, Mattson and Haack 1987*a*, *b*). For example, moderate stress increases herbivory on: herbaceous native species, such as annual sunflower *Helianthus annuus* (Lewis 1979, 1984), Rocky Mountain bee plant *Cleome serrulata* (Louda et al. 1987*b*), and some of the forbs in montane meadows (Louda et al. 1987*a*, *c*); on crop plants, such as tomatoes and soybeans (Hughes et al. 1982*a*, *b*, Hughes 1988); and, on a variety of forest trees (see Mattson and Haack 1987*a*, *b*, Heinrichs 1988). Two main exceptions are common. Sap-feeding insects, such as psyllids (Fig. 2D, E) and stem gallers (e.g., Waring and Price 1988) seem to respond to nitrogen availability rather than to stress-altered characters, such as sugars.

Finally, fourth, if the hypothesis is correct, then increased losses should translate into decreased relative fitness for stressed plants. Although a previous study showed a significant impact of herbivory on fitness parameters of bittercress (Louda 1984), the negative trends observed here, on height (Fig. 4A), leaf survival (Fig. 4F), and number of fruits (Fig. 4C) of the moderately stressed plants, were not statistically significant (Table 5). Ending the experiment early, in order to do chemical tests on still vigorous plants, most likely contributed to this result.

In sum, stress contributed significantly to the pattern of herbivory caused by the adapted insects to a native forb within its typical habitat. The level of stress imposed was moderate, as estimated by small, but significant increases in transient leaf water deficits. These

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results are consistent with the hypothesis that responses by foliage-feeding arthropods to stressed plants are not linear; damage appears to increase and then decline as the intensity of stress intensifies (Louda 1986, 1988, Louda et al. 1987*c*, Mattson and Haack 1987*a*, *b*, English-Loeb 1989). Thus, our results appear to highlight the importance of *moderate*, rather than severe, intensities of stress in the facilitation of herbivory by chewing insects on foliage.

Plant compensation for stress and herbivory

Herbivory following moderate stress prevented full compensation for early season reproductive differences (Table 5), in spite of increases in cauline leaves (Fig. 4D). Fruit production was lower on stressed plants (Fig. 4C) in at least some replicates (Table 5). One hypothesis to explain the increase in cauline leaves is based on the way in which we imposed stress. Carbohydrates are normally shunted to roots and rhizomes for vegetative reproduction and clonal integration (e.g., Hartnett and Bazzaz 1983). With root-cutting, carbohydrates may have been reallocated to aboveground growth.

Differences in herbivore guild responses

Leaf mining damage was a significant part of the total damage to leaves (Fig. 2B, C). Mines were more abundant, larger, and distributed onto more leaves on stressed plants (Fig. 3). One month after roots were cut more leaves had mines (Fig. 2F), more mines were initiated per leaf (Fig. 3A), and the median amount of mining damage per leaf increased (Fig. 3D). The observation that mines were both more abundant and larger on stressed plants is consistent with other experiments on this system (Louda 1986, 1988, Collinge and Louda 1988*a*, *b*). Leaf miners choose leaves that improve larval survival and growth (Bultman and Faeth 1986, Faeth 1988).

Alternately, however, the damage and occurrence of sap-sucking herbivores was not clearly enhanced by stressing host plants (Fig. 2). During the first half of the experiment psyllid damage (Fig. 2D), and the frequency of psyllid eggs (Fig. 2E), increased more on ramets in the stress treatment than on those in the controls (Fig. 2D). Few eggs were observed in either treatment in the second half of the experiment. These results suggest the psyllids may have responded to plants in the stress treatment during the oviposition phase of their life cycle; sap-feeding insects may have favored stressed plants, or sap-feeding insects may have preferentially used plants with lower frequencies of previous use by chewing insects. We have no data with which to distinguish between these alternatives.

By the end of the month, sap-feeding insects did not show any increased use of stressed plants (Fig. 2D). The lack of response should be expected. Performance of sap-feeding insects is usually correlated with available nitrogen (e.g., Wearing and van Emden 1967, van Emden and Bashford 1968, 1971, White 1969–1984, Wearing 1972*a*, *b*, McNeill 1973, Miles et al. 1982*a*), and we did not find major differences in total or available nitrogen (Table 3). In a previous experiment, flooding of bittercress increased psyllid occurrence on the stressed plants (Louda 1986). These results would be consistent with our present data if flooding increased nitrogen availability.

Nutrient and allelochemic concentrations

Nitrogen and secondary compounds are generally thought to mediate insect use of their host plants. Herbivore load on bittercress was not related to differences in plant nitrogen. Perhaps this result should have been expected since total nitrogen concentrations in bittercress were relatively high overall (3.6–3.9%, Table 3). Among the primary nutrients, variation in carbohydrate concentrations is more likely to explain differences in use of bittercress by adapted insects (Table 3; Collinge and Louda 1988*b*).

Glucosinolate concentrations in our experiment were relatively low, but averaged 25% higher in stressed plants (Table 3). Elevated concentrations would be consistent with observations of increased glucosinolates under conditions that stress plants (Neil and Bible 1972, Louda and Rodman 1983*a*, *b*, Gershenzon 1984, Mattson and Haack 1987*a*). However, the direct relationship between stress and glucosinolates still requires testing. In this system, variation in glucosinolate concentrations in bittercress is large (Louda and Rodman 1983*a*, *b*, Rodman and Louda 1984, 1985) and cannot explain differences in herbivory between adjacent habitats (Louda and Rodman 1983*a*, *b*; S. M. Louda, *unpublished manuscript*). However, glucosinolates appear to play a role in the variation in bittercress resistance to herbivory within its usual habitat (Louda and Rodman 1983*a*, *b*, Louda 1988).

In addition, we examined ratios of primary-to-secondary compound concentrations. We expected to find plants with increased nutrient-to-defensive compound ratios to be less resistant to insect herbivory (Janzen 1974, Coley et al. 1985, Bazzaz et al. 1987). We did not find this to be the case for nitrogen. Although herbivory increased, none of the nitrogen-to-glucosinolate concentration ratios increased with stress (Table 3). However, both herbivory and the soluble carbohydrate-to-glucosinolate ratio increased for stressed plants (Table 3). We conclude that when nitrogen content is high and similar among co-occurring plants, as in this system, other differences such as sugar content will mediate herbivory by adapted insects and its impact on plant performance.

Crucifer use by insects: conflicting results

Our results are consistent with most observations on stress in the resistance of herbaceous plants to insect herbivory, especially crucifers. For example, Josefsson (1970) found that insect damage decreased establishment and growth of *Brassica napus* when nutrients or soil moisture were limited. Van Emden and Bashford (1968, 1971), Wearing (1972*a*, *b*), and Miles et al. (1982*a*) recorded improved growth by aphids on water-stressed crucifers. Hicks and Tahvanainen (1974) found that increased herbivory led to higher mortality of *Dentaria diphylla* transplanted from forest to open field. And, Wolfson (1980, 1982) found that oviposition and growth of *Pieris rapae* increased on *Brassica nigra* on plants with limited water.

Our results conflict, however, with two studies of oviposition and larval growth of the cosmopolitan, cabbage white butterfly, *Pieris rapae*. We found differences in insect use and damage by chewing insects without finding differences in total nitrogen, free amino nitrogen, or total amino acid concentrations (Table 3). In contrast, Myers (1985) found that oviposition by the cabbage white butterfly was higher on fertilized cabbage and unrelated to watering regime. And Miles et al. (1982*b*) found that feeding and growth of *P. rapae* larvae were not related to leaf water status of *Brassica oleracea*, but positively correlated with glucosinolate concentrations.

Our hypothesis to explain the differences observed among studies reflects the fact that the plants used by Myers (1985) and Miles et al. (1982*b*) were grown in pots in the greenhouse, whereas ours were in the field. Use of greenhouse-grown plants involves at least four potentially confounding assumptions. These are that (1) leaf quality of greenhouse and naturally occurring plants is similar, (2) plants in pots are not stressed, (3) cultivation methods cause no modification of the relationship among parameters influencing insect choice and feeding, and (4) interactions of a cosmopolitan insect with a cultivar are similar to interactions of indigenous insects with native plants.

These assumptions appear questionable. First, plant growth is plastic and related to growing conditions (e.g., Nobel 1983). Plants grown under greenhouse conditions usually differ substantially from plants grown outside, including traits that influence insects (see Slansky and Rodriguez 1987), such as leaf size, thickness, toughness, and water and nitrogen content. Choice among greenhouse-grown plants and larval rearing on them may reflect only choice or response among very similar, tender, nutritious leaves of greenhouse-grown plants. Second, *all* plants in pots may be moderately stressed, at least comparable to the levels measured in the field in our study. Third, nitrogen and sugars may interact to determine crucifer attractiveness to adapted insects. Levels of nitrogen in bittercress are relatively high, compared to usual levels in brassicas. Perhaps when leaf nitrogen is low or variable, the nitrogen status of leaves forms the primary criterion of oviposition and feeding, as Myers (1985) and Miles et al. (1982*b*) found, whereas when leaf nitrogen is high, as in bittercress, the increases in the concentration of leaf sugars associated with moderate stress may be more important, as we found. Finally, fourth, our results suggest that a cosmopolitan pest species on a cultivar does not represent a general model for the interaction of indigenous insects with native crucifers, such as bittercress.

Intraspecific variation in stress and herbivore response

The existence of early, large, and persistent differences in damage among the replicates (Tables 4 and 5) was a striking, unexpected but important, outcome of this study. Experimental stress induced increased herbivory generally (Fig. 2). However, the replicates varied significantly in the overall amount of damage that they experienced (Table 4). Replicate V was consistently the most damaged, and replicate III the least, with or without the experimental imposition of stress. These differences were established early and persisted. Stress altered the relative ranking among replicates with intermediate levels of damage, shifting ordering: from II > IV > I to IV > I > II.

The clone receiving the most damage, replicate V, was exposed longest to direct sunlight (Fig. 1) and had the highest average level of glucosinolates (2.19 mg/g). Clones in the open are phenologically advanced (Fig. 4), having longest exposure to direct sun and thus earliest snow melt. Early growth, such as by plants in the open, coincides with early insect activity and leads to increased leaf damage (Collinge and Louda 1989). Also, clones in the open have been found to be generally more vulnerable to water deficit stress (S. M. Louda, *unpublished manuscript*). Insect damage also varies between plants across small-scale habitat discontinuities, such as a sun/shade transition (Louda and Rodman 1983*a*, *b*), or along short soil-moisture gradients (Louda 1988). So, the magnitudes of both insect herbivory and stress induced by our treatment were related to the clone's specific position within the environment.

These results combine with earlier ones to suggest that a substantial heterogeneity in the intensity interaction of plants with their adapted insects occurs within bittercress populations. In fact, heterogeneity in use generally characterizes the field data on insect herbivory in plant populations (see Harper 1977, Crawley 1983, Louda 1988). Such variation is often consistent and spatially ordered (e.g., Louda 1982, 1983). We propose that environmentally related physiological variation among plants within a plant population often disproportionately distributes insect herbivory onto a predictable subset of the individuals in that population.

Spatially explicit patterns of differential damage by insects have demographic, distributional and, potentially, evolutionary consequences (Louda 1982). First, since herbivory can significantly decrease growth and reproduction of bittercress (Louda 1984), the demographic consequences are straight-forward. The relative contribution of stressed individuals to the next generation will be decreased. And, when plants in one part of the environmental mosaic suffer dispropor-

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tionately, as in this case, then the distribution of plants in the population is likely to be altered, and often reduced, from its potential distribution (Louda 1982, 1983). Finally, when there is a spatial pattern in the occurrence of stress, and thus reduced plant resistance to insect herbivory, the genotypes in one portion of the habitat will contribute less to the next generation. This effect should be amplified by the fact that genetic relatedness is often spatially correlated in plants (see Harper 1977). Spatially arrayed, differential contributions among genotypes will alter population structure, and create the potential for microevolution and local differentiation.

Thus, our study illustrates significant *indirect* effects of environmental variation. We found physical environmental differences, such as those that induce differences in water deficit stress, could modify plant physiological status and create a predictable, spatially explicit pattern of insect herbivore damage to plants. Since such variation in insect herbivore–plant interactions has major demographic, distributional and evolutionary implications, further examination of this hypothesis is warranted.

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Invasion of the Meadow Vole (Microtus pennsylvanicus) in Southeastern Kentucky and Its Possible Impact on the Southern Bog Lemming (Synaptomys cooperi)

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ABSTRACT.—Robinson Forest is a 4450-ha eastern deciduous forest located in southeastern Kentucky on the Cumberland Plateau. Historically, the southern bog lemming (*Synaptomys cooperi*) was the dominant microtine rodent in forest clearings. However, within the last 15 yr, the meadow vole (*Microtus pennsylvanicus*) has expanded its range southward into southeastern Kentucky and has invaded clearings in Robinson Forest. Recent trapping efforts revealed that *M. pennsylvanicus* was the most abundant microtine in clearings, accounting for 48% of all small mammals caught. It invaded an isolated, grass-dominated clearing within 3 yr of tree removal. By contrast, *S. cooperi* was the most rarely caught small mammal in these clearings and tended to occupy herb-dominated clearings where fewer *M. pennsylvanicus* occurred. *Synaptomys cooperi* has become rarer since the arrival of *M. pennsylvanicus*, possibly due to competitive exclusion. Extensive deforestation, coupled with a 50-yr period of climatic cooling, may have led to the range expansion of *M. pennsylvanicus*.

INTRODUCTION

From the 1930s to the 1980s, mild climatic cooling and increased precipitation have caused species of small mammals belonging to the boreal faunal element to expand their distributions southward in the midwestern United States (Frey, 1992). Such a spread could have drastic impact on existing mammalian communities as new species invade and form new sympatric relationships. This is because interspecific competition is considered one of the major factors influencing structural organization of small mammal communities (Linzey, 1984). If, for example, two species with similar diets and habitat preferences come in contact with one another, one of the species may decline in abundance or shift to other habitats as a result of competitive exclusion.

The meadow vole (*Microtus pennsylvanicus*) is one member of the boreal faunal element spreading S in Kansas, Missouri and Illinois (Frey, 1992; Hoffmeister, 1989). In the past, *M. pennsylvanicus* was confined to the Bluegrass Plateau of N-central Kentucky, whereas the southern bog lemming (*Synaptomys cooperi*) was the dominant microtine on the Cumberland Plateau of southeastern Kentucky where it was isolated from *M. pennsylvanicus* (Barbour and Davis, 1974).

Barbour and Hardjasasmita (1966) provided a checklist of the mammals of Robinson Forest in Kentucky based on a 10-wk survey conducted during 1960 and 1961 in addition to Barbour's 12 yr of working in the forest. These authors considered *Synaptomys cooperi* to be common in forest clearings, collecting 20 specimens during the 10 wk. Many of these animals were caught in clearings near Camp Robinson (a research camp near the forest's western boundary). The pine vole, *Microtus pinetorum*, was the only other microtine rodent

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trapped during their study. Barbour never reported *M. pennsylvanicus* from Robinson Forest during 20 yr of collecting from the 1950s to the 1970s (Wayne Davis, pers. comm.).

In 1980, a single *Microtus ochrogaster* was collected from the clearing adjacent to Camp Robinson (Wayne Davis, pers. comm.). By 1983, Bill McComb (pers. comm.) was collecting both *M. pennsylvanicus* and *M. ochrogaster* on reclaimed surface mines adjacent to the forest. He also reported that both *M. pennsylvanicus* and *Synaptomys cooperi* were present in the forest clearings near Camp Robinson. Specific data are not available, although McComb reported that both species were trapped together, with *M. pennsylvanicus* being more abundant. From a 1987–1988 study on bobcats (*Lynx rufus*) in Robinson Forest, Frederick *et al.* (1989) and J. Whitaker (pers. comm.) found *M. pennsylvanicus* in 50% of all bobcat scats during the autumn and winter months and 67% of the scats in the spring and summer months. The frequency of *S. cooperi* in scat was 4% in autumn and winter and 11% in spring and summer. No additional information is available for Robinson Forest until the beginning of our study in 1992.

The purpose of this study was to determine the distribution of *Microtus pennsylvanicus* in Robinson Forest, which microhabitats it occupies, and its relative abundance compared to other small mammals. In addition, these results were compared to the microhabitat use and relative abundance of *Synaptomys cooperi*.

STUDY SITE

This study was conducted on the main body of the University of Kentucky's Robinson Forest, a 4450-ha, second-growth forest located in Breathitt, Knott and Perry counties in southeastern Kentucky. This is the largest remaining forest stand of any kind on the Cumberland Plateau. Elevations range from 240 to 490 m above sea level. It is completely surrounded by 1 to 20-year-old reclaimed surface mines and some active mining. The forest is a maze of deep, narrow valleys, steep slopes and narrow winding ridges (Overstreet, 1989). Clearings occur along streams flowing through the valleys. Most clearings are man-made with some over 70 yr old which are maintained by periodic mowing or periodic flooding. Robinson Forest includes four general habitats:

Mixed mesophytic forest.—Robinson Forest is near the center of the mixed mesophytic region (Braun, 1950). Such deciduous forest is the predominant habitat at our study site. Approximately 50 woody species dominate the area (Overstreet, 1989). Tree species vary from the most mesic beech-dominated areas characterized by beech-poplar (*Fagus-Liriodendron*) and hemlock (*Tsuga*) zones, to intermediate moisture levels characterized by oak-hickory (*Quercus-Carya*) and oak-red maple (*Quercus-Acer*) zones to the most xeric oak-dominated areas characterized by oaks and pines (*Pinus*; Kalisz *et al.*, 1987).

Low-elevation wildlife clearings.—Approximately 26 clearings ranging in area from 0.1–3.0 ha existed adjacent to the three major streams. These included narrow, mowed roadsides and other, larger mowed areas. Elevations ranged from 250–300 m. Many of these clearings were extremely wet. They varied greatly with respect to dominant vegetation, but generally were either grass-dominated or herb-dominated. Any one grass-dominated site had from 3–5 species of grass including broomsedge (*Andropogon virginicus*), smooth crabgrass (*Digitaria ischaemum*), tall fescue (*Festuca elatior*), canus (*Microstegium nominium*), redtop panicgrass (*Panicum rigidulum*), switch grass (*P. virgatum*), bushy panic grass (*P. dichotomum*), and tall redtop (*Triodia flava*). No exposed earth was present at these sites. In contrast, herb-dominated sites were sparsely vegetated and dominated by smartweeds (*Polygonum* sp.), tall ironweed (*Vernonia gigantea*), goldenrods (*Solidago* sp.) and horse-nettle (*Solanum carolinense*). Only two grasses were present in these clearings (small crabgrass, *Digitaria*

ischaemum, and spreading witchgrass, *Panicum dichotomiflorum*) and both were subdominants.

High-elevation wildlife clearings.—Periodically, ridgetops have had trees removed and successional plant communities have become established. During the current study, a single 2.0-ha high-elevation clearing existed. It was formed in 1989 and was 3 yr old at the beginning of our study. It was located on a ridgetop and the adjacent steep slopes; the elevation ranged from 320–430 m. This clearing was isolated from the nearest low-elevation clearings by 6 km of dense forest. The entire area was covered with a dense stand of broomsedge.

Reclaimed surface mines.—Reclaimed areas ranged in age from 1–20 yr and completely surround the forest. These areas were generally sparsely vegetated and the characteristic vegetation was quite variable. They range from being damp with small ponds to well-drained and dry. The soil is very hard and compact (resembling a desert hard-pan surface) and comprised of shale, sandstone and coal ranging in size from fine to coarse gravel. Some areas were littered with small stones. Virtually no leaf litter or organic matter was present. These areas were sparsely vegetated with bunch grasses, herbaceous species, and a variety of introduced plants used for their nitrogen-fixing abilities.

Four distinct subhabitat types were present on the reclaimed surface mines. First, low-lying areas typically had small, shallow ponds dominated by cattails (*Typha* sp.), bulrush (*Scirpus cyperinus*) and rushes (*Juncus* sp.). The second subhabitat was higher, drier habitat surrounding the cattails and characterized by a mixture of grasses that included broomsedge, redtop (*Argostis gigantea*), spreading witchgrass and purpletop (*Tridens flavus*). Other characteristic plants included goldenrod, horseweed (*Conyza canadensis*), and three species of lespedeza (Chinese lespedeza, *Lespedeza cuneata*; Korean clover, *L. stipulacea*; Japanese clover, *L. striata*). Small (up to 5 m tall) black locust (*Robinia pseudoacacia*) were typically scattered though this habitat. A third subhabitat type was dominated by crowned vetch (*Coronilla varia*) and up to five species of lespedeza (the three species listed above plus violet lespedeza, *L. violacea*, and the bush, *L. bicolar*). Redtop (*A. gigantea*) was the only grass present and was subdominant. The fourth subhabitat type was on the steep rubble slopes along the forest boundary. These slopes were sparsely vegetated and dominated by tall fescue (*Festuca elatior*) that was planted to stabilize the soil. The slopes sampled were N- or NE-facing.

METHODS

We trapped at 45 sites in Robinson Forest and the surrounding reclaimed surface mines. During our study, active mining began at the northern boundary of Robinson Forest destroying two of our 45 trap sites before the study was completed. Distances between sites varied from 200 m to 6 km. Trapping was conducted on a total of 22 nights during March, April, September and October of 1992; during January, February, March, September and December of 1993; and in April of 1994. Several sites were trapped repeatedly; however, we waited 4–6 mo between trapping periods. A total of 23 low-elevation wildlife clearings were trapped along the three major streams in the forest. Eighty percent of all high-elevation trapping was conducted on the single 2.0-ha ridgetop site. In addition, we trapped three small roadside clearings near this clearing. Six sites were trapped on reclaimed surface mines, and 12 sites in the mixed-mesophitic forest. Forest sites were within 500 m of wildlife clearings. We trapped these forest sites to determine if they were used as marginal habitat by either *Microtus pennsylvanicus* or *Synaptomys cooperi*.

We used a combination of snap traps (museum specials and rat traps) and Sherman live traps in trap lines. Snap trap bait was a mixture of bacon grease, peanut butter and rolled oats. For live traps, this bait mixture was combined with additional rolled oats and bird seed

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mix. Traps were used in approximately equal proportions (50% live traps, 50% snap traps) in the largest wildlife clearings, reclaimed surface mines, and in the forest habitat. To avoid impacting small populations, we relied more on Sherman live traps (80–100% live traps; 0–20% snap traps) in the small wildlife clearings and in larger clearings where we trapped repeatedly. Voucher specimens were prepared from each site and are currently deposited in the University of Kentucky vertebrate collection. Specimens were kept whenever their identification was in question.

In the eastern part of its range, *Synaptomys cooperi* is noted for being elusive and difficult to trap (Linzey, 1983). To compensate for this, we tried to improve capture success by searching clearings for active runs wherein we placed traps. *Synaptomys cooperi* uses other voles' runs and tends to be caught when traps are placed in their paths, as opposed to being attracted to bait (Linzey, 1983). We also searched for their characteristic shiny, green droppings; and if any were found, traps were placed in all nearby runs. Most of this trapping was done during the winter, when *Synaptomys cooperi* in Kentucky tends to be more easily captured (Robinson, 1981).

We used a nonparametric ANOVA (SAS, 1985) to compare trap success of *Microtus pennsylvanicus* and *Synaptomys cooperi* in habitats where the two species were found. The following within-species comparisons were made: (1) for capture rates in grass-dominated vs. herb-dominated low-elevation clearings; (2) for capture rates in all low-elevation clearings vs. reclaimed mines; and (3) for capture rates in grass-dominated clearings vs. reclaimed mine sites. Only data collected from December through March were used. These were the months of highest trap success and when all habitats were trapped during a given collecting trip.

RESULTS

Based on 2817 trap nights over 2 yr, *Microtus pennsylvanicus* was the most abundant rodent in low-elevation clearings and second most abundant in all other open habitat, whereas *Synaptomys cooperi* was the least commonly collected rodent at all sites (Table 1). One *M. pennsylvanicus* was caught in the forest habitat. *Microtus pennsylvanicus* were caught 18 times more often than *S. cooperi* in the low-elevation wildlife clearings (47.0% vs. 2.6% of all small mammals caught, respectively) and 4.3 times more often on reclaimed surface mines (26.5% vs. 6.1%, respectively). Furthermore, *M. pennsylvanicus* accounted for 31% of all small mammals caught on the high-elevation clearing where no *S. cooperi* were captured.

Microtus pennsylvanicus were most often trapped in grass-dominated habitats. This included low- and high-elevation wildlife clearings as well as some areas on the reclaimed surface mines where grass was one of the dominants. Cattail habitats were the only exception. *Microtus pennsylvanicus* were trapped at the edge of this habitat and active runs were in abundance through stands of sedge in the cattail habitat. Some grasses were present along these edges; however, active mining destroyed this habitat before mature grasses could be sampled. No small mammals were caught in areas where only crowned vetch and lespedeza dominated and grasses were virtually lacking.

Of the six small mammal species trapped in forest clearings, only *Microtus pennsylvanicus* was caught during each of the 7 mo. The other five species were missing from 2–5 of the months sampled (Fig. 1a). *Synaptomys cooperi* was caught less frequently than any other species, and only one individual was caught during any given month from October to February. Drastic seasonal fluctuations in trap success were experienced over the 2 yr of the study (Fig. 4b). Trap success in forest clearings was highest in January and December (20 mammals per 100 trap nights), intermediate from February to April (11 mammals per 100 trap nights), and lowest in September and October (1.5 mammals per 100 trap nights).

TABLE 1.—Trap results for Robinson Forest from March 1992 to April 1994. Values represent number of individuals per 100 trap nights. Numbers in parentheses represent the total number caught

	Habitat types				
	Wildlife clearings		Mixed mesophytic forest	Reclaimed surface mines	Totals
Species	Low elevation	High elevation			
Northern short-tailed shrew (*Blarina brevicauda*)	0.97 (14)	0.00 (0)	0.26 (2)	0.97 (3)	0.49 (19)
Eastern woodrat (*Neotoma floridana*)	0.00 (0)	0.00 (0)	0.52 (4)	0.00 (0)	0.14 (4)
Eastern harvest mouse (*Reithrodontomys humulis*)	0.56 (8)	0.00 (0)	0.00 (0)	0.00 (0)	0.28 (8)
White-footed mouse (*Peromyscus leucopus*)	2.09 (30)	2.93 (9)	3.53 (27)	9.71 (30)	3.41 (96)
Meadow vole (*Microtus pennsylvanicus*)	5.15 (74)	1.95 (6)	0.13 (1)	4.21 (13)	3.34 (94)
Pine vole (*Microtus pinetorum*)	1.46 (21)	0.97 (3)	0.26 (2)	0.00 (0)	0.92 (26)
Southern bog lemming (*Synaptomys cooperi*)	0.28 (4)	0.00 (0)	0.00 (0)	0.97 (3)	0.25 (7)
Eastern chipmunk (*Tamias striatus*)	0.00 (0)	0.33 (1)	0.00 (0)	0.00 (0)	0.04 (1)
Total mammals caught	151	19	38	49	255
Total trap nights	1437	307	764	309	2817
Trap success (individuals per 100 trap nights)	10.51	6.19	4.71	15.86	9.05

This sharp drop in trap success was most extreme in September, when a total of 476 trap nights during September 1992 and 1993 yielded a single *M. pennsylvanicus*. This low yield occurred despite our efforts to rebait traps during the night to offset the high rate at which invertebrates removed the bait. With very few exceptions, we failed to find signs of active runs.

Microtus pennsylvanicus and *Synaptomys cooperi* were both caught during October, December, January and February (Fig 1a). Thus comparing trap success for the different habitat types during these months, *M. pennsylvanicus* was significantly more likely (15.2 times more likely) to be trapped in grass-dominated clearings than in herb-dominated clearings ($F = 34.11$, $P = 0.0001$; Table 2), whereas *S. cooperi* was only 3.5 times more likely to be caught in grass-dominated clearings than herb-dominated clearings ($F = 0.719$, $P = 0.41$; Table 2). *Synaptomys cooperi* was 7.2 times more likely to be trapped on reclaimed surface mines ($F = 4.16$, $P = 0.053$), whereas *M. pennsylvanicus* was as likely to be caught on reclaimed mines as in forest clearings (5.2% vs. 5.3%, respectively; $F = 0.00$, $P = 0.99$; Table 2). *Microtus pennsylvanicus* was 2.6 times more likely to be caught in grass-dominated forest clearings than on reclaimed mines ($F = 3.4$, $P = 0.09$; Table 2), whereas *S. cooperi* was 3.9 times more likely to be caught on reclaimed mines ($F = 1.06$, $P = 0.33$; Table 2).

DISCUSSION

Documented distributions in the midwestern United States and available information for Kentucky suggest that the presence of *Microtus pennsylvanicus* in Robinson Forest is recent.

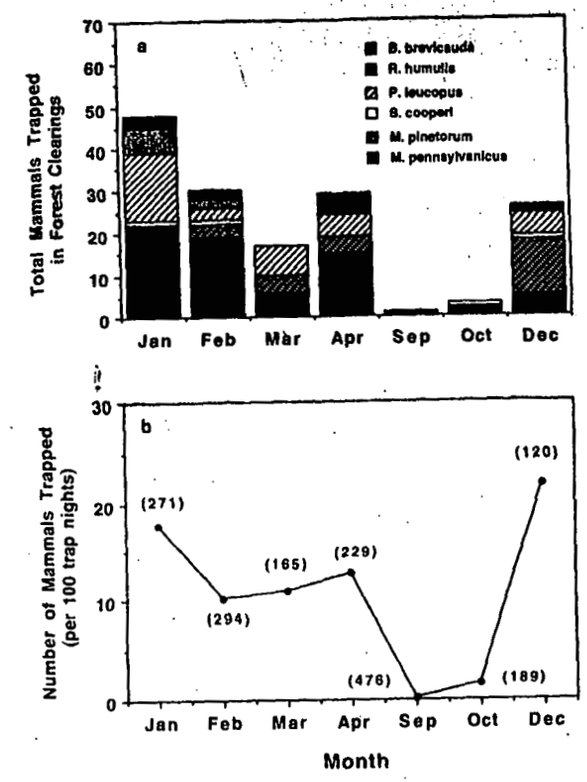

FIG. 1.—Combined trapping data for all wildlife clearings (high- and low-elevation) in Robinson Forest. March represents pooled data from 1992 and 1993, April represents pooled data for 1992 and 1994, and September represents data pooled for 1992 and 1993. January, February and December data are from 1993, and October data from 1992; (a) represents the total number of each species collected during each of the 7 mo; (b) represents the number of all small mammals trapped per 100 trap nights during each of the 7 mo. The numbers in parentheses are the total number of trap nights for each month

This range expansion has probably been the combined result of climatic cooling (as suggested by Frey, 1992) and deforestation (as suggested by Linzey, 1984). This species is extending its range southward in the midwestern states (Frey, 1992). *Microtus pennsylvanicus* was not known in Kansas until 1963 but is now well-established (Frey, 1992). Meadow voles were first reported in Missouri in 1973 and have become increasingly more abundant in

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TABLE 2.—Comparison of trap success for *M. pennsylvanicus* and *S. cooperi* among habitat types from trapping during the months of October, December, January and February during winter trapping (n = the number of sites trapped). Mean values represent number of individuals per 100 trap nights ± SE. Within-species comparisons revealed that the only significant difference in capture rates occurred for *M. pennsylvanicus* in grass-dominated vs. herb-dominated clearings

	n	*M. pennsylvanicus*	*S. cooperi*
Low-elevation clearings	20	5.26 ± 1.69	0.21 ± 0.15
Grass-dominated clearings	7	13.39 ± 2.89	0.39 ± 0.39
Herb-dominated clearings	13	0.88 ± 0.39	0.11 ± 0.12
Reclaimed surface mines	6	5.23 ± 3.34	1.52 ± 1.11

southeastern Nebraska (Frey, 1992). Hoffmeister (1989) noted that *M. pennsylvanicus* has been extending its range southward in Illinois since the late 1950s. The apparent southeastern expansion in Kentucky is concordant with the fact that other members of the boreal faunal element have recently become more widespread in Kentucky. This is the case for *Zapus hudsonicus* (Houtcooper, 1982), and is most striking for the least weasel (*Mustela nivalis*). The least weasel was first reported from Kentucky in 1976 (Davis and Barbour, 1979) and since then, abundant records have become known for N-central Kentucky (Meade, 1992). Frey (1992) considered the mild decrease in temperatures and increase in precipitation in the midwest from 1935 to 1985 to be a likely explanation for the southward expansion of the northern boreal faunal element in the midwest. Similar cooling trends in the southeastern United States (Trapasso and Al Kolibi, 1994) may suggest a similar scenario in Kentucky.

Generally, *Synaptomys cooperi* is rare and elusive in the eastern part of its range (Linzey, 1983). This characteristic coupled with the lack of quantitative data, makes it difficult to determine how its population at Robinson Forest may have changed over the years or how it has been affected by the arrival of *Microtus pennsylvanicus*. We do know that *S. cooperi* is now rarely caught in forest clearings, whereas *M. pennsylvanicus* is the most commonly caught small mammal in forest clearings. One *S. cooperi* was caught for every 20 *M. pennsylvanicus*. During our study, we failed to collect *S. cooperi* or find signs of it in clearings (especially those near Camp Robinson) where Barbour and Hardjasasmita (1966) found them to be common. It is the same spot where, W. McComb (p[illegible]) found them in the early 1980s (when *M. pennsylvanicus* probably first arrived).

Linzey (1983) stated that isolated, man-made clearings in eastern forests are not readily colonized by *Microtus pennsylvanicus* and are favored by *Synaptomys cooperi*, although the clearing of eastern woodlands and replacement of native grasses by introduced species favors *M. pennsylvanicus*. These conditions are similar to those seen in Robinson Forest. First, forest clearings in southeastern Kentucky were more isolated in the 1950s and 1960s before extensive deforestation from surface mining. Second, an increase in the number of paved highways, coupled with the planting of fescue grass along the roadsides, occurred during the 1960s and 1970s (W. Davis, pers. comm.). Both the deforestation and grassy roadsides reduced the isolation of Robinson Forest and may have favored the spread of *M. pennsylvanicus*.

The current rarity of *Synaptomys cooperi* in Robinson Forest is more difficult to explain. Linzey (1983, 1984) emphasized that *S. cooperi* is difficult to trap; nonetheless, Barbour and Hardjasasmita (1966), W. Davis (pers. comm.) and W. McComb (pers. comm.) caught it readily in Robinson Forest and in near-by Cumberland Gap National Historical Park (Barbour *et al.*, 1979) from the 1950s to the early 1980s. Two possible explanations for the rarity of *S. cooperi* include: (1) the population may be at a low point in its population cycle in Robinson Forest, or (2) *Microtus pennsylvanicus* may be competitively excluding *S. cooperi* from the forest clearings.

Linzey (1984) demonstrated in a study 170 km E of Robinson Forest that *Microtus pennsylvanicus* competitively excludes *Synaptomys cooperi* from high-quality habitat (damp areas with dense grass), forcing them to move into lower quality habitat (areas with less grasses and more herbaceous species). A similar situation may be occurring at Robinson Forest. *Microtus pennsylvanicus* is now present in grassy clearings once occupied by *S. cooperi*, and the few *S. cooperi* caught were in herb-dominated clearings. Barbour and Davis (1974) considered it a general phenomenon in Kentucky for *S. cooperi* to avoid competing with *M. pennsylvanicus* by occupying habitat that cannot support *M. pennsylvanicus*.

Establishing the relationship between *Microtus pennsylvanicus* and *Synaptomys cooperi* in Robinson Forest will require long-term trapping and/or experimental manipulations. Competitive exclusion may be operating if either *S. cooperi* abundance increases when *M. pennsylvanicus* population cycles reach low densities or if experimental manipulations of *M. pennsylvanicus* numbers in clearings influence *S. cooperi* abundance. Without such studies, we can only speculate how species that are expanding their ranges affect the small mammal communities they invade.

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Sex-biased Response of Raccoons (Procyon lotor) to Live Traps

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ABSTRACT.—Heterogeneity of response to traps has important implications when interpreting mark-recapture data. We used radiotelemetry to investigate variations in recapture probability for adult raccoons (*Procyon lotor*) during live trapping conducted in S Texas from 1990–1992. Both sexes had higher recapture rates in winter/spring trapping periods than summer/autumn (males $P < 0.001$, females $P < 0.001$). Adult males were consistently captured more frequently than adult females in all trapping periods. There was a higher proportion of 'available' males captured while some females avoided capture. In addition to differences in movement patterns, intersexual behavioral differences in response to live traps were suggested.

INTRODUCTION

Mark-recapture techniques have been instrumental in providing information on population demographics, and a series of models have been developed to estimate population size from mark-recapture data. Ascertaining capture heterogeneity among individuals, and between classes of individuals, is essential to selecting the appropriate model for analyses, as well as interpreting demographic characteristics.

Numerous studies have described raccoon (*Procyon lotor*) demographics from mark-recapture data (Stuewer, 1943; Mech *et al.*, 1968; Urban, 1970; Hoffmann and Gottschang, 1977; Moore and Kennedy, 1985a; Kennedy *et al.*, 1986), but parameter estimates, such as sex ratios, may be biased because males are more readily trapped than females. Researchers reporting raccoon demographics (using mark-recapture or harvest data) have suggested estimates may be affected by an increased vulnerability of males as a consequence of their greater movement and activity (Sanderson, 1951; Stains, 1956; Johnson, 1970; Urban, 1970) or other unknown differences in their behavior (Sanderson and Hubert, 1981). Johnson (1970) further suggested that biases may be seasonal; males may be more prone to capture during the mating season and again during parturition when movements of females are reduced. Some mark-recapture estimators of population size assume equal catchability among all members of the population; therefore, violations of this assumption can bias estimates generated with these models (Pollock *et al.*, 1990).

Little is known concerning the heterogeneity of capture and trap response among raccoons. Moore and Kennedy (1985b) examined raccoon response to live trapping, but did not account for raccoons that were not recaptured. This could have affected their assessment of raccoon trappability and density estimators. For example, failure to recapture an animal could be due to 'trap-shyness', the animal encounters the traps but avoids recapture; emigration, the animal left the trapping area, or mortality. Thus, we used radiotelemetry to assess heterogeneity among adult raccoons in response to live traps, and the effects of heterogeneity of response to traps (Pollock *et al.*, 1990) on interpretations of mark-recapture data.

Specifically, we addressed two null hypotheses: (1) there are no seasonal differences in

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Attractiveness of scents varies with protein content of the diet in meadow voles

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Abstract. The diet consumed by animals can influence their physical condition and potential for reproductive success. Do differences in diet quality affect the attractiveness of secondary sexual characteristics to the opposite sex? This study addressed this question by examining the attractiveness of odours produced by meadow voles, *Microtus pennsylvanicus*, that were fed diets that differed in protein content. Meadow voles that served as scent donors were maintained on one of three diets, consisting of 9, 15 or 25% protein, all of which are sufficient to maintain voles in reproductive condition. These diets influenced the attractiveness of all three odours tested (anogenital area, urine and faeces). Both male and female subjects preferred odours from donors on high-protein diets: subjects preferred odours of opposite-sex conspecifics fed a 15 or 25% protein diet over odours from donors fed a 9% protein diet. Females preferred two odours of males on a 25% protein diet over the same odours of males on a 15% protein diet. These results suggest a mechanism for mate choice via odour preferences based on the protein content of the food consumed by potential partners. Because animals compete for access to higher-quality diets in nature, the choice of a mate with a high-quality diet may also be a means of choosing a higher-'quality' individual.

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Diet quality can have a profound impact on the *life history* characteristics of fish (Kodric-Brown 1985, 1989), amphibians (Walls et al. 1989; Jaegar et al. 1991), birds (Hill 1991, 1992) and mammals (Porter & Doane 1977; Skeen & Thiessen 1977; Batzli 1985; Rissman & Johnston 1986; Bucyanayandi & Bergeron 1990; Galef 1994). For instance, among arvicoline rodents such as voles and lemmings, individuals that consume plants that have low phenol and fibre contents and moderate protein contents (near or above 12–15% protein) usually grow faster, reach sexual maturity earlier, produce more young and overwinter more successfully than those that consume lower-quality diets (Bergeron et al. 1990; Jones 1990; Batzli & Lesieutre 1991).

Diet may also have more specific effects on morphological characteristics used in social communication and mate choice. For example, in house finches, *Carpodacus mexicanus*, the amount of carotenoids in the diet is directly related to the redness of a male's plumage, and redness is a characteristic preferred by females when choosing a mate (Hill 1991, 1992). Similarly, in guppies, *Poecilia reticulata*, higher levels of carotenoids in the diet lead to brighter red and orange spots on the males, and females prefer males with such brighter spots (Kodric-Brown 1985, 1989). Thus, diet quality may influence secondary sexual characters important for successful advertising for mates: animals that consume high-quality foods should have attractive secondary sexual characters and be preferred as mates (Kodric-Brown & Brown 1984). Choosing a mate that has consumed a high-quality diet may influence fitness in a number of ways. Such a mate may be in better

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physical condition or have access to high-quality food and thus be able to devote more energy and resources to care or feeding of the young.

Among many species of rodents and other mammals, the most important signals involved in social communication are odours (Johnston 1983; Brown 1985), and it is well known that diet can influence body odour. In humans, some foods such as onions, garlic, cabbage and asparagus change the scent of the body, urine or breath (Sastry et al. 1980). Consumption of garlic by nursing mothers not only changes the flavour of breast milk, but also may influence ingestion of milk by the infant (Mennella & Beauchamp 1993). In guinea pigs, the odour of urine from animals on some diets elicits more investigation than that from animals on other diets, and these effects occur within 22 h of starting on a new diet (Beauchamp 1976). In spiny mice, differently flavoured diets cause distinctive differences in body odours that become incorporated into the signatures learned by pups from their litter-mates and are used by them to identify kin (Porter et al. 1977; Porter & Doane 1977).

Although these studies show that diet influences odours, only a few studies have examined the influence of the quality of the diet on functionally significant responses, such as preferences for odours of potential mates. In Australian cashmere goats, *Capra hircus*, conspecifics investigated bucks fed a high-quality diet more than those fed a low-quality diet (Walkden-Brown et al. 1994). In red-backed salamanders, *Plethodon cinerus*, females preferred staying in a burrow next to a faecal pellet from a male fed a high-quality diet as opposed to a burrow next to a faecal pellet from the same male when he was fed a low-quality diet (Walls et al. 1989). In this case there was no difference, however, in the attractiveness of the two types of faecal pellets themselves.

Protein content is an important determinant of diet quality for mammals (Glass & Swerdloff 1980; Lindroth & Batzli 1984; Bergeron & Jodin 1987; Walkden-Brown et al. 1994); it affects reproductive maturation, maternal behaviour, growth of young, nesting patterns and space use (Massaro et al. 1974; Glass & Swerdloff 1980; Bergeron & Jodin 1989; Bergeron et al. 1990; Bucyanayandi & Bergeron 1990; Jones 1990). If high-quality food resources are distributed in patches, information about diet quality of a potential mate could be an indicator of its ability to gain or defend such resources. Many species of microtine rodents inhabit areas where food resources are patchily distributed (Batzli 1985). In the present study, we examined whether differences in protein content of the diet cause differences in the attractiveness of the odours of male and female meadow voles, *Microtus pennsylvanicus*. Meadow voles have a polygynous/promiscuous mating system, and competition for mates is intense (Madison & McShea 1987; Boonstra et al. 1993).

GENERAL METHODS

Animals

We used voles that were second- and third-generation offspring of field-caught animals born and raised under long photoperiod (14:10 h light: dark; lights on at 0700 hours Eastern Standard Time). This photoperiod simulates day length prevalent during the spring and summer breeding season. Animals were weaned at 18 days of age, housed with litter-mates until 35 days of age, and housed singly in clear plastic cages thereafter (30.5 × 35.5 × 22.8 cm); cages contained cotton nesting material, water and standard mouse chow (Purina Mouse Chow #5015, St Louis, MO, U.S.A.). Scent donors were 24 male and 24 female voles between 70 and 120 days of age. All scent donors were sexually naive, and within each sex donors were of similar weight (less than 15% difference between scent donors of the same sex). All voles were raised on the 15% diet and then assigned to one of three treatment groups. Each treatment group contained eight animals of each sex. The treatment groups differed only in the food they were given: 9% protein, 15% protein diet (standard mouse chow) or 25% protein. The body weight for each scent donor was recorded at the onset and conclusion of the study. We began collecting odours from scent donors after they had been in the treatment groups for 4 weeks.

Protein Diets

We chose diets containing 9, 15 and 25% protein because they corresponded roughly to the range of protein content available to meadow voles in free-living populations during the breeding season (Batzli 1985). The 9% diet simulates the quality of food (e.g. hay) that a vole may encounter when living in a marginal or poor habitat in nature. This diet contains the lowest protein content that is sufficient for animals to maintain good health, mature gonads and sexual behaviour (Lindroth & Batzli 1984). The 15% diet represents the quality of food (e.g. alfalfa) that a vole may encounter when living in a good habitat. This is also the protein content that we and others generally feed to captive voles (Lindroth & Batzli 1984). The 25% diet simulates the quality of food (e.g. legumes) that a vole may encounter when it lives near a cultivated field (Lindroth & Batzli 1984). The 9 and 25% diets were especially prepared by Purina Test Diets, Richmond, IN, U.S.A.); the 15% diet was Purina's standard mouse chow. The 9% protein diet contained 11% fat, 5.91% fibre and 69.23% carbohydrate. The 15% diet contained 11% fat, 5.29% fibre and 63.25% carbohydrate. The 25% diet contained 11% fat, 4.29% fibre and 53.30% carbohydrate. The three diets were isocalorie and calculated to provide 4 kcal/g of digestible energy.

EXPERIMENT 1: DIET EFFECTS ON SCENTS OF FEMALES

The purpose of this experiment was to determine whether male meadow voles were differentially attracted to the odours of female voles fed high (25%), medium (15%) or a low (9%) protein diets.

Methods

Animals

We used 15 males that were housed singly for at least 3 weeks before they were tested as subjects. Male subjects were 120–150 days of age, sexually experienced and had been fed the 15% protein diet since birth.

Experimental Procedure

We examined the time that males investigated the scents from females on different diets. Males were simultaneously presented with scents of females fed two different diets using three comparisons: (1) 9% protein diet versus 25% protein diet, (2) 9% versus 15%; (3) 25% versus 15%. For each comparison, we examined the responses of males to three different female scents (anogenital area, urine or faeces). Thus we tested nine groups of males ($N = 10$ per group). We randomly selected males for each group from the pool of 45 males. At least 5 days intervened between use of a subject; in two tests, no subject was used in more than two tests, and scent donors and subject voles were unfamiliar and unrelated to each other. We used a unique pair of female scent donors for each trial. The sequence of tests for each subject was randomly determined.

Odour-testing Procedure

We presented scents on a clean glass microscope slide (2.5 × 7.6 cm) following procedures used in previous experiments for assessing odour preferences in voles (Ferkin et al. 1994; Ferkin & Johnston 1995a, b). We divided each slide into three equal sections (each 2.5 cm); one end section contained a stimulus odour from one animal (e.g. faeces), the other end section contained the same type of odour from a donor in a different treatment condition, and the middle section contained no stimulus odour. We suspended the glass slide by a wire hook and clasp 1 cm above the substrate in the subject's home cage, against the wall opposite the animal's nest. During the 3-min trial, we recorded the time that subject voles spent investigating the two scented sections of the slide. We did not record the time spent investigating the middle section of the slide. Criteria for investigation of an odour were that a vole sniffed or licked one end section of the slide and/or that its nose was directed towards and within approximately 1 cm of a scented section of the slide. Each trial began when the slide was placed in the subject's cage. At the end of a trial, the slide was discarded. The placement of stimulus odours on the left or right side of the slide was random. We used Wilcoxon matched-pairs signed-ranks test to determine significant differences between the time spent investigating each pair of odour stimuli. We used a one-way analysis of variance (ANOVA) followed by a t-test to determine whether significant differences existed in weight gained by scent donors in different treatment groups. Lastly, we used chi-square tests to determine whether voles displayed a bias towards either the left or right side of the slide. In all statistical analyses, significant differences were accepted at $P < 0.05$.

Collection of Odours

We collected fresh anogenital area and faeces scents for each trial. To collect anogenital area scent, we rubbed the donor's anogenital area

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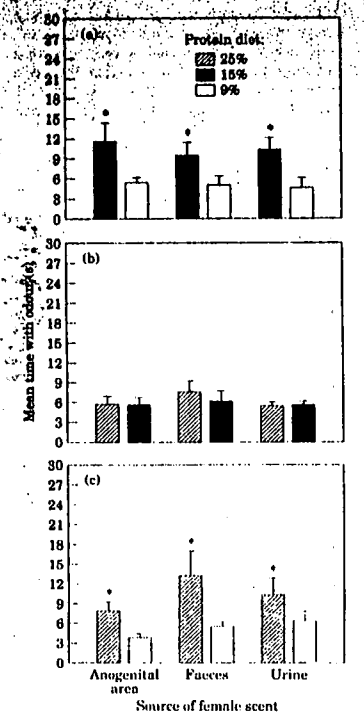

Figure 1. The mean + SE amount of time that male meadow voles investigated scents from the anogenital area, faeces and urine of (a) a female fed a 15% protein diet versus a female fed a 9% protein diet, (b) a female fed a 25% protein diet versus a female fed a 15% protein diet and (c) a female fed a 25% protein diet versus a female fed a 9% protein diet. *$P<0.05$, Wilcoxon matched-pairs signed-ranks test.

against a clean glass microscope slide for 3–5 s. The anogenital area scent may contain components of scent from the preputial gland, sebaceous glands and sex organs. Although this scent may contain traces of urine and faeces, animals often respond differently to anogenital, urine and faecal scents; thus scent from the anogenital area must contain additional components of importance (Ferkin et al. 1994; Ferkin & Johnston 1995a). We collected faeces and urine by placing an animal in a metabolic chamber for 2–4 h. Faecal scent was provided by picking up 1–2 fresh faecal boli with clean forceps and rubbing each bolus onto a glass microscope slide with a water-moistened cotton swab. Urine was placed in a clean vial and stored at −5°C until the day of testing, then thawed at room temperature and rubbed on a clean microscope slide with a cotton swab. The experimenter wore disposable latex gloves to minimize human scent transfer while handling slides.

Results

The diet of female scent donors influenced the responses of males to their odours. Males spent significantly more time investigating the scents of females fed either a 15 or a 25% protein diet than scents from females fed a 9% protein diet (Fig. 1a, b). Males did not; however, show preferences for any of the three scents from females fed a 25% protein diet versus those fed a 15% protein diet (Fig. 1c). Males investigated both stimulus odours on all trials. None of the nine groups displayed a left- or right-side prefer[illegible] tests, $P>0.10$ for all conditions).

The different diets did not differentially affect body weight or weight gain in female scent donors. At the beginning of the experiment the mean ± SE weight of the 24 female scent donors was 43.2 ± 5.0 g. At the completion of the experiment, 6 weeks later, they weighed 45.7 ± 5.3 g, having gained an average of 2.5 g (range = 0.9–4.3 g), which was not a significant increase ($t_{23}=0.86$, $P>0.1$). More importantly, the three groups of scent donors did not differ in body weight, either at the beginning or at the end of the experiment ($F_{2,23}=1.29$, $P>0.1$). At the end of the experiment females fed a 9% protien diet weighed 45.6 ± 4.7 g, females fed a 15% protein diet weighed 46.9 ± 5.1 g, and females fed a 25% protein diet weighed 44.7 ± 6.1 g.

EXPERIMENT 2: DIET EFFECTS ON SCENTS OF MALES

In this experiment, we investigated females' responses to odours from male meadow voles fed diets differing in protein content.

Methods

Animals

We used 47 female voles housed singly for at least 3 weeks before they were tested as subjects. These females were 120–150 days of age, were fed a 15% protein diet since birth and had reared at least one litter; females housed in such conditions will mate within a few hours of being paired with a male (Meek & Lee 1993).

Experimental Procedure

There were nine groups of subjects ($N=10$ per group). We tested their preferences for three different odours (anogenital area, urine or faeces) of males fed three different diets (9, 15 or 25% protein) as described in experiment 1. We randomly selected females for each group from the subject pool. At least 5 days intervened between use of a subject in two tests, no subject was used more than twice, and scent donors and subject voles were unfamiliar and unrelated to each other. We used a unique pair of male scent donors in every trial. The sequence of tests for each subject was random. All other procedures, odour testing and the collection of odours were the same as those in experiment 1.

Results

The diet of male scent donors influenced the responses of females to their odours. Females spent significantly more time investigating the anogential area, faeces or urine scents of a male fed a 15% protein diet compared with the same scent from a male fed a 9% diet (Fig. 2a). Similarly, they preferred all three scents from a male fed a 25% protein diet over the same scent from a male fed a 9% protein diet (Fig. 2b). Unlike the male subjects in experiment 1, females also showed a preference for two scents (anogential area and faeces) of males receiving the 25% protein diet over those receiving the 15% protein diet (Fig. 2c). All female subjects investigated both stimulus odours, and none of the groups showed a side preference (chi-square tests, $P>0.10$ for all conditions).

The different diets did not differentially affect body weight or weight gain in male scent donors. At the beginning of the experiment the average ± SE weight of the 24 male scent donors was 46.1 ± 4.3 g. At the completion of the experiment, 6 weeks later, male scent donors had gained a mean of 4.9 g (range = 2.0–6.3 g) for a final mean weight of 51.0 ± 4.0 g; this increase in weight was not statistically significant ($t_{22}=1.40$, $P>0.1$). The protein content of the diet did not

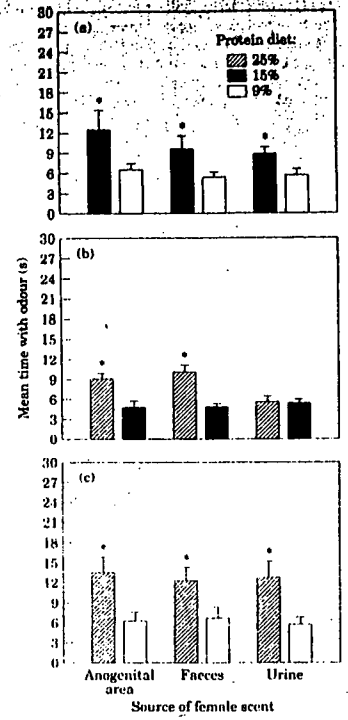

Figure 2. The mean + SE amount of time that female meadow voles investigated scents from the anogenital area, faeces and urine of (a) male fed a 15% protein diet versus a male fed a 9% protein diet, (b) a male fed a 25% protein diet versus a male fed a 15% protein diet and (c) a male fed a 25% protein diet versus a male fed a 9% protein diet. *$P<0.05$, Wilcoxon matched-pairs signed-ranks test.

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results in significant differences in body weight between groups of scent donors, either at the beginning or at the end of the experiment ($F_{2,21}=1.70$, $P>0.1$). At the end of the experiment, males fed a 9% protein diet weighed 52.6 ± 5.3 g, males fed a 15% protein diet weighed 48.9 ± 2.7 g, and males fed a 25% protein diet weighed 51.7 ± 3.9 g.

DISCUSSION

These experiments show that the protein content of the diet influenced the attractiveness of several odours of meadow voles. When tested with odours from voles of the opposite sex, both males and females preferred scents from animals that consumed the two diets high in protein content compared with the diet low in protein content. Voles showed such preferences for all three scents that we tested. None the less, some scents may reflect protein content of the diet more faithfully than others. Females showed graded preferences for odours of male anogenital area and of faeces across all three diet groups, but they did not respond differently to urine from males in the 15 and 25% protein groups. The attractiveness of urine scent appears to reach a plateau in animals fed a diet that contains 15% protein, although we do not know what might happen if the diet had had more than 25% protein. These results suggest that urine does not contain as much information about dietary protein content. Previous work on voles indicates that urine provides more information about circulating testosterone titre than faeces or other male odours (Ferkin et al. 1994). Taken together, these findings are consistent with the recently developed view that different scents provide some overlapping and some different information about sex and reproductive state (Johnston 1983; Drickamer 1989; Ferkin & Johnston 1995a; Lai et al. 1996).

We do not know what chemical changes occurred in the three scents or how protein content of the diet influenced each scent. An increase in protein in the diet could change the composition of the scents directly by increasing the concentration of proteins, amino acids, fats, sulphur compounds or other metabolic products (Sastry et al. 1980; Galef et al. 1988; Mason et al. 1994). It is also possible that an increase in protein content of the diet could change the size or activity of the scent-producing tissues, thereby altering the quantity or quality of the secretion and thus the attractiveness of scent from these areas of the body. Alternatively, odours could be indirectly influenced by changes in some other physiological processes, such as secretion of gonadal hormones, which are known to affect odour quality and attractiveness (Powers et al. 1985; Ferkin & Johnston 1993; Walkden-Brown et al. 1994). Although we did not measure gonadal hormone titres of scent donors, the percentage of protein in all three diets we used is sufficient to maintain reproduction in microtine rodents (Lindroth & Batzli 1984). Thus, it is not likely that the diets we used influenced gonadal hormone titres in donors sufficiently to affect the attractiveness of their odours (but see Walkden-Brown et al. 1994). The effects we report are more likely to be due to direct influences of protein content on the chemical composition of these scents, resulting in a change in odour.

An alternative explanation of our results might be that the voles showed preferences for the diet itself. That is, food particles, by adhering to the body, could potentially be mixed with each of the scents we collected, and preferences could be for the diet (Galef 1988, 1994). If this were the case, one would expect preferences for odours of like-sex stimulus animals on a higher protein diet. Preliminary data suggest that this is not the case. In observations using the same methods as in experiment 1 and 2, we found that male meadow voles ($N=6$) spent a similar amount of time investigating the anogenital area scent of male donors fed a 9% or 15% protein diet ($\bar{X} \pm se = 5.5 \pm 2.1$ s and 6.3 ± 2.4 s, respectively). Similarly, female voles ($N=5$) spent approximately an equal amount of time investigating this same scent from female donors fed a 9% and 15% protein diet (6.7 ± 2.5 s and 6.9 ± 2.8 s, respectively; M. H. Ferkin, C. J. Lee & R. E. Johnston, unpublished data). These data thus suggest that the observed preferences were not due to preferences for the diet itself, but were due to differences in the odours of donors caused by consumption of the diet.

We hypothesize that the functional explanation for our results is that preferences we observe reflect mate preferences. There are three reasons for this interpretation. First, the type of preferences for opposite-sex odours that we observed indicates actual mate preferences in other studies

(Brown 1985; Salo & Dewsbury 1985; M. H. Ferkin, N. K. Noyd & K. Hudson, unpublished data). Second, cross-sex odour preferences in meadow voles are correlated with other variables that are associated with mate preferences, such as time of year, being housed under long versus short photoperiods, and the hormonal status of the animals involved (Ferkin & Johnston 1993, 1995a, b; Ferkin et al. 1994, 1995). Third, preferences of females for males that consume high-quality diets have been reported in other species. Female red-backed salamanders were more attracted to a burrow in close proximity to faecal pellets of males that were fed termites, a high-quality diet, than to those from males fed ants, a low-quality diet, and females also mated more with males fed termites (Walls et al. 1989; Jaeger & Wise 1991). In both house finches and guppies, females prefer to mate with males that have brighter red plumage or red spots, and the brightness depends on the carotenoid content of the diet (Kodric-Brown 1985, 1989; Hill 1991, 1992). Thus, in these examples, the quality of the diet influences the signals that affect mate choice, and could be used by individuals as a basis for mate choice. Such diet-induced differences in secondary sexual characteristics would be most pronounced in species that have a non-monogamous mating system, in which competition between males for females is intense (Kodric-Brown & Brown 1984).

Why should males or females prefer as mates individuals that consume high-quality diets? Differences in diet quality may reflect differences in successful competition for food resources. For house finches, the degree of red coloration in males is also correlated with the attentiveness of males at the nest, suggesting that a male's ability at obtaining a diet high in carotenoids is related to a male's value as a parent. For voles, it may be beneficial for females to choose males that consume a high-quality diet, since this may indicate the male's ability to locate and gain access to such resources. Males may also benefit from similar choices of females. Females occupy mutually exclusive territories in transitional grasslands containing patches of food of widely varying quality (Batzli 1985; Madison & McShea 1987; Bergeron & Jodin 1989), and thus their territories may differ considerably in quality (Bergeron et al. 1990). Presumably, females compete for these resources (Ostfeld 1985). Maintenance of a territory containing food that is rich in protein and low in tannins and phenolics will result in the production and rearing of more young than a territory that is low in protein and high in tannins and phenolics (Iris 1987; Jones 1990; Norrie & Miller 1990; Wong & Bondrup-Nielson 1992; Bondrup-Nielsen 1993). A high-quality maternal diet and/or diet for the pups may also enhance reproductive development (Rissman & Johnston 1986; Nelson 1991; Meek et al. 1995). If this interpretation is correct, our results are some of the first to show that males in a promiscuous or polygynous species of vertebrates exert preferences for females based on the quality of the female's diet.

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MOVEMENT OF MEADOW VOLES IN RESPONSE TO FOOD AND DENSITY MANIPULATIONS: A TEST OF THE FOOD-DEFENSE AND PUP-DEFENSE HYPOTHESES

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The space-use patterns of female voles are believed widely to be driven by food availability, whereas male voles respond primarily to availability of receptive females. Alternatively, female voles may maintain exclusive territories to prevent infanticide. We manipulated population densities and levels of food availability in replicate populations of the meadow vole, *Microtus pennsylvanicus*, to determine the impact of each on movement distances. Sex differences occurred in the responses of voles to food and density treatments. Adult male voles responded to food supplementation by decreasing movement distances, irrespective of density. Adult female voles only contracted movement distances under high densities. Male voles may respond to changes in food availability when female voles are dispersed widely and do not constitute a defensible resource. Female voles may retain fairly constant home ranges in the face of increased food availability to prevent infanticide. Our data suggest that habitat characteristics are important in the spacing behavior of male voles and food abundance is not the primary determinant of the spacing behavior of female voles.

Key words: *Microtus*, voles, food availability, density, movement distance, space use

Territoriality can serve several adaptive functions, including defense of limited resources, increased access to mates, and prevention of infanticide. Furthermore, space requirements of each sex may vary among species with different mating and social systems. The meadow vole, *Microtus pennsylvanicus*, has a promiscuous breeding system. Both males and females may have multiple mates: male voles contribute nothing to reproduction beyond insemination (Wolff, 1985*a*). Reproductive success of male and female meadow voles may be limited by different factors due to the dichotomy in their reproductive roles. Female meadow voles are territorial during the breeding season and exclude other females but not males (Madison, 1980). Territoriality of female voles may be related to distribution and renewability of their food resources; territoriality ultimately serves as a form of food defense (Ims, 1987*a*; Jones, 1990; Ostfeld, 1985, 1990). Alternatively, females may maintain exclusive territories as a form of pup defense. Space use per se may be the source of interspecific competition to defend offspring and protect against infanticide (Wolff, 1985*b*, 1993; Wolff and Schauber, 1996).

Male meadow voles do not maintain exclusive territories, their ranges overlap extensively with females and other males (Madison, 1985). Reproductive success of male voles is supposedly less dependent on food availability and more responsive to distribution of potential mates (Ims 1987*b*, 1988*a*, 1988*b*; Nelson, 1995*a*, 1995*b*; Ostfeld, 1985). If this hypothesis is correct, male voles should not alter movements based on changes in food availability unless

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movements of female voles change. The dichotomy in space-use requirements of each sex should be manifested in a differential response of each sex to perturbations in population density and food availability.

Contrary to that expectation, numerous studies have shown a similar change in the space-use patterns of both sexes in response to experimental alterations of food availability. An increase in food availability often produces a decrease in the home-range size or movement distances of both male and female rodents (Andrzejewski and Mazurkiewicz, 1976; Boutin, 1990; Sullivan et al., 1983; Taitt, 1981; Taitt et al., 1981; Taitt and Krebs, 1981, 1983). This uniformity in response is surprising, given the different reproductive roles and space-use patterns in each sex. These results may be due in part to confounding effects of uncontrolled changes in density. Food supplementation invariably produces an increase in population density in unfenced populations of small rodents because of increased reproductive success or increased immigration. Thus, populations receiving supplemental food also are subjected to pronounced and simultaneous changes in density.

Increases in density alone can cause a decrease in movements of both sexes (Abramsky and Tracy, 1980; Ostfeld and Canham, 1995). Increases in density may affect food availability by producing a decrease in quantity or quality of available forage as competition increases for a finite set of resources. Changes in either population density or food availability may produce similar responses in the space-use patterns of each sex. However, each sex may actually be responding to a different parameter of the environment. Our goal was to manipulate independently food availability and population densities to investigate their impact on movement distances in the meadow vole. We predicted that if female meadow voles are limited by food, they should contract their movement distances in the presence of increased food availability under both high- and low-density conditions. Conversely, if territoriality is a function of pup defense, changes in food availability should produce no change in movement distances of female voles if density is held constant. If male meadow voles alter movement distances solely in response to movements of females, they should not respond to changes in food availability under constant density conditions unless movements of females also have changed. An understanding of the movement patterns of each sex under different food and density regimes will provide an indirect test of the food-defense (Ostfeld, 1985) and pup-defense (Wolff, 1993) hypotheses and further explain the dichotomous patterns of space use in male and female meadow voles.

Materials and Methods

Study area.—Replicate populations of meadow voles were maintained in 0.17-ha enclosures on an oldfield habitat located at the Broadmoor Audubon Sanctuary in South Natick, Massachusetts. The flora consisted of a number of common grasses including quack grass (*Agropyron repens*), bluegrass (*Poa pratensis*), goldenrod (*Solidago*), and milkweed (*Asclepias syriaca*). South Natick is in the coastal climatic zone, which is generally milder and drier than inland zones. However, winter of 1993 was unusually severe with the second highest snowfall recorded to date for Boston.

Study design.—Eight adjacent grids were enclosed with corrugated metal fencing buried to a depth of ca. 30 cm and extending 1 m above ground. Fencing did not eliminate access by avian or mammalian predators (Tamarin et al., 1984). Each population was founded with four pairs of meadow voles in July 1993. Originally, the study was to consist of a two-by-two factorial design with replicate populations subjected to one of four possible treatments: food supplementation at both high and low density and no food supplementation at high and low density. Densities >34 animals per grid were considered high. This criterion was determined by calculating the number of home ranges of female voles that could fit onto each grid. Ranges of females were selected because only female meadow voles defend spatially exclusive territories (Madison, 1980). Using a conservative estimate of 100 m², we determined that 17 home ranges of female voles could fit on each of the 0.17-ha grids. Thus, with unbiased sex ratios, grids should not have been spatially saturated at densities of <34 individuals per grid. During the course of the study, nonsupplemented plots never reached densities of >17 adult female voles or >34 animals total; thus, only three treatment groups were possible: food-supplemented populations at high density, food-supplemented populations at low density, and nonsupplemented populations at low density. Voles never were added to any of the grids after initial establishment due to confounding hormonal and behavioral changes that accompany introduction of unfamiliar voles (Carter and Getz, 1985; Fortier et al., 1996)

Food and density manipulations.—Levels of food were manipulated on supplemented grids by adding 5.7 kg of sunflower seeds to each weekly with a broadcast spreader. Sunflower seeds were chosen for their high caloric value. Hulls of these seeds were repeatedly found in tunnels and nesting areas throughout the study, indicating that this supplemental food was both acceptable and accessible to the voles. To evaluate the efficiency of our food supplementation, we placed 1-l plastic containers filled with sunflower seeds at 40 stations on each supplemented grid. We were able to quantify the amount of seed taken by voles at densities of up to 40 voles per grid. We then added supplemental food with a broadcast spreader at three times that level for the duration of the study. In this way, we attempted to ensure that ample seed was available for all voles at any given level of density. Any differences observed between food-supplemented grids at low and high density should be due to some facet of the density change itself, rather than a difference in availability of food.

Animals were removed from low density plots every 2 weeks to maintain consistent densities between food-supplemented low-density treatments and nonsupplemented control grids. On the first day of every trapping period, sex and age ratios were calculated for each of the plots to be cropped. Individuals removed on the second day of trapping were selected to minimize effects of cropping on sex ratio and age structure of the population.

Collection of trapping data.—Voles were trapped using multiple-capture traps (Ketch-alls, Kness Manufacturing Co., Albia, IA) baited with crimped oats and supplied with cotton bedding material. Each trapping station consisted of a single Ketch-all trap covered with a piece of particle board to provide protection from the sun and precipitation. Twenty-five traps were arrayed on each grid in a 5 by 5 array with 6.1 m between trapping stations. Trapping occurred biweekly from August 1993 to December 1994; trapping was not conducted from January through March 1994 due to deep snow cover. Traps were set late in the afternoon of the first day and checked on the following 2 mornings. At first capture each animal received a uniquely numbered ear tag and was toe-clipped for future identification. We recorded tag number, mass, sex, location, and reproductive condition for all captures. All individuals were released at their point of capture. In addition, small numbers of white-footed mice (*Peromyscus leucopus*) and meadow jumping mice (*Zapus hudsonius*) were captured and removed from the grids. Short-tailed shrews (*Blarina brevicauda*) and masked shrews (*Sorex cinereus*) were captured occasionally and released.

Data analysis.—Voles were placed into one of two size classes based on weight: individuals weighing 20–29 g were classified as subadults and individuals weighing >30 g were classified as adults. Juveniles (≤19 g) were caught occasionally, but their numbers were small and they were omitted from analyses of movement data. Data were pooled into two time intervals: a breeding period and a nonbreeding period. The breeding season extended from April through October and ended when <50% of the adult female voles were lactating on unmanipulated control grids. Analysis of movement distances during the nonbreeding season was limited to movements of adult voles because of the small number of subadult voles captured during this period. Movements of all animals were determined by the distance between successive captures at 2-week intervals. Repeated-measures analyses of variance were used to test for significant effects of density and food availability on movement distances; logistic transformation was required to normalize the distribution of distances. Enclosures of each food and density treatment maintained independent populations of voles; thus, enclosures, not individual voles, were used as the unit of replication. Scheffe's *F* test was used for post-hoc comparisons of means

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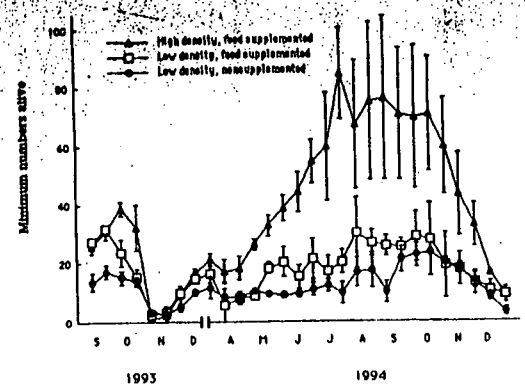

FIG. 1.—Population densities (minimum number alive per grid) of voles in the three treatment groups. Values are means of the replicates for each treatment ± *SE*. No trapping occurred between January–March 1994 due to deep snow cover.

when the RMANOVA indicated that effects of the food and density treatments were significant.

RESULTS

Density effects.—During the study, 1,352 voles were captured 3,780 times. Trappability was high on all grids, averaging 87%; thus, enumeration was used to estimate density (Krebs, 1966). The addition of supplemental food resulted in increases in the density of voles on the uncropped food-supplemented grids (Fig. 1). The low-density, food-supplemented grids were cropped to maintain densities comparable to those on the unsupplemented control grids. Densities in the low-density, food-supplemented grids tended to be slightly higher than those in nonsupplemented grids, although these differences were not significant. That difference was due to the fact that low-density, food-supplemented grids were cropped according to the number of animals caught but trappability was <100%; thus, actual densities tended to be slightly higher than in control grids. All grids showed seasonal fluctuations; peak densities occurred near the end of each breeding season (Fig. 1).

Movement distances.—Movements of voles were determined indirectly in this study by capture locations of voles caught in successive trapping periods. All data were taken from the second year of the study, after differences in density had been firmly established across treatment groups. There were two high-density, food-supplemented plots, two low-density, food-supplemented plots, and four low-density, nonsupplemented plots. Movement distances of adult voles were affected significantly by sex, season, and food and density manipulations (Table 1). Sexes differed in response to treatment, as indicated by the significant sex by treatment and sex by season interactions. Adult male voles were influenced by food supplementation and decreased their average distance moved in both low- ($F = 28.97$, $d.f. = 1,5$, $P < 0.05$) and high-density ($F = 25.60$, $d.f. = 1,5$, $P < 0.05$) supplemented treatments relative to the low-density nonsupplemented populations

TABLE 1.—*Repeated measures analysis of variance for effects of sex, season (breeding and nonbreeding), and treatment (food and density levels) on the movement distances of adult voles between successive captures at 2-week intervals. Grids were used as the unit of replication; thus all movements of individual voles were averaged within a season by sex by treatment grouping prior to analysis.*

Source	*F*	*P*
Model	20.16	0.004
Sex	18.78	0.007
Season	86.11	0.269
Treatment	43.51	0.001
Sex by season	7.46	0.041
Sex by treatment	10.16	0.017
Season by treatment	4.56	0.075

during the breeding season (Fig. 2). Movement distances of adult male voles were higher on the low-density nonsupplemented grids than on the high-density food-supplemented grids ($F = 16.49$, $d.f. = 1,5$, $P < 0.05$) during the nonbreeding seasons (Fig. 3). No significant differences were observed between the low-density, food-supplemented grids and either the high-density, food-supplemented grids or the low-density, nonsupplemented grids during the nonbreeding season.

Conversely, adult female voles were affected by density during the breeding season (Fig. 2) and moved shorter distances on the high-density supplemented grids than on either the low-density supplemented grids ($F = 47.55$, $d.f. = 1,3$, $P < 0.01$) or low-density nonsupplemented grids ($F = 38.11$, $d.f. = 1,5$, $P < 0.01$). Differences between the low-density supplemented treatments and the low-density, nonsupplemented controls were not significant. During the nonbreeding season, female voles responded to only supplemental food, exhibiting a sharp increase in movement distances on the low-density, nonsupplemented grids relative to the high- ($F = 58.59$, $d.f. = 1,5$, $P < 0.01$) and low-density ($F = 116.84$, $P < 0.01$) food-supplemented treatments (Fig. 3). Repeated-measures analyses of variance indicated that there were no significant effects of sex or treatment on movement distances of subadult voles.

DISCUSSION

Male and female meadow voles exhibited markedly different responses to experimental treatments. Contrary to our expectations, male voles contracted their movement distances in the presence of supplemental food, even when density was held constant. The ranges and activity patterns of male voles may be more responsive to nutritional and energetic factors than has previously been hypothesized (Bondrup-Nielsen and Ims, 1990; Nelson, 1995*a*; Ostfeld, 1985). Male voles may shift their ranges periodically during the breeding season to maximize the number of receptive female voles that they encounter, but their short-term movements may be based more on food availability, particularly when female voles are widely dispersed and do not constitute a defendable resource.

Female voles did not respond to food supplementation during the breeding season when population densities were held constant. We suggest that female meadow voles at low density are not food limited; there is no evidence to suggest that size of female territory is based on energy demands during the breeding season (Wolff, 1993). Movement distances of female meadow voles only contracted under high-density conditions during the breeding season. Furthermore, during the nonbreeding season, female voles contracted their movement distances on all food-supplemented grids, irrespective of density (Fig. 3). These results indicate that patterns of space use during the breeding season in female meadow voles are not tied to food but to some other factor, such as intruder pressure. Previous work with the prairie vole, *Microtus ochrogaster*, has shown that supplemental food has no effect on home-range size when grids are compared at similar density levels (Desy et al., 1990). A similar relationship between density, food availability, and

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FIG. 2.—Average movement distances of adult voles during the breeding season. Animals weighing ≥30 g were classified as adults. Movement distances represent the mean distance moved between consecutive trapping periods ± *SE*. Movements were significantly farther for males under nonsupplemented conditions relative to all food-supplemented grids; movement distances of females were significantly lower under high-density food-supplemented conditions relative to both low-density food-supplemented and nonsupplemented treatments.

home range has been found in chipmunks (*Tamias*). Supplemental food produces no change in home-range size of chipmunks when population density is held constant (Lacki et al., 1983).

During the breeding season, female meadow voles exclude other adult females from their territories; males maintain ranges that overlap extensively with individuals of both sexes (Madison, 1980, 1985). Yet, nonterritorial male meadow voles were most responsive to changes in food availability; female meadow voles were more sensitive to changes in density during the

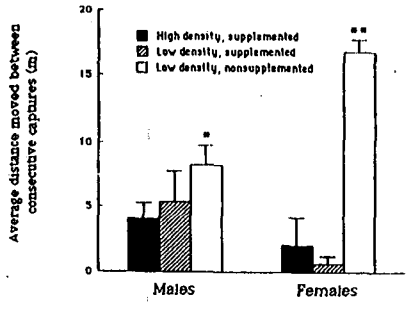

FIG. 3.—Average movement distances of adult voles during the nonbreeding season. Animals weighing ≥30 g were classified as adults. Movement distances represent the mean distance moved between consecutive trapping periods ± *SE*. Movements were significantly farther for both male and female voles under nonsupplemented conditions relative to all food-supplemented grids.

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breeding season. This sensitivity to density only occurred during breeding; adult female voles did not exhibit any difference in movement distances between high-density food-supplemented grids and the low-density food-supplemented grids during the nonbreeding season. Gaines and Johnson (1982) found a significant negative correlation between density and home-range size for only adult female voles. High population densities also have been found to affect subsequent reproductive performance of juvenile female voles but not juvenile males (Kviljo et al., 1992). Our results support predictions of the *pup-defense hypothesis*; the function of female territoriality may be defense of young rather than defense of food. As density increases, female meadow voles may contract their ranges to reduce infanticide (Wolff, 1985*b*, 1993; Wolff and Cicirello, 1989; Wolff and Schauber, 1996). This hypothesis is further supported by our finding that subadult female voles, which are weaned but not yet reproductively active, do not exhibit contractions in movement distances at high density.

Ims (1987*a*) demonstrated that food supplementation alone could produce smaller home ranges in female grey-backed voles, *Clethrionomys rufocanus*, which also exhibit intrasexual territoriality of females and nonterritoriality of males. However, food availability was manipulated by adding discrete patches of high-quality food at a small number of stations. Under these conditions, the observed reduction in home-range size was likely to be a product of the clumped distribution of food as opposed to its relative abundance. Our findings indicate that movement distances of females are not altered by an increase in food availability if the food resources are widely and evenly distributed.

For breeding male voles, availability of sexually receptive females is believed to be the key factor regulating spacing. When female voles are artificially clumped via caging or feeding stations, males are observed to contract their ranges or increase their range overlap (Ims, 1988*b*, 1990; Ostfeld, 1986; cf. Agrell et al., 1996). In natural populations, however, female meadow voles typically maintain exclusive territories without significant range overlap during the breeding season (Madison, 1985). Thus, female voles are unlikely to exhibit the patchy distribution that would constitute a defendable resource; males may be more influenced by food availability under these conditions. If female voles remain widely distributed and indefensible, movement patterns of male meadow voles may vary in response to food availability. Previous work has indicated that multiple paternity occurs in field populations of voles (Boonstra et al., 1993) and the variance in male reproductive success may actually be lower than the variance in female reproductive success (Sheridan and Tamarin, 1988), suggesting that male voles are unable to monopolize females under natural conditions.

Our results challenge conventional wisdom that food is the key resource for females and males are driven by availability of receptive females (Fleming, 1979; Ims, 1987*a*, 1988*b*; Trivers, 1972). Male meadow voles alter their movement distances in response to food supplementation; use of space by female meadow voles appears to be a product of population density rather than simple food availability. Our results support the pup-defense hypothesis as an explanation of territoriality in female meadow voles. Although we did not measure infanticide rates directly, our results may be consistent with other hypotheses as well. There may be competition for space to provide cover from predators, or territoriality may foster long-term resource availability (Boonstra and Rodd, 1983).

Clearly, effects of increased food availability cannot be fully understood without isolating confounding effects of immigration and changes in density. Our understanding of the relationship between these variables would benefit from additional studies on variability in the reproductive success of males at different densities and

detailed information concerning effects of use of space on growth and survival of offspring.

Acknowledgments

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LONG-DISTANCE HOMING IN MEADOW VOLES, *MICROTUS PENNSYLVANICUS*

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During a field experiment on density-dependent processes in meadow voles (*Microtus pennsylvanicus*), we removed 848 voles from field enclosures and released them 1,200 m away. Eleven animals (1.3%) returned to the enclosure from which they had been removed, which entailed traversing inhospitable habitat (forest, wetland), obstacles (permanent stream, roads), and climbing a 0.9-m hardware-cloth fence surrounding the enclosures. For six of the 11 voles, returning home was accomplished in >2 but <4 weeks; the others returned in ≤2 weeks. Voles returning home, which averaged ca. 30 g, lost on average 5.3% of their body mass during homing, unlike their resident counterparts, which gained mass. The voles that homed could not have used familiar objects as cues for navigation, but whether they used distant points of reference or wandered randomly is unknown. Our findings suggest that meadow voles are capable of travelling >1 km toward home, and thus, it is likely that they could travel similar distances while dispersing.

Key words: *Microtus pennsylvanicus*, meadow vole, dispersal, long-distance homing, movement distances

Animals displaced from their home ranges may return, a process known as homing. Most research on homing in small mammals has been concerned with elucidating the proximate mechanisms involved. Some support exists for both orientation using familiar cues in the environment and navigation using remote cues, such as landscape features, sun, stars, or magnetic fields (August et al., 1989; Drickamer and Stuart, 1984; Etienne et al., 1986; Fisler, 1962; Fluharty et al., 1976; Joslin, 1977; Karlsson, 1984; Robinson and Falls, 1965). Alternatively, displaced mammals may wander in random directions and succeed in finding their original home ranges by chance alone.

The evolutionary and ecological significance of homing in small mammals is poorly understood, in part because little information exists to indicate the likelihood or frequency that animals are displaced from home. However, studies of homing are useful in evaluating the capacities of animals to travel long distances over unfamiliar terrain. If animals can return home from great distances once displaced, it is likely that they have the capacity to disperse long distances away from home. The ability to travel long distances is believed to be particularly important in species such as the meadow vole (*Microtus pennsylvanicus*), which probably occupied patchy and ephemeral habitats throughout much of its evolutionary history (Christian, 1970; Getz, 1985). In such landscapes, the ability to disperse long distances through unfamiliar terrain to locate and colonize suitable habitat should have been favored by selection (Christian, 1970). The chances of finding new, suitable habitats during explorations generally may have been low, thus favoring the ability to return to known suitable habitat.

In this paper, we report data collected during an experiment in which we removed large numbers of meadow voles to control population density within field enclosures (Ostfeld and Canham, 1993, 1995). We did not expect the removed voles to return, but took advantage of their having done so to

examine their capabilities of long-distance movements.

MATERIALS AND METHODS

Our study was conducted in a mesic, fertile, old field at the Institute of Ecosystem Studies in Millbrook, Dutchess Co., New York (41°50′N, 73°45′W). The field had been abandoned from agricultural use in the early 1970s and mown about once per year until 1990, when we began our study. Vegetation consisted of grasses (*Bromus inermis, Poa pratensis, Arrhenatherum elatius, Phleum pratense*) and forbs (*Galium mollugo, Solanum carolinense, Glecoma hederacea, Oxallis repens, Potentilla, Hieracium pratense, Solidago*). Further details of habitat and vegetation are in Ostfeld and Canham (1993).

In May and June 1990, we built nine 40- by 40-m enclosures using 1.4-m wide galvanized hardware cloth (1.3-cm mesh) with 0.5 m extending belowground and 0.9 m aboveground. Trapping grids, consisting of 5 by 5 arrays of Longworth livetraps placed 7.5 m apart, were established inside enclosures. To detect escapees from the enclosures, we occasionally set a ring of Longworth traps surrounding the enclosures. Four percent of the 3,094 voles we marked inside enclosures were captured outside fences or moved between enclosures (Ostfeld, 1994); thus, the fences were not completely impermeable. Because holes beneath the fences were rare and filled upon discovery, we suspect that most voles that crossed fences did so by climbing.

Our study was designed to examine density-dependent processes (Ostfeld and Canham, 1993, 1995; Ostfeld et al., 1993) and consisted of experimentally reducing the density of meadow voles inside six of the nine enclosures. From early June 1990 to April 1992, we trapped for 2 consecutive days every other week. We estimated density of voles on the 1st day of each trapping session, and removed voles on day 2 to manage populations at either low or medium density, with three replicates of each. During periods of rapid population growth, we also trapped selected low- and medium-density enclosures in the intervening weeks. We marked voles with numbered metal ear tags. For each vole, we recorded tag number, gender, body mass, reproductive condition, and trap station. Most animals were released at the site of capture, but some were removed to achieve desired densities.

Voles selected to be removed were returned to their live traps until all traps had been checked, usually by late morning or early afternoon. We then placed traps in the trunk of a car and drove them in a direct path to one of two release points. Release points were in grassy fields managed by mowing once or twice per year. The straight-line distance between both release points and the field enclosures was 1,200 m. Between one release point (weather station) and the enclosures lay ca. 300 m of deciduous forest, 600 m of wetland dominated by purple loosestrife (*Lythrum salicaria*) and willows, and 300 m of grassy, lowland fields. From the other release point (Conover House) to the enclosures, ca. 50 m is forested, 800 m is wetland, and 350 m is grassy fields. A dirt road, two narrow, low-traffic, paved roads, and a permanent stream separated the release points from the enclosures. The stream is third order, has a mean annual flow volume of 1 m^3/s, and is spanned by a few fallen trees as well as a road bridge. Voles were released by opening traps and allowing animals to walk or run out; those that did not leave immediately were gently shaken out. Voles that exhibited homing were detected during the regular live-trapping schedule inside enclosures. Up to 30 voles were removed from enclosures in any given week.

RESULTS

We removed 848 voles from six of the nine experimental enclosures and released 712 at the weather station release point and 136 at the Conover House release point. Voles were removed during all seasons in both years, with a slight peak in late summer to mid-autumn. We preferentially chose subadults (20–30 g) to remove from the enclosures (Ostfeld and Canham, 1993), although some voles were >30 g.

Eleven voles returned to the enclosures of their origin; nine from the weather station and two from Conover House. One of three voles that was removed a second time returned again. Of the 11 animals that homed, five were females and six were males; the one that returned twice was a male. Three voles returned in spring (April or May), six in summer (late June–mid September), and two in autumn (October).

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None of the voles removed was captured in the ring of traps placed outside the enclosures. Thus, all voles that returned home climbed a 0.9-m-high hardware-cloth fence to enter their enclosure of origin. None of the 11 voles had climbed a fence to disperse between enclosures before being removed, and none of the voles returned to an enclosure other than that from which it had been removed.

The average (±1 *SD*) mass of voles that returned home was 30.73 ± 4.1 g, which was not significantly different from the average of all voles removed (t_{10} = 1.82, P = 0.10). Of the 11 voles, five had returned by the trapping session following that of their removal (2 weeks later), and six returned 2–4 weeks after removal. The male that homed twice returned 4 weeks after his first and 8 weeks after his second removal. On average, voles that returned home lost 1.64 ± 3.47 g, or 5.3%, of body mass between the day of removal and the 1st day captured following their return home. This loss of mass, averaging 0.28%/day, was in marked contrast to resident voles of ca. 30 g, which tended to gain ca. 1–2% of their mass each day (Ostfeld and Canham, 1995).

Discussion

We do not know the mechanism by which the 11 voles might have oriented themselves and then navigated home. However, because all of the voles we removed had been born and raised within an enclosure, they could not have been familiar with habitat features at the release sites 1,200 m away (cf. Joslin, 1977; Robinson and Falls, 1965). Navigation by distant landscape or celestial features seems unlikely, because voles tend to travel beneath dense vegetation or litter, which would seriously hinder their view of distant objects. At best, their horizon is a few meters away. Orientation by auditory cues (the enclosures are near a busy road) seems unlikely because the large distance of displacement placed them out of range of road noises. If voles had begun by orienting toward the site of origin using a directional sense, a sun-compass (Fluharty et al., 1976) or magnetic orientation (August et al., 1989), they may have been able to draw close enough to orient toward local cues, such as road noise. Because only 1.3% of the 848 voles returned home, we cannot rule out the possibility that voles departed the release points in random directions, and the few that successfully homed did so by fortuitously choosing the right direction (Fisler, 1962).

Homing behavior by voles has been reported in a few studies. The maximum distance from which displaced California voles (*Microtus californicus*) homed was 183 m (Fisler, 1962). In an extensive study of meadow voles, Robinson and Falls (1965) found that none of >700 animals returned home from >427 m. Rodents such as deer mice (*Peromyscus maniculatus*), which typically occupy home ranges much larger than those of voles, show good homing ability from distances >1,500 m (Teferi and Millar, 1993). Cooke and Terman (1977) found that white-footed mice (*Peromyscus leucopus*) homed well from 335 m, but not from 671 m. Kirkland (1988:83) trapped three meadow voles in a forest clearcut that was "... at least 2.6 km from the nearest appreciable suitable habitat for this species." However, he had no direct evidence regarding distance traveled by the voles. To our knowledge, the 1,200-m homing events we observed represent the longest homing distance described for voles.

Although homing is not synonymous with dispersal, we believe our results indicate the capacity of meadow voles to travel long distances, whether that travelling is toward or away from the home range. More than one-half of the voles required >2 weeks to return home, and, on average, homing voles lost >5% of their body mass. We believe that homing was costly in terms of time and energy. Much of the distance covered by homing voles was through inhospitable habitat (forest, wetland), through suitable habitat (grassy fields) in which they could have settled, and past obstacles

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(stream, roads, and fences). Thus, we believe that the voles that homed were highly motivated to return. The motivation to return may have been enhanced by high-habitat quality in the home enclosures, which was due in part to our management of the populations of voles at levels considerably below carrying capacity (Ostfeld and Canham, 1995). High motivation to return home may have been advantageous for meadow voles in their historical landscapes, in which explorations may rarely have been successful in locating new, suitable patches. Whether dispersing voles experience levels of motivation similar to homing voles is not known. Nevertheless, the physical ability of meadow voles to travel >1 km through unsuitable habitat, and potentially to locate new and suitable patches is evident.

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ES Riparian area management.
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Root biomass allocation in the world's upland forests

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Abstract Because the world's forests play a major role in regulating nutrient and carbon cycles, there is much interest in estimating their biomass. Estimates of aboveground biomass based on well-established methods are relatively abundant; estimates of root biomass based on standard methods are much less common. The goal of this work was to determine if a reliable method to estimate root biomass density for forests could be developed based on existing data from the literature. The forestry literature containing root biomass measurements was reviewed and summarized and relationships between both root biomass density (Mg ha^{-1}) and root:shoot ratios (R/S) as dependent variables and various edaphic and climatic independent variables, singly and in combination, were statistically tested. None of the tested independent variables of aboveground biomass density, latitude, temperature, precipitation, temperature:precipitation ratios, tree type, soil texture, and age had important explanatory value for R/S. However, linear regression analysis showed that aboveground biomass density, age, and latitudinal category were the most important predictors of root biomass density, and together explained 84% of the variation. A comparison of root biomass density estimates based on our equations with those based on use of generalized R/S ratios for forests in the United States indicated that our method tended to produce estimates that were about 20% higher.

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Key words Root biomass · Forests · Aboveground biomass · Root:shoot ratio

Introduction

There is increased interest in estimating the biomass of forests because of their role in regulating the cycling of carbon and nutrients. There are a variety of established methods for estimating the biomass in aboveground tree components, but biomass of root systems is difficult to measure in any forest ecosystem (Sanford and Cuevas 1996). Therefore, our knowledge of biomass allocation to roots lags behind that of its aboveground counterpart. A better understanding of the allocation of forest biomass, and the factors that regulate it, is needed for many applications including assessing change in forest structure, biogeochemical cycles, and various aspects of global change (Brown et al. 1993; Dixon et al. 1994; Sanford and Cuevas 1996).

Various factors are thought to determine the relative biomass allocation between roots and aboveground plant parts, commonly expressed as a root:shoot ratio (R/S) (Klepper 1991). Early studies assumed a static allometric relationship for R/S determinations (Bray 1963). More recent studies indicate that R/S varies with stand/tree age (Gerhardt and Fredriksson 1995), or is a function of tree species and differs between gymnosperms and angiosperms (Cuevas et al. 1991; Rodin and Bazilevich 1967; Sanford and Cuevas 1996). In addition to these biotic factors, several abiotic factors are thought to influence biomass allocation to roots. For example, decreasing soil moisture produces higher R/S (Axelsson 1981; Brown and Lugo 1982; Chapin 1980; Keyes and Grier 1981; Kramer and Kozlowski 1979; Murphy and Lugo 1986; Nadelhoffer et al. 1985; Nihlgård and Lindgren 1977). Soil characteristics, such as nutrient availability (Cavelier 1992; Gower 1987) and texture (Gerhardt and Fredriksson 1995; Keyes and Grier 1981; Vitousek and Sanford 1986; Vogt et al. 1995; Waring and Schlesinger 1985) are also purported to have a sig-

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... particularly in nutrient-poor spodosols (Vitousek and Sanford 1986; Vogt et al. 1995; Waring and Schlesinger 1985). How generally applicable the conclusions reached by the above cited studies are to the world's forests is not clear because most of the studies were done over a relatively narrow range of biotic and abiotic conditions.

The objective of our study was to review data from all major biomes to determine what environmental and ecological characteristics best predict the allocation of biomass to roots. We examined the effects of latitude, tree type, temperature, precipitation, age, soil texture, and aboveground biomass density (ABD) on the allocation of biomass to tree roots. Our approach was to (1) review and summarize the literature, (2) test various statistical relationships between total RBD, including both live and dead roots, and R/S as dependent variables against the various edaphic and climatological independent variables, singly and in combination, and (3) develop equations that may be used to estimate RBD and associated uncertainty given ABD and data on one or more of the other factors. We were particularly interested in predicting RBD from ABD because of issues related to the total carbon pools in forests. Forest inventory data are useful for reliably estimating ABD, as has been done for many regions of the world (Birdsey 1992; Brown et al. 1993; Brown and Gaston 1995; Kurz et al. 1992). However, forest inventories do not provide a direct way of estimating RBD, so other means must be sought.

Methods

Building the database

We reviewed the literature to obtain sources that reported root and aboveground biomass in forest ecosystems. All data were critically reviewed using these criteria:

1. Did the methodology sufficiently indicate that all root biomass was quantified?
2. Were biomass densities reported on an oven dry weight basis?
3. Did the studies adhere to standard methods leading to comparable estimates?

In general, standard methods included spatially distributed soil cores or pits for fine to medium roots and partial to complete excavation and/or allometry for coarser roots. Most studies did not report or quantify root biomass by size classes. Further, because authors generally did not distinguish between live and dead, total RBD was reported as the sum of both live and dead roots.

Root sampling depth was either ≥ 100 cm (15%), from 40 to < 100 cm (20%), or unknown (65%). Although many sources did not specify depth, the studies were designed to quantify total root biomass. Therefore, we assumed that the investigators sampled to a depth to capture practically all the roots.

Although the sites were not randomly distributed and did not equally represent all latitudinal zones, we feel that they represent a wide range of environmental conditions. The site characteristics of the data set showed a broad range of biotic and climatic conditions, with trees ranging in age from 2 to 350 years, mean annual precipitation from 269 to 4000 mm, and mean annual temperature from −3.4 to 28°C (Table 1). Most studies were done in the temperate zone (44%), followed by the boreal (32%) and tropical zones (24%). Information on soil texture was available for about half of the sites. Further, the data came from 25 countries on six continents.

We excluded data from forested wetlands, i.e., mangroves, bogs, and swamps. We also excluded data from sites subject to recent harvesting activities that likely reduced ABD but not RBD (e.g., coppiced stands). The resultant total number of records was 165 (Table 1) and the sample size in the various analyses ranged from 68 to 165 because some records contained certain data (e.g., temperature), but not others (e.g., age).

We also sought to determine trends and relationships between the fine:total RBD ratio and factors which may influence this ratio. Approximately 25% of the data records contained explicit estimates of fine root biomass. Sources used various definitions of fine roots, the most frequent being all roots < 5 mm diameter. We examined the 27 estimates so defined.

Based on current understanding, the major factors influencing biomass allocation to roots appear to be latitude, tree type, age, precipitation, temperature, temperature:precipitation ratio [T/P, an index of water availability (Brown and Lugo 1982)], and soil texture. In many cases latitude and longitude were not specified, but enough information was given (e.g., country) to place sampling sites in a latitudinal zone, generally defined here as: tropical forests 0–25°, temperate forests 26–50°, and boreal forests ≥ 51° (Dixon et al. 1994). Tree type was coarsely categorized as either angiosperm (generally broadleaf) or gymnosperm (generally coniferous). Age (years) of the dominant trees, when given by the sources, was noted. Mean annual temperature (°C) and total mean annual precipitation (mm) were used in the analyses, along with ratios of temperature to precipitation (Brown and Lugo 1982).

Soils were classified into three texture classes: coarse, medium, and fine, based on FAO (1971–1981). These were assigned by using descriptions in the data sources and a standard soil texture chart. This was accomplished using either the percent composition of sand, silt, and clay (if reported) or by aggregation of subclasses.

Statistical analysis

For practical purposes of this global synthesis, we assumed that all field observations were random and independent. In some cases where allometric regression equations were used for estimating ABD and coarse RBD based on tree diameter alone, this may not be strictly the case. As part of the process of developing predictive regression equations, we tested the standard assumptions of linear regression (Neter et al. 1989) as applied to these data. Histograms and scatterplots of the variables used in our analysis revealed that transformations were required for ABD, RBD, age and R/S. A natural log transformation was used to help stabilize the nonconstant variance of ABD and RBD and to help correct skewness of the age and R/S distributions (Ramsey and Schafer 1996). Temperature, precipitation, and their ratios did not require transformation.

Both R/S (a variable derived from total RBD and total ABD) and RBD were tested for statistical relationships with a series of biotic and abiotic site characteristics. General descriptive statistics and the Student-Newman-Kuehl multiple comparison procedure (Kuehl 1994) were applied to the discrete, or categorical, site characteristics (latitudinal zone, soil texture index, and tree type) with R/S as the response variable at an $\alpha = 0.05$ level of significance. Both the continuous and discrete independent variables were then separately fit to R/S using simple linear least squares regression (Myers 1990).

Following the examination of R/S predictability, we tested our ability to estimate RBD directly from ABD and other climatic and edaphic factors with a forward stepwise least squares regression algorithm (Myers 1990). A set of *a priori* two-way interactions was included in this analysis with the stipulation that no two-way in-

Table 1 Site descriptions and data sources. Each source represents one or more data points (electronic version of complete data base available from authors). *ABD* aboveground biomass density, *RBD* root biomass density (values in parentheses are the ratio of fine root (< 5 mm diameter) biomass density to total *RBD*), *MAT* mean annual temperature, *MAP* mean annual precipitation, *M* mature forest, but specific age not reported. Soil texture *C* coarse, *ME* medium, *FI* fine), *N/A* data not reported

Country	ABD (Mg/ha)	RBD (Mg/ha)	MAT (°C)	MAP (mm)	Age (year)	Texture	Forest type[a]	Source
Tropical ≤ 25° lat.								
Malaysia	431	43	25	1810	M	ME	Lowland rain	Bandhu 1973; Kira 1990
Zaire	123	32	24.5	1700	18	N/A	Moist	Bartholomew et al. 1953
Venezuela	182	128	26	3600	M	CO	Tall bana woodlands	Bongers et al. 1985
Brazil	406	69 (0.58)	27.2	2771	M	ME	Lowland rain	Brunig and Klinge 1976; Fittkau and Klinge 1973; Klinge 1973, 1976; Klinge et al. 1975; Klinge[b]
Brazil	5–88	1–9	25	1750	3–8	FI	Evergreen rain	Buschbacher et al. 1988; Uhl et al. 1988
Mexico	74	31	23.5	707	M	ME	Dry deciduous	Castellanos et al. 1991
Panama	13	2	25	2000	2–5	N/A	Moist secondary	Ewel 1971
Puerto Rico	223	60	19.7	3725	M	N/A	Lower montane rain	Frangi and Lugo 1985
Ghana	233	54	25	1650	40	N/A	Moist semideciduous	Greenland and Kowal 1960
Venezuela	348	56 (0.44)	12.6	1500	M	N/A	Montane humid	Grimm and Fassbender 1981
Jamaica	229	55	15.5	2500	M	N/A	Upper montane	Grubb and Tanner 1976; Tanner 1980
French Guyana	323	42	N/A	N/A	M	N/A	Lowland rain	Humbel 1978; Lescure et al. 1983
Ivory Coast	513	51 (0.56)	26.2	2095	M	CO	Lowland rain	Huttel 1975; Lemee[b]
Malaysia	81	6	25.5	4000	12.5	ME	Evergreen wet, secondary	Koopmans and Andriesse 1982
Sri Lanka	32	17	28	1050	32	ME	Mixed evergreen and dry deciduous	Koopman and Andriesse 1982
Puerto Rico	32–125	6–22 (0.25–0.71)	22.3	2330–3920	5.5–60	FI	Lowland wet secondary and paired plantations	Lugo 1992
Surinam	415	66	25	2250	M	N/A	Lowland rain	Odier 1980, cited in Klinge and Herrera 1983
Puerto Rico	198	65	22.3	3920	M	N/A	Lower montane rain	Ovington and Olson 1970
Brazil	97–394	32–60	25	2300	8.5–M	CO	Lowland wet mature and plantation	Russell 1983
Venezuela	58–255	10–59	25	3500	11.5–M	N/A	Lowland moist mature and secondary	Saldarriaga et al. 1988
Puerto Rico	226	75 (0.03)	22.3	3500	M	FI	Wet tabonuco	Scatena et al. 1993
Venezuela	20–34	3–4	25	3500	3–5	ME	Lowland young successional rain	Uhl 1987
Temperate · 26–50° lat.								
United States	12	3	1.5	1000	350	CO	Subalpine	Arthur and Fahey 1992
Australia	312	75	11.2	982	51	N/A	Eucalyptus	Attiwill[b]
Czechoslovakia	161	76	10	570	60	N/A	Fageto-Quercetum	Bielcupsky[b]
Spain	160	62	9.5	870	75	ME	Montane Mediterranean sclerophyllous	Canadell and Roda 1991
Canada	117–313	37–78 (0.08–0.12)	N/A	N/A	70–78	CO-N/A	Subalpine coniferous	Comeau and Kimmins 1989
United States	130	36 (0.23)	14.5	1390	43	ME	Mesic deciduous hardwood	Cox et al. 1978
Belgium	121	35	8.5	952	80	N/A	Mixed oak	Duvigneaud and Galoux[b]
United States	386–430	93–99 (0.01–0.06)	9.4	1440	45	N/A	Coniferous lowland	Edmonds 1980, 1987; Vogt 1991; Vogt et al. 1983, 1987

Table 1 (continued)

Country	ABD (Mg/ha)	RBD (Mg/ha)	MAT (°C)	MAP (mm)	Age (year)	Texture	Forest type[a]	Source
India	27–241	14–67	8.0–12.1	2170	N/A	ME-CO	Deciduous [illegible]	[illegible]
United States	174	31	9.8	1360	36	N/A	Douglas fir plantation	[illegible]
Canada	122–462	28–106	4	1242	84–212	N/A	Spruce	Gordon[b]
United States	500–982	105–206 (0.05–0.09)	8	2300	M	ME	Douglas fir	[illegible] et al. [illegible]
United States	53–447	23–139 (0.09–0.40)	5.4	2700	23–180	ME	Cold, wet subalpine Pacific silver fir	[illegible]
United States	90	22 (0.14)	15.5	1160	N/A	N/A	Warm coniferous loblolly pine plantation	[illegible]
United States	109–138	33–34	13.3	1400	30–55	N/A	Oak-hickory, pine, chestnut oak, yellow poplar	[illegible]
Hungary	222	36	9.9	582	66.5	N/A	Oak woodland	[illegible]
United States	248–467	57–89 (0.05–0.18)	10.2	1000	40	ME-CO	Lowland coniferous	[illegible]
United States	93	22	15.6	1150	15	ME	Pine plantation	[illegible]
Japan	192	64	4.2	1455	290	N/A	Sub-alpine coniferous	[illegible]
France	262	50	12.4	987	150	N/A	Mediterranean evergreen oak	[illegible]
United States	266	66	6.9	777	130	N/A	Oak-prairie border	[illegible]
Poland	243	49	7.8	729	100	N/A	Oak-hornbeam	[illegible]
Former USSR	446	67	17.3	1856	20–40	N/A	Taiga	[illegible]
United States	276	28	N/A	N/A	N/A	N/A	Deciduous riverine	Mulholland [illegible]
United States	–[c]	–[c]	N/A	N/A	110	N/A	*Pinus contorta*	Pearson et al. [illegible]
Spain	204	53	8	802	90	N/A	Pine-holly	[illegible]
Japan	93–169	23–37	10.2–11.3	1467–1806	20–39	N/A	Pine & larch plantations	Satoo[b]
Japan	292	44	11.3	2788	150	N/A	Beech	Shidei[b]
India	92–640	21–146	9.3–23	800–3500	52-M	ME-FI	Monsoon mixed deciduous evergreen	Singh et al. [illegible]
United States	175	35	9.8	1370	34	CO	*Abies rubra*	Turner et al. [illegible] Stoutz [illegible]
Czechoslovakia	314	47	N/A	N/A	N/A	N/A	Deciduous riverine	Vyskot 1976
United States	26	8	11.6	970	N/A	ME	Mediterranean climate pygmy forest	Westman and Whittaker [illegible]
Canada	75	24	0.5	384	N/A	N/A	Aspen	Wilson 1959
United States	147–210	32–42	N/A	N/A	20–50	FI	Rain deciduous	Zavitkovski and Barnes [illegible]
Boreal – ≥ 51° lat.								
Former USSR	–[c]	–[c]	N/A	N/A	N/A	N/A	Taiga	Alexeyev and [illegible]
Sweden	201	34 (0.24)	7.5	644	158	FI	Mixed deciduous woodland	Andersson 1971
Former USSR	218	65	6.1	1063	70	N/A	Luzulo-gagetum	Dylis 1971
Germany	275	36	N/A	N/A	122	N/A	*Fagus sylvatica*	Ellenberg
Former USSR	251–307	65–126	6	537	80–250	ME	Quercetum Pilosicaricosum & Tilieto-quercetum Aegopodiosum	Gorynina[b]
Finland	102	38	0	500	260	N/A	Hylocomium-myrtillus	Havas[b]

Table 1 (continued)

Country	ABD (Mg/ha)	RBD (Mg/ha)	MAT (°C)	MAP (mm)	Age (year)	Texture	Forest type[a]	Source
Former USSR	206	74	3.4	640	110	ME	Taiga. Picetum-myrtillosa *Oxalidosum*	Karpov[b]
Former USSR	25–209	6–48	2.2	650	22–138	N/A	Myrtillosum	Kazimirov and Morozova[b]
Sweden	226–315	36–44	6–7	650–900	90–100	N/A	Beech, Deschampsia type	Lindgren and Nihlgard[b]
Sweden	308–324	52–58	7	800	60–87.5	N/A	Beech, Stellaria-larmium & planted spruce	Nihlgard[b]
UK	62–164	17–49	7.7–N/A	762–N/A	23–55	FI-N/A	Coniferous plantations & deciduous	Ovington 1962
Former USSR	133	41	−1.2	499	125	N/A	Northern taiga. Picetum Hylocomiosum	Rednaeva et al.[b]
UK	128	76	7.8	1115	80	N/A	Mixed deciduous	Satchell[b]
Former USSR	61–207	19–43	N/A	N/A	20–67	N/A	Deciduous	Smirnova and Gorodenskaya [illegible]
Denmark	221	44	7.1	660	87.5	N/A	Beech	Thamdrup[b]
United States	231	51	−3.4	269	130	N/A	Conifer	Van Cleve[b]
Netherlands	273	41	8.6	780	140	N/A	Oak	Van Der Drift[b]

[a] As reported by the source authors
[b] Cited in DeAngelis et al. 1981: names of International Biological Programme investigators
[c] Only R/S ratio reported

Results and discussion

Root:shoot ratios

The range in ABD (4.7–982.5 Mg ha^{-1}), RBD (1.2–206.3 Mg ha^{-1}), and R/S (0.05–0.70) varied by orders of magnitude. Examination of the basic descriptive statistics for the discrete predictive variables showed that the overall mean R/S was approximately 0.26 and the tendency was for values to be between 0.20 and 0.30, independent of latitude, soil texture, or tree type (Table 2). Aside from the slight difference in mean R/S for tropical sites, none of the three discrete predictive variables (latitudinal zone, soil texture, tree type) showed differ-

Table 2 Root:shoot biomass ratios (R/S) by latitudinal zone, soil texture, and tree type. Mean, standard deviation (SD), coefficients of variation (% CV), median, lower (*LQ*, 25%) and upper (*UQ*, 75%) quartiles, and sample size (*n*) are also given. The sample size varies by characteristic because of the lack of data for that characteristic in the original source. Significant differences in means are shown by different *lower case letters* (Student-Newman-Kuehl test: $\alpha = 0.05$)

	Mean (SD)	% CV	Median	LQ	UQ	*n*
LATITUDINAL ZONE						
Tropical	0.24 (0.14) a	58	0.21	0.14	0.31	39
Temperate	0.26 (0.07) b	27	0.24	0.22	0.28	73
Boreal	0.27 (0.10) b	37	0.25	0.22	0.30	53
SOIL TEXTURE						
Coarse	0.29 (0.17) a	58	0.26	0.20	0.33	10
Medium	0.27 (0.11) a	41	0.25	0.21	0.36	34
Fine	0.24 (0.11) a	46	0.23	0.20	0.27	24
TREE TYPE						
Angiosperm	0.25 (0.12) a	48	0.24	0.17	0.31	102
Gymnosperm	0.26 (0.07) a	27	0.24	0.22	0.29	63

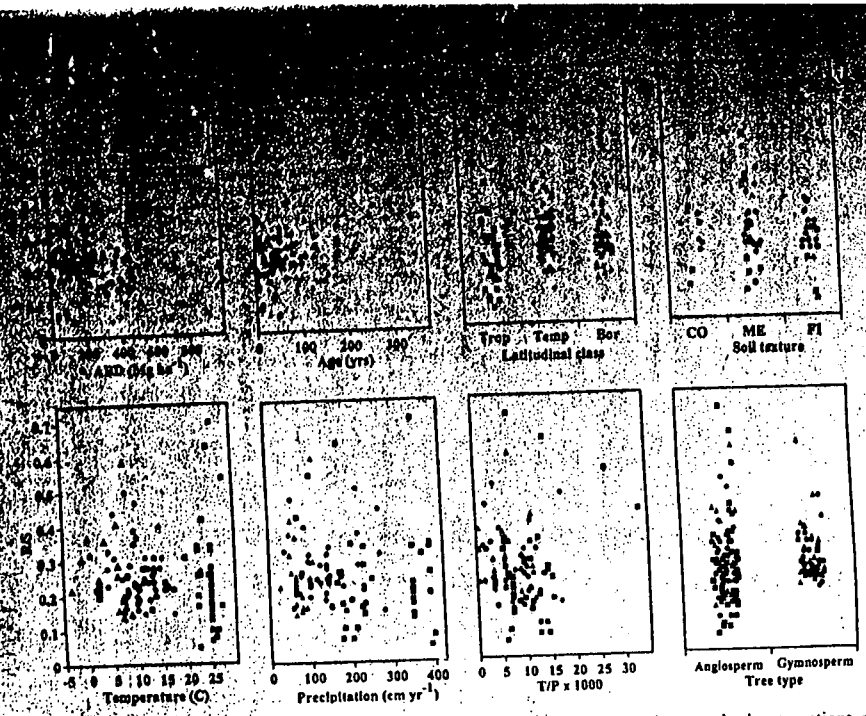

Fig. 1. Scatterplots of root:shoot ratios (*R/S*) versus aboveground biomass density (*ABD*), age, latitude, soil texture, mean annual temperature (*T*), mean annual precipitation (*P*), *T/P* (°C/mm) ratios, and tree type. The discrete variables (latitudinal zone, soil texture, and tree type) are plotted in a staggered manner for clarity

ences in mean R/S with a change in parameter values. A multiple comparison test indicated that the R/S in tropical sites was significantly lower than in the other latitudinal zones. As might be expected, the R/S was higher in coarse soils than in the other soil texture classes; although this trend was not statistically significant. The coefficient of variation was higher in the tropics than in the other two zones, reflecting a greater heterogeneity of forest types. Similarly, the higher coefficient of variation for angiosperm R/S, despite the larger sample size (Table 2) reflects the greater heterogeneity of these tree types compared to gymnosperms.

Scatterplots of R/S versus eight possible predictive variables showed no apparent relationships with any of the independent variables tested (Fig. 1). Simple linear regressions of transformed and untransformed data revealed that none of the independent variables alone exhibited predictive value for R/S. Natural log transformations aided in meeting standard assumptions of linear regression and were thus used in such analyses. Although the model parameters for ABD, latitudinal zone, and mean annual temperature were statistically significant ($\alpha = 0.05$) in explaining the variation in R/S, the highest coefficient of determination was an adjusted R^2 of 0.05 for latitudinal zone, indicating little practical significance. Age, soil texture index, tree type, temperature:precipitation ratio, and mean annual precipitation, alone or in combination, were not statistically significant ($\alpha = 0.05$) in explaining variation in R/S.

Root:shoot ratios are routinely used to partition plant biomass into aboveground and root component (e.g., Klepper 1991; Russell 1977). Our lack of a predictive relationship between R/S and eight biotic and abiotic factors (Fig. 1) was in contrast to previous conclusions (e.g., Rodin and Bazilevich 1967). Our results also contrast with those of Körner (1994) who reviewed 73 studies on biomass partitioning in temperate and boreal zone forests. He reported R/S for conifers of 0.24, which is higher than the 0.19 he reported for deciduous trees. By comparison, Cannell (1982) reported R/S of 0.26, 0.25, and 0.31 for coniferous, deciduous, and tropical forests, respectively.

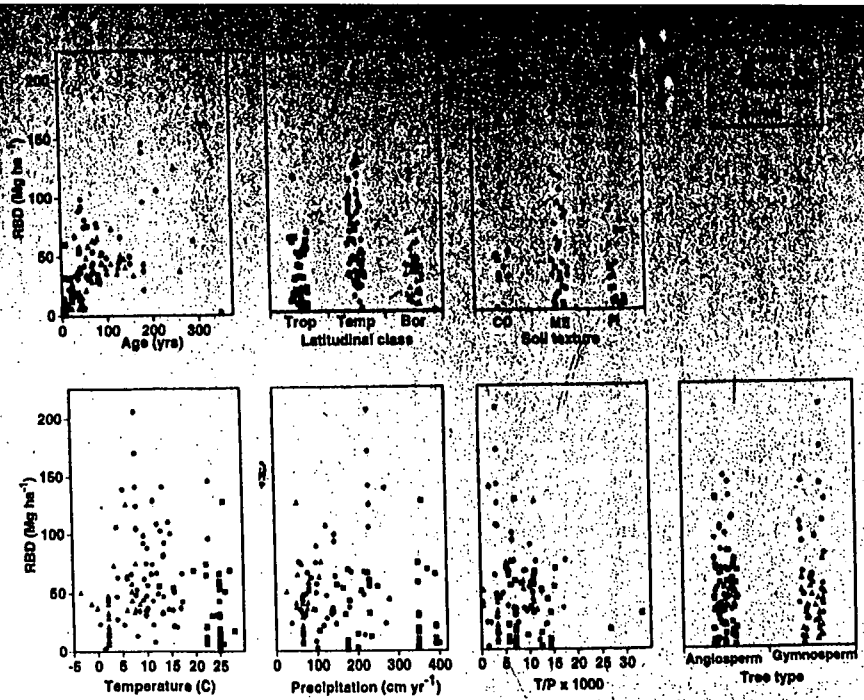

Fig. 2 Scatterplots of root biomass density (*RBD*) versus age, latitude, soil texture, mean annual temperature (*T*), mean annual precipitation (*P*) *T/P* (°C/mm) ratios, and tree type. The discrete variables (latitudinal zone, soil texture, and tree type) are plotted in a staggered manner for clarity

Root biomass density

Scatterplots of RBD versus seven possible predictive variables showed a possible relationship with age and no apparent relationships with any other independent variables (Fig. 2). Forward stepwise least squares linear regression of the various site characteristics revealed that ABD alone accounted for 83% of the variation in RBD (Fig. 3). After accounting for ABD, age and latitudinal zone also significantly improved the predictive utility of RBD (Table 3). When age was included along with ABD, the adjusted R^2 increased slightly, to 0.84. The combination of ABD and latitude also resulted in a slightly increased adjusted R^2 value (Table 3). No other combinations were significant. Examination of six interactions, chosen *a priori* (ABD × age, ABD × latitudinal zone, ABD × mean annual temperature, age × mean annual temperature, ABD × mean annual precipitation, and age × mean annual precipitation) revealed no significant effects.

While highly significant, variability was large around RBD estimates calculated from ABD, producing wide 95% prediction bands (Fig. 3). For example, mean estimates of RBD from Eq. 1 (Table 3) at ABDs of 200 and 400 Mg·ha^{-1} are 46 and 87 Mg·ha^{-1}, respectively. The corresponding upper and lower 95% prediction bands are 24 and 87 and 45 and 165 Mg ha^{-1}, respectively. Another way of looking at this variability is that the true RBD may be up to 91% higher or 47% lower than the mean estimate. This variability is likely the result of not only differences in sampling methodology, but also the natural variability of biological systems. Additionally, our equation was developed from the data available in the literature, not from a systematically, statistically rigorous experimental design executed with the same sampling methods. We expect that if data points were proportionally derived in the same manner from all conditions of latitude, soil texture, age, ABD, tree type and climatic factors, the prediction bands would be narrower. We would, however, also expect the prediction bands to deviate from the mean more at older ages (= larger ABDs) because of the inherent hetero-

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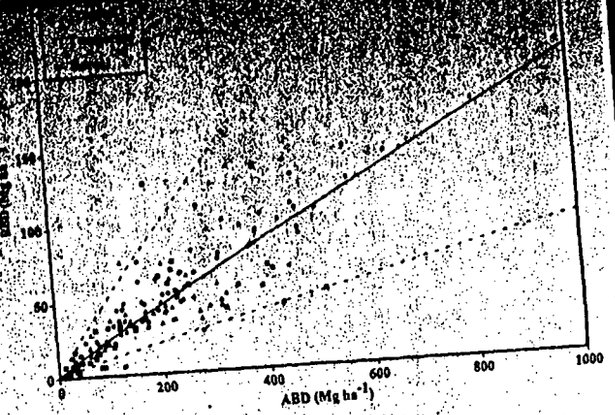

Table 3 Regression equations for predicting root biomass density (RBD). All equations are of the form Y (RBD, Mg/ha) = exp [intercept + $a(\ln A) + b(\ln B) + c(C) + d(D)$]. ($A$ ABD (Mg/ha), B age (year), C 1 in temperate sites, both C and D 0 in tropical sites, and 0 in temperate sites and 0 in boreal sites, D 1 in boreal sites and 0 in temperate sites). Equation 1 estimates RBD based on aboveground biomass density (ABD) only, Equation 2 adds age, and Equation 3 includes ABD and latitudinal zone. The standard errors of regression coefficients (SE) are in parentheses. All model parameters were statistically significant (α = 0.05) in accounting for variation in RBD

Equation	Intercept	a	b	c	d	n	Adjusted R^2
Equation 1	−1.0850	0.9256	N/A	N/A	N/A	151	0.83
SE	(0.177)	(0.035)	–	–	–		
Equation 2	−1.3267	0.8877	0.1045	N/A	N/A	109	0.84
SE	(0.203)	(0.053)	(0.044)	–	–		
Equation 3	−1.0587	0.8836	N/A	0.2840	0.1874	151	0.84
SE	(0.175)	(0.036)	–	(0.079)	(0.084)		

getelty of larger and older stands. It should also be noted that estimates from our equations have measures of variability and most reported RBD estimates from R/S ratios do not.

As a test of practical significance, we ran the three equations (Table 3) with hypothetical values of the predictive variables. We found that for each doubling of ABD, the estimated mean RBD increased by a factor of 1.9 in Eq. 1. When we maintained a fixed level of ABD and doubled age in Eq. 2, the mean RBD increased by 8%. Although Eq. 2 only marginally increased the adjusted R^2 over Eq. 1 (Table 3), the effect of adding tree age was of both practical and statistical significance. Holding ABD constant, the estimated mean RBD from Eq. 3 was 33% higher in the temperate latitudes than in the tropics, 10% higher in the temperate latitudes than in the boreal latitudes, and 21% higher in the boreal latitudes than in the tropics.

Multicollinearity appeared not to be a problem in Eq. 2 and 3, as evidenced by the relative stability of both parameter estimates and their associated standard errors (Table 3). For example, the three parameter estimates for ABD were similar, as were their standard errors.

Our results generally agree with Bray (1963) who suggested that biomass allocation to roots can be estimated based on ABD allometries. Our finding that soil texture had no predictive value for RBD contrasted with others (Sanford and Cuevas 1996; Vitousek and Sanford 1986) who indicated that coarse tropical soils produce greater RBD. Our larger data base may be more representative of global forests than those of either Sanford and Cuevas (1996) or Vitousek and Sanford (1986). Our analysis also contrasts with other studies indicating that available soil moisture is strongly correlated with root biomass allocation, with water stress causing greater biomass allocation to roots (Kramer and Kozlowski 1979; Murphy and Lugo 1986; Sanford and Cuevas 1996). This is consistent with the theory that trees should allocate more resources to roots on infertile sites to optimize nutrient uptake (Bloom et al. 1985). Allocation of biomass to roots versus shoots on fertile sites has not been well documented (Vitousek and Sanford 1986).

The ratios of fine:total RBD among the 27 data records ranged from 0.01 to 0.71, with a mean of 0.23 (Fig. 4). Angiosperm fine root ratios were generally greater than 0.2, while those for gymnosperms were less than 0.2, with one exception. Fine root ratios also appear to be high at low RBDs, decrease rapidly as RBD increases, and then level at RBDs greater than 75 Mg

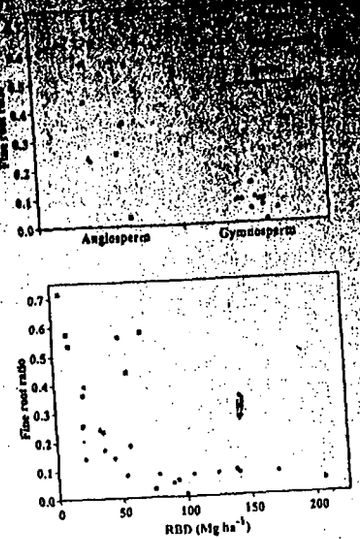

Fig. 4 Scatterplots of fine root ratios (biomass density of roots < 5 mm diameter to total RBD) versus tree type and root biomass density. Tree type, a discrete variable, is plotted in a staggered manner for clarity

ha^{-1} (Fig. 4), a trend in close agreement with Kurz et al. (1996).

Most of the sites with high fine root ratios were in tropical latitudes. This may be due to the continual growing season, tree architecture, water stress, or soil nutrient status (e.g., exchangeable and total nutrient concentrations, pH, organic matter content, trace nutrient concentrations, and cation exchange capacity). Thus, although total RBD may not relate to soil moisture, texture, or nutrients, fine roots, which are purported to be active in nutrient and water uptake, may.

Implications for estimates of carbon storage in the world's forests

Estimates of RBD are fundamental to understanding carbon storage and the biogeochemical dynamics of forest ecosystems. At the stand level, combinations of soil cores or pits and species-specific regression equations are often developed to estimate fine and coarse RBD, respectively. At larger spatial scales, average R/S ratios are commonly developed from the literature to quantify RBD at regional scales when only ABD is known (e.g., Birdsey 1992; Brown et al. 1993; Schroeder and Winjum

[illegible] estimates of ABD [illegible] Mg ha⁻¹ [illegible] RBD of 12–30 Mg ha⁻¹ [illegible] Table [illegible] for softwood, yielding RBD of 12–30 Mg ha⁻¹ [illegible] forests. The resulting corresponding R/S values of 0.24–0.26 for eastern and 0.23–0.25 for western forests. These are somewhat higher than those used by Birdsey (1992), particularly for softwood stands. We believe that these differences are large enough to urge the adoption of the statistically stronger regression equations developed in the present paper.

A recent report focused on boreal and temperate forest RBD estimation from ABD alone, without considering edaphic and climatic variables, and reported separate regression equations for hardwood and softwood species (Kurz et al. 1996). Although our analysis showed no differences between free types, and our Eq. 1 had a higher R^2 value [0.83 for ours versus 0.71 and 0.77 for softwood and hardwood species, respectively, in Kurz et al. (1996)], results were similar to each other. Kurz et al. (1996), while not reporting prediction bands, estimated 42 and 46 Mg ha^{-1} RBD for hardwoods and softwoods, respectively, at an ABD of 200 Mg ha^{-1}. The corresponding estimate from our Eq. 1 is 46 Mg ha^{-1}. At the same ABD of 200 Mg ha^{-1}, our Eq. 3 estimates a temperate latitude RBD of 50 Mg ha^{-1} and a boreal latitude RBD of 45 Mg ha^{-1}.

The equations presented here can be used to make point and interval estimates of root biomass allocation in the world's upland forests based on knowledge of aboveground biomass, age, and latitude. Use of these equations in unique forest ecosystems, such as wetland forests, may not be appropriate because of additional overriding site or climatic characteristics. However, this analysis clearly indicated that RBD could be estimated directly, rather than by using R/S ratios.

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IMPROVING THE SUCCESS OF WETLAND CREATION AND RESTORATION WITH KNOW-HOW, TIME, AND SELF-DESIGN

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Abstract. The creation and restoration of new wetlands for mitigation of lost wetland habitat is a newly developing science/technology that is still seeking to define and achieve success of these wetlands. Fundamental requirements for achieving success of wetland creation and restoration projects are: understanding wetland function; giving the system time; and allowing for the self-designing capacity of nature. Mitigation projects involving freshwater marshes should require enough time, closer to 15–20 yr, than 5 yr, to judge the success or lack thereof. Restoration and creation of forested wetlands, coastal wetlands, or peatlands may require even more time. Ecosystem-level research and ecosystem modelling development may provide guidance on when created and restored wetlands can be expected to comply with criteria that measure their success. Full-scale experimentation is now beginning to increase our understanding of wetland function at the larger spatial scales and longer time scales than those of most ecological experiments. Predictive ecological modelling may enable ecologists to estimate how long it will take the mitigation wetland to achieve steady state.

Key words: achieving successful wetland mitigation; creating wetlands; ecological engineering; ecological modelling; freshwater marshes; functional analysis of wetlands; mitigation of wetland loss; Olentangy River Wetland Research Park, Ohio; wetland succession.

INTRODUCTION

[redacted]

Success in the general sense here means the establishment of a biologically viable and sustainable wetland ecosystem. Some call a wetland a success when it replaces the functions lost in a wetland that is being replaced; others would gauge success of a created or restored wetland against natural reference wetlands in the region. Unfortunately, there has been little formal published follow-up of the poorly named (see Renner 1994) "mitigation wetlands" that are constructed to replace wetlands that are unavoidably lost and there are few satisfactory methods for assessing replacement of the functions lost with the original wetland (Mitsch and Gosselink 1993). Regulators and consultants have chosen to use simple indicators of "success" to expedite the process and to keep monitoring costs low. Normally 3–5 yr of simple once- or twice-per-year monitoring is required, with easily measured parameters such as plant lists, animals witnessed, and percentage vegetation cover as the overall indicators. Assessing success is then based on comparing these easily measured parameters with a relatively simple set of criteria that were stipulated in the original permit for the project; these criteria may or may not accurately reflect wetland function.

After reviewing pertinent literature, we discuss three fundamental requirements for achieving success of wetland creation and restoration projects: understanding wetland function, giving the system time, and appreciating the idea of self-design. Our hypothesis is that most attempts to measure and achieve success of created and restored wetlands—caused by a lack of application of good wetland science to the problem and compounded by the existing construction-schedule-driven process—are flawed because of misunderstanding or misapplication of these factors. We then argue that ecosystem-level research and ecosystem modelling may provide better guidance on when created and restored wetlands can be expected to comply with criteria that measure their success.

STUDIES ON WETLAND MITIGATION SUCCESS

[redacted] improvement in the building of wetlands. Maguire (1985) used area, vegetative cover, and implementation of permit conditions to estimate mitigation success in Virginia and found that only 50% of 23 mitigation wetlands [redacted] the mitigation project had not been implemented. An additional study by Reimold and Cobler (1985) conducted for the U.S. Environmental Protection Agency (EPA) gave similar results. Glubiak et al. (1986) and Quammen (1986) both suggested the need for better management of mitigation wetlands. Additionally Glubiak et al. (1986) predicted that while the protection

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[2] For reprints of this group of papers on wetland mitigation, see footnote 2, page 33.

[illegible] it should.

[illegible] involved in wetland [illegible] that mitigation was [illegible] (1986), while others suggested that more research needed to be done and that, if not properly conducted, a wetlands mitigation project could easily fail (Race 1986). Kusler and Groman (1986) raised concerns about the granting of Section 404 permits to contractors when alternative sites are available. Many questions and issues were raised by Kusler and Groman (1986) and Golet (1986) regarding permitting processes and the actual success of wetland mitigation projects. Their major issues were: When should destruction/damage and subsequent creation/restoration be permitted? How is the damage to the original system measured and how is the creation/restoration deemed sufficient? Golet (1986) suggested that under no circumstances should damage to a wetland be allowed unless there is absolutely no alternative.

[redacted] this concept has already been codified in several parts of the country. For example, in Massachusetts, vegetation cover of ≥75% is the major success criterion, even if vegetation composition is very different [redacted] original wetland (Jarman [redacted]

Recent investigations of wetland mitigation projects, as a greater number of mitigation sites have become available for scrutiny, generally reinforce the early concerns. For example, Erwin (1991) found that, of 40 mitigation projects in south Florida involving wetland creation and restoration, only about half of the required 430 ha of wetlands had been constructed and that 24 of the 40 projects (60%) were judged to be incomplete or failures. The most significant problems identified with created wetlands were improper water levels and hydroperiod. Sifneos et al. (1992) collected information from permits on Louisiana, Alabama, and Mississippi wetland mitigation projects and found that in Louisiana *(their primary area of interest)* only 8% of areas impacted by dredge-and-fill activity was compensated for, and >50% of the areas receiving permits covered <0.4 ha. Additionally, only 10% of the mitigation wetlands were monitored by at least one site visit. The lack of standardized record-keeping from state to state made the study difficult. The study suggests that follow-up monitoring and information on wetland *functions* be required in future permit decisions. Kentula et al. (1992) investigated several mitigation wetlands in Oregon and Washington and found a net loss in wetland area of 43% for Oregon and 26% for Washington. Data were either incomplete or of poor quality and up-to-date standardized databases were recommended. In a similar study, but without field checks, Holland and Kentula (1992) examined >300 Section 404 permits issued in California from 1971 to 1987 and found that while 1260 ha of compensatory mitigation (wetland creation, restoration, or preservation) had been required for impacts to 1180 ha of wetlands over that period, there was little follow-up of the permits and fewer than one-third (31.5%) required any field monitoring. Confer and Niering (1992) found that when comparing five created freshwater marshes with five nearby natural ones, the created marshes generally had greater water depth and thus more open water. They state that most of their created wetlands were highly dependent on highway runoff as a water source. Roberts (1993), quoting several ecologists, summarizes the skepticism by calling wetland trading "a loser's game."

Improving the Odds of Wetland Success

We propose three general concepts that will need attention of those involved in wetland mitigation if we are truly going to address the issue of creating and restoring viable wetland ecosystems: (1) Understand *wetland function; (2) Give the system time; and (3)* Allow for the self-designing capacity of nature. These points are discussed in detail below.

Understand wetland function

Mitsch and Cronk (1992) proposed that the "know-how" of building and restoring wetlands is based on an empiricism with little scientific backing, and is learned and relearned every time a new wetland is built. Wetland restoration and creation are relatively new fields and few engineers are trained in ecology and few ecologists have any experience in engineering methods. Engineers, consultants, scientists, and landscape architects can, and frequently do, claim to be experts with little experience or little knowledge of wetland ecology; without any certification standards for individuals involved in wetland creation and restoration, projects are often carried out by organizations and individuals not well versed in wetland ecology. A relatively high number of "failures" of mitigation wetlands can be attributed to a general lack of understanding of first principles of wetland science.

For example, an understanding of wetland hydrology as the fundamental forcing function of wetlands is well understood conceptually (Mitsch and Gosselink 1993) yet not always put into practice by many of those involved in wetland mitigation. The importance of hydrology is discussed in detail in a companion paper by Bedford (1996). Erwin (1991) pointed out that a number of Florida wetlands were considered failures in his Florida study because they lacked suitable hydrology. In so-called "on-site mitigation," wetlands are developed in watersheds near the wetlands being drained or lost; their success is often problematic because of the usual proximity of the mitigation project to a human-altered landscape and the accompanying changes in hydrologic conditions. In these settings, created and restored wetlands can be subjected to "flashy" streams and human-regulated hydrologic conditions. In urban and suburban settings, floods are often greater and occur more quickly after precipitation; low-flow conditions are drier than in a "natural" hydrology (Dunne and Leopold 1978). Both of these conditions lead to *generally greater water level fluctuations compared to* those in more natural settings (Fig. 1). Unpredictable and rapidly fluctuating hydrology can lead to washouts, scouring, planting failure, and animal and macroinvertebrate emigration, leading to decreased biodiversity and even loss of water quality function.

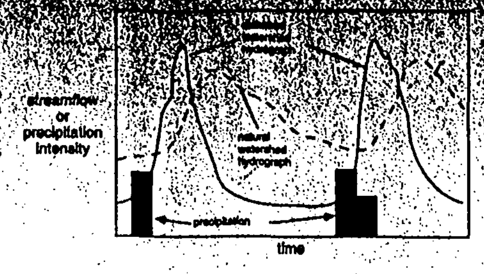

FIG. 1. Comparison of a hypothetical stream hydrograph in a natural watershed vs. one from a highly disturbed urban or suburban watershed. Placing the wetland in either of these two watersheds would probably lead to significantly different wetland structure and function.

Give the system time

A flaw in the measurement of mitigation wetland success is the limited amount of time that regulators and the land development process allow for newly created wetlands to develop before passing judgment. The legal and economic necessities seem to dictate the ecological patterns of nature, encouraging "quick-fix" wetlands while *not allowing for the stochasticity of* nature. Engineers have long recognized the probabilistic nature of hydrologic events (e.g., precipitation and streamflow) yet relatively deterministic indicators such as wetland plant viability, open water area, endangered species, and waterfowl are expected to develop in a relatively short time span, usually 5 yr. The very best that we can have after 5 yr of monitoring a mitigation wetland is a general idea of the wetland's ecological trajectory and even less understanding of its function.

In one of the longest-running documentations of a constructed wetland in this country, an 8-ha freshwater tidal marsh (Windmill Point), was constructed in 1974–1975 within dikes in the James River in eastern Virginia, USA. Early indications, from 1978 to 1982, considered the wetland a success as it supported a diversity of herbaceous vegetation typical of tidal freshwater marshes (Newling and Landin 1985). At that time the monitoring was referred to as "long-term." But the dikes were breached in 1986 due to flooding on the James River, eliminating the vegetation and submersing the wetland in the river (Landin 1994, *personal communication*). Sixteen years after construction the project could be termed by some as a hydrologic and ecologic failure if long-term survival of the wetland was one if its goals.

Because of the stochastic nature of hydrologic events and the slow development of ecosystems, sometimes *in spurts, sometimes in the slow process of recruitment* and growth, the 5-yr time horizon can be viewed as arbitrary and probably much too short. As ecological models show (see e.g., Jørgensen 1994), the further initial conditions are from steady-state, the longer it will take for that system to reach or approach steady state (Fig. 2). Short monitoring times favor measuring success *with transplanted vegetation and pioneer organisms*; long-term success is less dependent on these initial conditions.

Allow self-design

There are two general approaches for introducing vegetation (and other organisms) in wetland creation *and restoration projects. One is the "designer" approach* of introducing species and expecting their survival in Gleasonian zones, akin to gardening or landscape architecture. The other emphasizes the "self-design" or "self organization" capacity of Nature to both recruit species on its own and to make choices from those species introduced by humans (Odum 1989, Mitsch 1993). In self-design the emphasis is on the introduction of as many species as possible, knowing that natural forces will help in the ultimate design by choosing the most appropriate species. Self-design also recognizes the importance of natural colonization of species in wetlands.

In one of the few studies to make a preliminary comparison of these two general approaches [redacted]

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FIG. 2. Hypothetical trajectories of the pattern of one wetland criterion (e.g., "success," e.g., percentage vegetation cover) for two different initial conditions in the same hypothetical wetland site. In Case 1 the wetland would be considered a "success" after 5 yr, while in Case 2 the wetland would be considered a "failure." Each wetland case could end up eventually at the same level, but well after 5 yr. In reality, a multiplicity of criteria would be used in this comparison.

[redacted] plants in the [redacted] increased with age, size, and proximity to the nearest wetland source even though *Typha* spp. comprised 15% of the vegetation for 1-yr-old wetlands, and 55% for 3-yr-old wetlands. Seeded wetlands had a high species diversity and richness after 2 yr and *Typha* cover in the seeded sites was lower than in the naturally colonized sites after a 2-yr period.

Many studies to date (e.g., Confer and Niering 1992, McKnight 1992), especially those on restoration of non-coastal wetlands, have probably over-predicted—because of short time horizons and small spatial scales—the survivability of transplanted species in "designer" wetlands. (An exception to this short time horizon is the long-term observation of Frenkel and Boss [1988], through aerial photography, of the spread of *Spartina patens* in areas along Oregon's coastal wetlands.) With enough time and space, introduced species may be less successful than we initially believed. A better idea is to give the wetland system many possibilities through multiple-seeding, multiple-transplanting, and establishment of hydrologically open systems; this allows nature to participate in the wetland design.

Providing the Needed Research Tools

In addition to the above suggestions for wetland managers and ecological engineers who are attempting to design and monitor wetlands, there are some important approaches that wetland scientists can use to reduce the uncertainty of wetland mitigation.

Select the proper experimental scale

The limited ability of science as we generally practice it to both understand and solve our dilemmas in natural resource conservation was argued by Ludwig et al. (1993) and debated in the pages of *Ecological Applications* (Levin 1993). Taking the cue from Holling (1993) and Costanza (1993) in that discussion, we question whether reductionistic experimental science, with its short time scales (often the time required for a Ph.D. dissertation) and its small spatial scales (often in laboratories or small field plots) can correctly prescribe how to build large wetlands. A holistic systems approach, with the appropriate time and space scales, should at least have equal emphasis.

As one example, a number of studies of wetland function were carried out with four full-scale constructed wetlands at the Des Plaines River Wetland Demonstration Project in northeastern Illinois (Sanville and Mitsch 1994). Hydrologic conditions were varied for high- and low-flow conditions for entire wetlands (average size: 2.4 ha), not just experimental plots; the studies were carried out over 3 yr. Researchers had important findings in estimating detention and mixing (Kadlec 1994), water quality function (Hey et al. 1994, Phipps and Crumpton 1994), sedimentation (Brueske and Barrett 1994, Fennessy et al. 1994*a*), vegetation development (Fennessy et al. 1994*b*), aquatic metabolism (Cronk and Mitsch 1994*a*, *b*), and avian success (Hickman 1994) in created wetlands, most as a function of hydrology.

In a comparison of two natural tidal marshes with a 0.65-ha constructed marsh in coastal Virginia 5 yr after construction, Havens et al. (1995) found seasonal differences in fish and shellfish abundances between natural and constructed marshes, with lower numbers in the latter. They attribute the differences to relative lack of organic carbon and less morphometric heterogeneity (e.g., stream rivulets, microtopography) in the created marsh.

We recently initiated a full-scale comparison of "self-design" and "designer" approaches to wetlands at the Olentangy River Wetland Research Park at The Ohio State University (Fig. 3; Mitsch and Wu 1995, Mitsch 1995). In one newly constructed wetland basin (1 ha), we planted, in approximately the stratification that we would find in nature, ≈2500 individuals representing 14 species of wetland plants. In an identical constructed wetland basin nearby, we planted nothing. Hydrologic conditions are being maintained as similar as possible in the two basins and there is no predetermined completion date to our experiment. We believe that our "experiment" is closer to the scale necessary for documenting the forces, e.g., plant recruitment, geese and muskrat invasions, etc., that influence ecosystem development. Working at this full scale precludes extensive replication because of land and construction costs, yet our understanding of ecosystem development and other wetland functions will come only

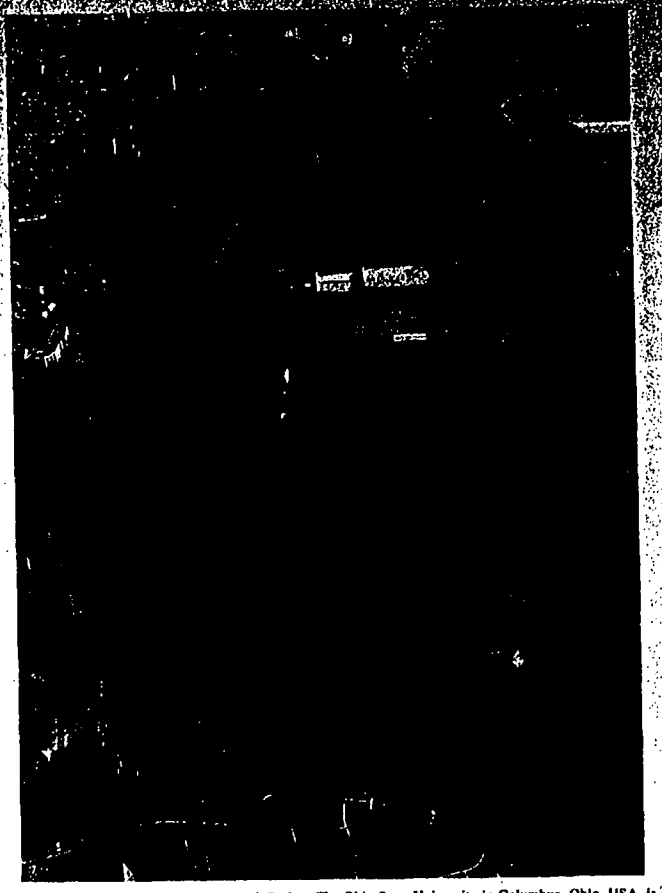

FIG. 3. The Olentangy River Wetland Research Park at The Ohio State University in Columbus, Ohio, USA, is a whole-ecosystem long-term experiment begun on 14 May 1994 with the planting of one of the deep-water marshes shown in foreground (right basin) with ≈2500 plants representing 15 wetland species. The second deep-water marsh (left basin) remains unplanted. Each basin is 1 ha in size and water is supplied by pumps in the lower right-hand corner of the site to create a similar hydrology for each basin. The Olentangy River, shown flowing from bottom right to the top of the picture (with the university ≈0.5 km downstream of the site on the horizon of the picture), is the source of the water, which is pumped in proportion to the river flow in the same patterns for each wetland basin. The photo was taken in November 1993 prior to the introduction of water to the wetlands (photo by Mark Myers, Apex, Columbus, Ohio).

[illegible] and not the [illegible]

[illegible] significant contributions [illegible] mitigation needs to [illegible] ecological science, not a [illegible] each time without theoretical understanding. Scientists need to make the connections between structural measures (e.g., vegetation density, diversity, productivity) and functions such as wildlife use, organic sediment accretion, or nutrient retention in quantitative and carefully designed experiments. Simply having a list of plant species is inadequate for regulators or managers to estimate ecosystem function. Simulation models and experimentation at the proper spatial and temporal scales should be able to help us predict the behavior of these wetlands and estimate proper designs.

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TRANSPIRATION IN UPPER AMAZONIA FLOODPLAIN AND UPLAND FORESTS IN RESPONSE TO DROUGHT-BREAKING RAINS

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Low availability of water for plant uptake may affect the phenology, function, and composition of vegetation in seasonal tropical forests (Fanjul and Barradas 1985, Becker et al. 1988, Reich and Borchert 1988, van Schaik et al. 1993). The rate of water use under a given microclimate depends generally on the soil moisture available for plant uptake, rooting volume, and species sensitivity to soil and atmospheric drought. By measuring the effect of water availability on the transpiration of trees, it is possible to compare functional properties of different forest types (Hinckley et al. 1978, Hsiao 1982). We compared transpiration of canopy trees of mature forests at a floodplain and an upland site, ≈2 km apart, near Cocha Cashu Biological Station in the Manu National Park, Madre de Dios, Peru (11°53′ S, 71°24′ W). Over the measurement period, coinciding with the end of the 4–5-mo dry season, plant water availability changed from low to high. We measured transpiration of trees representing layers from lower to upper canopy, to quantify the effects of limiting and nonlimiting soil moisture conditions in two extensive forest types, floodplain and upland, of the humid tropics.

Setting and Methods

Mean annual rainfall at Cocha Cashu is ~2100 mm (10-yr mean), 86% of which occurs during the 8-mo annual rainy period (October to May). The annual dry period varies appreciably in length and severity (Gentry 1990). A receding floodplain water table is apparent in a gradual lowering of water level in oxbow lakes through the dry season. Mean annual temperature is 24°C, with record extremes of 8° and 34°. On clear days during the dry season, the air vapor pressure deficit may exceed 30 Pa/kPa.

Measurements in a mature floodplain forest were made near the Cocha Cashu Biological Research Station, at an average distance of 30 m from an oxbow lake. The stand selected grows on level ground at an elevation of 335 m above sea level. During the measurement period, the ground surface was 2 m above the lake surface. Measurements in the upland forest were made ≈2.0 km to the southeast, on a 30% slope near a hilltop, ≈50 m from the river and 20 m above its surface. The measurement period, 9–16 September 1992, was chosen to coincide with the end of the annual 4–5-mo dry period, when there is high probability that a strong rainfall event will break the drought providing an opportunity to conduct measurements during both dry and moist soil conditions. A rain event delivered ≈90 mm of rain 20 d before the study began. Measurements began at the end of 3 wk without rain. Four days of measurements were completed prior to a major rain event (100 mm in 4 d), which began at pre-dawn on 13 September and lasted, at varying intensity, until the study ended on 16 September. Daily rainfall was measured at two places: in a 30 m diameter opening near the floodplain site, and on a sandbar protruding ≈10 m into the river near the upland site.

Ten trees of different species, located within a circle 25 m in radius, were selected at each site; two species were represented by one individual at both sites. Xylem sap flux density (g $H_2O \times m^{-2}$ sapwood $\times s^{-1}$) was measured in the stems of the trees over 8 d using a thermal constant energy input method (Granier 1985). The temperature difference between the stem and a heated, 20-mm probe inserted in the outer xylem (constant heat dissipation of 200 mWatt) was monitored every 30 s, and a 30-min mean was stored for each sensor in a data logger (DL-2, Delta-T Devices, Burwell, England). Whole-tree transpiration was estimated by multiplying the xylem flux density by the hydroactive xylem area (Granier 1985). For most palm species, the hydroactive xylem is represented by the total cross-sectional area inside the outer, inactive layer. The hydroactive xylem area in trees with relatively thin xylem can be estimated from the circumference, corrected for bark thickness, and the depth of hydroactive xylem. The circumference of each tree was measured at the sensor height, 1.4–2.5 m above ground (depending on the shape of the buttress, if any). Xylem thickness was estimated at the end of the study by drilling 1–2 mm consecutive intervals into the xylem near the position of the heated sensor and measuring the dielectric constant of the xylem with a c-band portable dielectric probe (Applied Microwave, Lawrence, Kansas). Typically, both real and imaginary parts of the dielectric constant increase appreciably past the bark tissue and decrease past the hydroactive xylem (Salas et al. 1991).

In order to calculate the vapor pressure deficit (VPD) in each stand, the temperature was measured with a linearized thermistor and the relative humidity was measured with a capacitive sensor (Skye, Delta-T Devices). Measurements were made at the base of the upper one-third of the canopy, a region representing highest leaf area per unit of canopy volume. Air temperature and relative humidity were checked against measurements made with a sling psychrometer (Baccarach, Pittsburgh, Pennsylvania). Photosynthetically active radiation (PAR) was measured just above the forest floor with three quantum sensors (LI190, LI-COR) and one spherical sensor (LI193, LI-COR). Soil temperature was measured at 0.15 m depth with thermistors (Siemens, Erlangen, Germany). A pyranometer (LI200, LI-COR) and an additional spherical photosynthetically active radiation sensor were positioned as a reference 2 m above the lake surface, far enough from the shore that the top of the forest canopy was <30° above the horizon relative to the sensors. Data from all soil and micrometeorology sensors were acquired and recorded at the same temporal resolution as specified for the xylem flux density measurements.

To calculate the stand-level transpiration rate, transpiration of each tree was expressed per unit of projected crown area, averaged for all monitored trees in the stand, and then multiplied by the number of crown layers in the stand. Projected crown area was estimated by measuring the longest and shortest diameter of each tree crown, and calculating the area of an ellipse with like axes. The average number of tree crowns overlaying the ground in each site was estimated using a point intercept method. The number of crowns with bases >5 m above the ground (the lowest crown base found among trees selected for transpiration measurements) was counted above each of 25 points, 5 m apart, arrayed in a grid.

A canopy leaf area analyzer (LAI2000, LI-COR, Lincoln, Nebraska) was used to obtain relative estimates of the canopy leaf area index, percent canopy openness, and leaf angle at each site. Measurements were made on an overcast day along five 40-m transects in each site (five sampling units) at 10-m intervals (five subsampling units). Saturated conductivity of the mineral soil (K_{sat}) was measured near the center of the group of selected trees, in five 0.2-m intervals from the surface to 1 m depth, using an Amoozemeter (Ksat, Raleigh, North Carolina), a constant head permeameter (Amoozegar 1989). K_{sat} measurements were not replicated within depths at each site because, as a result of low soil conductivity, 1 d was necessary to measure all depths in each site. K_{sat} was thus used for site description; only when very large differences were found among depths or between sites was this variable used as a potential explanation of patterns in water relationships.

Linear regression was used to evaluate the relationships between the integrated daily air vapor pressure deficit and the daily transpiration of each tree before and after the rain event (N = 4). Note that the assumption of independence among data points is violated. The small number of data points precludes a meaningful statistical test of the hypothesis that the lines changed after the rain. Other comparisons rely on presenting means and standard deviations and performing Student t tests between the populations.

Results

After four rainless study days, a cold front moved in on 12 September, resulting in sharply lower temperature (Fig. 1). During the third rainy day (15 September), the rain gauge near the upland site was washed downstream. Thus, only 2 d of rain data are available for that site. The floodplain rain gauge data show that ≈90 mm of rain were delivered in 4 d. Based on the proximity of the two sites and their similarity in all environmental variables measured before and during the rain event (Fig. 1), we assume that a similar amount of precipitation fell in the upland forest site.

Xylem flux densities followed the diurnal trends in each of the microclimate variables (data not shown). The microclimate variable most closely approximating the leaf-to-air vapor pressure difference (ΔW), the driving force for transpiration, is the saturation water vapor pressure deficit of the air (VPD). This is based on the assumption that average leaf temperature within the canopy is equal to the air temperature if canopy leaf area is high and only a small proportion of the leaf area is directly illuminated at any time. The majority of the leaf area, receiving only diffuse radiation, actually may be somewhat cooler than the surrounding air. Because the forests were too tall for canopy temperature measurements, we assumed that VPD can be used as a surrogate for ΔW if the leaf area index is high and if stand-level comparisons are made only where canopy characteristics are similar. Employing this assumption, several recent studies successfully calculated canopy conductance using VPD (cf. Köstner et al. 1992).

Both environmental conditions (Fig. 1) and canopy characteristics were similar in the two forests. We did not find differences (t test, $P > 0.25$) in the canopy leaf area index (floodplain: 5.3 ± 0.4, mean ± 1 SD; upland: 5.5 ± 0.5), percent canopy openness (floodplain: 1.0 ± 0.5%, mean ± 1 SD; upland: 1.3 ± 0.7%), and percent inclination of leaves (floodplain: 39.2 ± 0.42%; upland: 41.6 ± 1.5%). The high leaf area index and similarities in environment and canopy characteristics at the two stands support use of VPD as a proxy for the force driving transpiration, consistent during the study period and comparable between the stands.

The height, circumference, projected crown area, and stratal position of each of the trees are shown in Table

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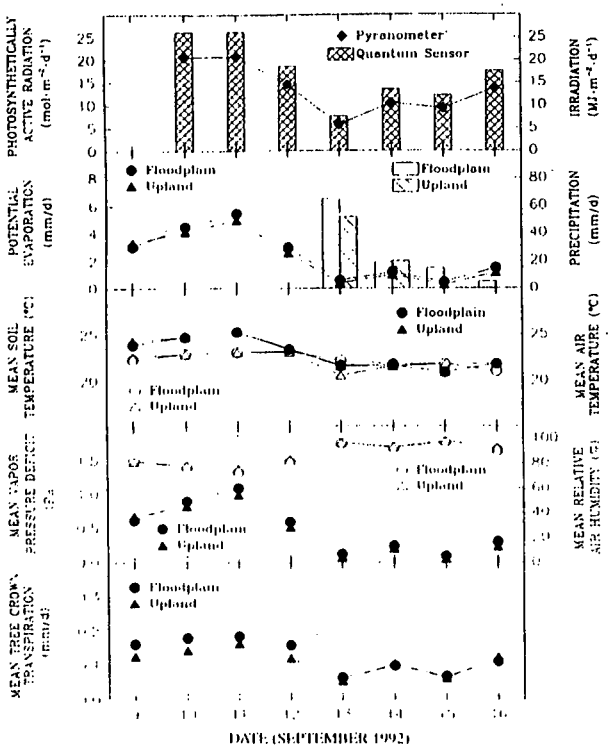

FIG. 1. Daily sums of PAR, irradiation, potential evaporation (calculated based on David 1936, cited in Singh 1988), and precipitation in an open reference site, as well as mean soil and air temperature, vapor pressure deficit, and relative humidity in the upper canopy, and transpiration (on a projected crown area basis) at floodplain and upland sites at Cocha Cashu, Rio Manu, Peru. To calculate tree canopy transpiration, values in the bottom panel of the figure must be multiplied by the mean number of crown layers superimposed on the ground in each stand.

1. Only two species were common to both sites: *Brosimum alicastrum*, the tallest tree at both sites, and *Astrocaryum chonta* (a palm), shortest of the measured trees. The floodplain forest was generally composed of taller trees with greater mean girth and crown spread. Accordingly, the projected crown area of the 10 floodplain trees was 1227 m² compared to 821 m² for the 10 upland forest trees. The point intersect method indicated a greater number (2.4 ± 0.8, mean ± 1 SD) of superimposed crowns at the floodplain site than at the upland site (1.9 ± 1.1; *t* test, $P < 0.071$).

Sensitivity of trees to atmospheric drought after rain was investigated by evaluating the relationship between whole tree transpiration and the standardized, time-integrated VPD during the daytime (VPD_I). Daytime was defined as the period during which the 30-min means of photosynthetically active radiation were >10 mmol. VPD_I was calculated as the sum of 30-min means of VPD during this daytime period, standardized by atmospheric pressure and by the ratio of daytime half hours divided by 48. Thus, VPD_I can be used as a basis for comparing transpiration behavior regardless of date and geographic location. Whole-tree transpiration was calculated as the product of the xylem flux density and the hydroactive xylem area. Except for the palm, xylem thickness (used for calculating xylem area) ranged from 7 to 14 mm in the upland forest and from 8 to 20 mm in the floodplain forest, averaging

TABLE 1. Taxonomy, height, projected crown area, stem circumference, and position in the canopy (E, emergent; UC, upper canopy; MC, mid-canopy; SC, subcanopy) of trees for which water uptake was measured in floodplain and upland forests. Letters are used to identify species in Fig. 2.

Species	Family	Height (m)	Crown area (m²)	Circumference (m)	Crown class
Floodplain forest					
a *Brosimum alicastrum*	Moraceae	55	165	2.900	E
b *Neea* sp.	Nyctaginaceae	50	53	1.450	UC
c *Swietenia macrophylla*	Meliaceae	50	384	3.660	E
d *Lecointea amazonica*	Fabaceae	45	153	1.700	MC
e *Terminalia oblonga*	Combretaceae	45	190	3.030	UC
f *Pseudolmedia laevis*	Moraceae	40	83	0.720	SC
g *Otoba parvifolia*	Myristicaceae	40	35	0.780	MC
h *Calycophyllum spruceanum*	Rubiaceae	40	82	1.670	E
i *Inga* sp.	Mimosaceae	35	74	1.320	SC
j *Astrocaryum chonta*	Palmae	15	8	0.500	SC
Upland forest					
k *Brosimum alicastrum*	Moraceae	30	251	5.734	E
l *Micropholis egensis*	Sapotaceae	26	282	3.202	E
m *Eschweilera* sp.	Lecythidaceae	23	61	0.801	UC
n *Jacaranda copaia*	Bignoniaceae	23	14	1.120	SC
o *Schizolobium parahybum*	Caesalpiniaceae	23	55	1.174	SC
p *Manilkara inundata*	Sapotaceae	21	47	1.150	UC
q *Hymenaea courbaril*	Fabaceae	16	20	0.545	MC
r *Sloanea ternifolia*	Elaeocarpaceae	15	54	1.200	UC
s *Himatanthus sucuuba*	Apocynaceae	14	4	0.446	MC
t *Astrocaryum chonta*	Palmae	9	3	0.326	SC

>2 mm thicker in the latter. Integrated daily whole-tree transpiration was strongly related to VPD_I in most trees (Fig. 2). After the rain, VPD_I explained more of the variation in transpiration, in most cases, and the slopes changed. No clear trend in xylem flux density in relation to position of trees in the canopy could be discerned. The maximum xylem flux density found in each tree during the study was also unrelated to the position

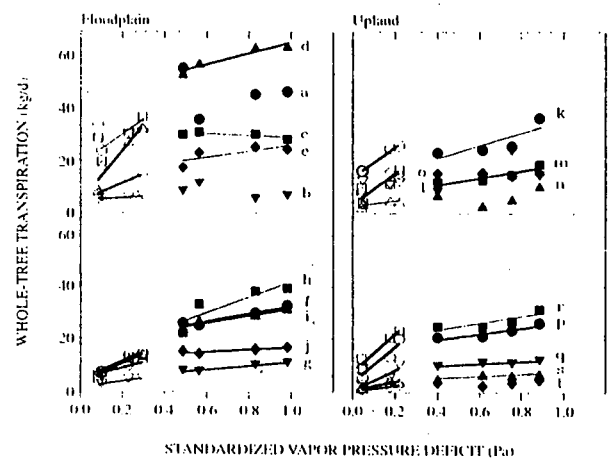

FIG. 2. Daily tree transpiration in relation to standardized vapor pressure deficit (VPD_I) in the two study sites. Closed symbols represent the period before onset of the rains; open symbols represent the period during the rain event (13–16 September 1992). Letters correspond to species as indicated in Table 1. Thick lines represent relationships with $r^2 > 0.8$ and $P < 0.1$; thin lines represent relationships of lower r^2, but similar P values.

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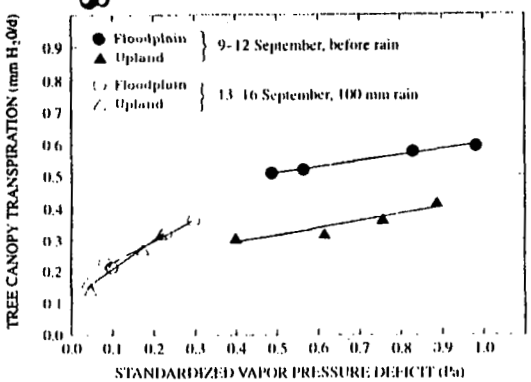

FIG. 3. Daily tree canopy transpiration in relation to standardized vapor pressure deficit at the two study sites, before and after the rain event of 13–16 September 1992.

of trees (data not shown). Thus, the weighted average of transpiration rate normalized to projected crown area could be calculated without need to account for the relative contribution to stand-level transpiration of trees in different canopy positions. The calculation was done by summing the daily transpiration of all the trees measured in each forest and dividing by the sum of their projected crown areas (Fig. 1, bottom). This value appeared greater for the floodplain forest before the onset of the rain event, but was very similar thereafter.

Estimates of integrated daily transpiration for the whole forest canopy were obtained by multiplying the crown area-normalized transpiration by the average number of superimposed crown layers in each forest. This value represents only a part of the total stand transpiration, as it neglects small trees whose crowns begin <5 m above ground, understory vegetation, and lianas.

Daily canopy transpiration showed different relationships with VPD_z for the two forests before the rain event. The floodplain forest transpired at a higher rate than the upland forest under similar VPD_z, although their leaf area indices were similar, indicating lower resistance to the transpiration flux (Fig. 3). However, differences between the forests were marginal after the rain event.

The K_{sat} in all soil depths at both sites was relatively low, with the maximum rate at the 0.4–0.6-m interval of the floodplain site reaching 4.9 mm/h. K_{sat} varied with depth in the floodplain forest soil, but remained > 1.1 mm/h in all depths, whereas K_{sat} in the upland soil declined with depth, reaching a rate of 0.1 mm/h at 0.6 m below the surface.

Discussion

Forest types in the Manu National Park, Peru, represent the two major topographic subdivisions of this portion of southwestern Amazonia: floodplain and upland. The floodplain forest is characterized by trees of great stature (emergents commonly reach 55 m), and a multilayered vertical organization; the upland forest is generally of lower stature, contains fewer large trees, and fewer superimposed crowns (Terborgh and Petren 1991). Our study stands conform to this general description. The floodplain site was located on deep, recently deposited alluvium (Entisol). The upland site was situated on a high, eroded Pleistocene terrace (Ultisol), and nearby soil pits revealed the presence of an impermeable clay hardpan at a depth of 0.6–0.7 m in some spots.

Transpiration was measured after a 4–5-mo dry season and through a drought-breaking rain. Trends in both heat-flux densities and whole-tree transpiration were unrelated to the size or vertical position of crowns (Fig. 2). Therefore, transpiration did not differ among trees due to a vertical gradient in the driving force (VPD) through the canopy, but was probably affected by differences among trees in resistance to water flux. Resistance to water flux from soil to atmosphere can be estimated from the inverse of the slope of the relationship between the flux and VPD_z through the origin. A steep slope in the relationship indicates a low resistance. After 3 wk without rain, water uptake by the floodplain canopy was nearly twice that of the upland forest canopy (Fig. 3). Transpiration of most individual trees in the upland forest was depressed (Fig. 2), whereas only one tree at the floodplain site (a large *Swietenia macrophylla*, species c in Fig. 2) had similarly reduced transpiration. The greater increase in slopes shown by many upland site trees after a rain reflects a larger reduction, relative to the floodplain site, in resistance to water uptake. As a result, many upland forest trees transpired at higher rates after the rain than before, despite a VPD_z less than half as great (Fig. 2: compare transpiration at the lowest VPD_z before the rain with the highest after the rain). Increased resistance to water uptake (soil–root resistance) or to transpiration (stem or stomatal resistance) in the preceding rainless 20 d dampened or eliminated tree response to VPD_z in the upland forest during the early part of the study. Uptake of water by trees after the onset of rain while VPD_z was zero (data not shown) demonstrated a relaxation of resistance in the soil–root interface.

Extrapolating to the stand level highlights the behavioral difference of these two forests (Fig. 3). The difference in canopy-level transpiration rates between the sites was caused equally by a greater number of overlayed tree crowns and a higher mean transpiration per crown in the floodplain forest. The relationships between transpiration and VPD_z after a 20-d rainless period, relative to those immediately following a rain, indicated a greater decrease in resistance to transpiration of canopy trees at the upland site, relative to the floodplain forest, as water became available.

Two edaphic features of the upland site could contribute to restricted water availability. First, the height of the terrain above the river (≈20 m) implies that the water table is deeper than at the floodplain site during the dry season. Second, a subsurface clay layer noted at some nearby sampling points (in accord with the low K_{sat} found at 0.6 m from the surface) suggests the possibilities of impeded root penetration (in accord with a higher incidence of treefalls in this forest, although none were apparent in the vicinity; J. W. Terborgh, *unpublished data*), and subsurface lateral loss of water to an area downslope.

The occurrence of a 100-mm rainfall made the relationships between tree canopy transpiration and VPD_z in the two forests practically indistinguishable (Fig. 3). The apparent non-zero intercept indicates a recharge of the stem storage as water became more easily accessible. The similar relationships between transpiration and VPD_z shown by the two forests in a period of unlimited water supply and low VPD_z suggest that they may transpire at similar rates during the rainy period, when there are many wet, cloudy days with low VPD_z. However, during the pronounced dry season in which rain is infrequent and VPD_z is often high, water limitation may develop within 20 d in upland forests, and transpiration there can be only 65 to 55% of that in floodplain forests. Thus, even in moist tropical climates, water limitation imposes water stress and may regulate species composition and productivity of forests.

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An Ecological Perspective of Riparian and Stream Restoration in the Western United States

By J. Boone Kaufman, Robert L. Beschta, Nick Otting, and Danna Lytjen

ABSTRACT

There is an unprecedented need to preserve and restore aquatic and riparian biological diversity before extinction eliminates the opportunity. *Ecological restoration* is the reestablishment of processes, functions, and related biological, chemical, and physical linkages between the aquatic and associated riparian ecosystems; it is the *repairing of damage* caused by human activities. The first and most critical step in ecological restoration is *passive restoration*, the cessation of those anthropogenic activities that are causing degradation or preventing recovery. Given the capacity of riparian ecosystems to naturally recover, often this is all that is needed to achieve successful restoration. Prior to implementation of active restoration approaches (e.g., instream structures, channel and streambank reconfiguration, and planting programs), a period of time sufficient for natural recovery is recommended. Unfortunately, structural additions and active manipulations are frequently undertaken without halting degrading land use activities or allowing sufficient time for natural recovery to occur. These scenarios represent a misinterpretation of ecosystem needs, can exacerbate the degree of degradation, and can cause further difficulties in restoration. Restoration should be undertaken at the watershed or landscape scale. Riparian and stream ecosystems have largely been degraded by ecosystem-wide, off-channel activities and, therefore, cannot be restored by focusing solely on manipulations within the channel. While ecological restoration comes at a high cost, it also is an investment in the natural capital of riparian and aquatic systems and the environmental wealth of the nation.

A fence-line contrast of a five-year-old exclosure (without livestock grazing) and an area grazed season-long on a tributary of the Deschutes River, Oregon. The cessation of those activities that are causing degradation or preventing recovery is the most important step in ecological restoration. Given the natural resilience capacity of riparian ecosystems, passive restoration such as halting excessive livestock grazing is all that is needed to restore degraded riparian ecosystems

J. B. Kaufman

Traditionally, the use and management of rivers, riparian zones, and wetlands have focused on activities that led to increases in the social well-being of material wealth of a [illegible] and the use of water for agricultural, industrial, and municipal uses (National Research Council 1992).

As a result of these practices, as well as activities such as channelization, road construction, timber harvesting, livestock grazing, mining, and water diversion, numerous riparian zones in the western United States have [illegible] (National Research Council 1992, 1994). The resulting decreases in diversity, functions, and productivity of riparian and aquatic ecosystems limit their future integrity, value, and use. This is an important societal concern since riparian zones are among the nation's most highly valued, yet threatened natural ecosystems (Johnson and McCormick 1979; National Research Council 1992).

Riparian and aquatic ecosystems are currently being altered, impacted, or destroyed at a greater rate than any time in history (National Research Council 1992).

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An estimated 70%–90% of all natural riparian areas in the United States have been extensively altered (Hirsch and Segelquist 1978); approximately 47.3 million ha (117 million acres) or 53% of all U.S. wetlands have been lost since the 1780s (Dahl 1990). Some widespread land uses that occur in both uplands and riparian systems exert their greatest impacts on streamside areas. For example, in the 11 western states, livestock grazing is permitted on [illegible] land. Of the 1.6 million ha (158 million acres) of Bureau of Land Management-administered lands, 5% is classified in fair to poor condition (i.e., the land has been moderately to severely desertified) as a result of long-term grazing (U.S. General Accounting Office 1988). Historical grazing impacts to riparian systems have been even more severe. On these public lands, 25,700 km (16,000 miles) of sportfishing streams have declined in quality as a result of land use practices (Armour et al. 1991).

Degradation of riparian zones and streams damages [illegible] functions, including [illegible] and retention and transformation of nutrients, purification of water, attenuation of floods, maintenance of stream flows and stream temperatures, recharging of groundwater, and establishment and maintenance of habitats for fish and wildlife. The most important factor contributing to the decline of aquatic biodiversity is the loss or degradation of habitats (i.e., habitat alteration, introduced species, and water pollution; Miller et al. 1989). Almost 40% of the perennial streams in the United States are affected by reduced flows, and 11% are influenced by siltation, bank erosion, and channelization (National Research Council 1992). More than half of the nation's rivers have fish communities harmed by turbidity, high temperatures, toxins, and low levels of dissolved oxygen (Council on Environmental Quality 1989). Almost 85% of historical Pacific Northwest anadromous salmon stocks are either extinct, endangered, threatened, or of special concern (National Research Council 1996). The current threat to aquatic biodiversity in North America is greater than the threat to terrestrial diversity (Nauman et al. 1995). While 11%–15% of the terrestrial vertebrates are considered rare or nearly extinct, 34% of the fishes, 63% of the crayfishes, and 75% of the bivalve mussels fall into these categories (Nauman et al. 1995). To date, not a single aquatic species has been delisted through Endangered Species Act procedures because of implementation of a successful recovery plan; in fact, the majority of the listed species do not have a formal recovery plan (Williams et al. 1989). An unprecedented need exists for ecological restoration of riparian ecosystems and their closely associated aquatic ecosystems.

What Is Ecological Restoration?

Ecological restoration in riparian ecosystems is defined as the reestablishment of [illegible] disturbance riparian functions and related chemical, biological, and physical processes (National Research Council 1992). *Restoration* is the process of repairing damage caused by humans to the diversity and dynamics of indigenous ecosystems (Jackson et al. 1995). While ecological restoration attempts to return riparian zones as closely as possible to predisturbance functions and processes, scientists must recognize that ecosystems are in a constant state of flux due to ever-changing environmental conditions. These changes, sometimes coupled with [illegible] conditions by natural processes, air pollution, may preclude our capability to precisely recreate ecosystem structure and function as that previously existed. Thus, the goal of restoration projects is to ensure that the dynamics of natural ecosystem processes are again operating efficiently so that both ecosystem structure and function can be recovered (National Research Council 1992).

Riparian areas are three-dimensional zones of biological, physical, and chemical interactions between terrestrial and aquatic ecosystems (Gregory et al. 1991). [illegible] riparian zones requires a holistic approach where activities and conditions across an entire watershed should be considered. Problems affecting riparian and aquatic resources are unlikely to be solved by ignoring deleterious land management practices, either historical or current, that occur at landscape or watershed scales.

While scientists strongly recognize the need to restore or conserve native fish throughout the Pacific Northwest and other nearby regions, less appreciation exists for local geomorphic settings and natural

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hydrologic disturbance regimes interact with native riparian plant communities to create sustainable habitats (Figure 1). Restoration of degraded riparian zones and their subsequent conservation after recovery requires knowledge of how these ecosystems function as well as the attributes responsible for their composition, structure, and productivity. The character and value of riparian zones arise as a result of an infinite number of complex interactions among three fundamental ecosystem features: (1) soils/geomorphology; (2) hydrology; and (3) biota (Figure 1). The soils/geomorphology features include streambank and floodplain form and development, channel gradient, geologic substrates influencing soil and channel composition, and subsoil features of the floodplain (e.g., gravel lenses important for hyporheic or subsurface flows). Hydrological features include the frequency, magnitude, and temporal distribution of stream flow (including peak and low flows), sediment availability and transport, subsurface hydrology, and water quality. Biotic features include vegetation, vertebrates, invertebrates, and microorganisms. In addition to live plants, the vegetation component also includes dead materials (necromass) such as snags, fallen logs, and fine organic debris (litter). Anthropogenic activities that either alter these components or sever the linkages between them will disrupt ecosystem dynamics, including species composition, productivity, structure, and function.

Among the most important ecosystem linkages are those interactions among vegetation, hydrology, and substrates as they influence geomorphic features such as channel morphology and channel dynamics (Figure 1). For example, naturally occurring pool habitats typically form as a result of interactions of hydrologic disturbance regimes, substrates, and streamside vegetation. If hydrologic patterns, sediment availability, or streamside vegetation are altered by land

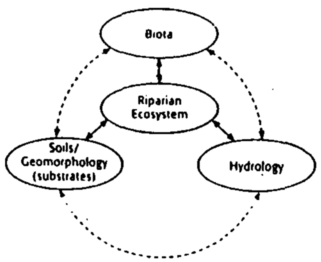

Figure 1 illustrates the linkages of the biotic, hydrologic, and geomorphic components combined to shape the unique structure and function of riparian and stream ecosystems. Each arrow represents an infinite number of biological and physical processes and interrelationships among these ecosystem features. Because of these inextricable linkages, human or natural actions that alter any one component or process will have feed-forward influences that can affect all other components of the ecosystem.

use activities, then channel morphology will subsequently adjust to these new conditions. This is often expressed by a simplification in stream structure (e.g., loss of pools, decreased channel sinuosity, and loss of channel diversity).

Another important interaction represented in Figure 1 is the influence of substrate characteristics and hydrology on plant community composition. For example, many riparian-obligate trees and shrubs have specific micro-site requirements for establishment. Successful natural establishment of cottonwood trees (*Populus* spp.) and willows (*Salix* spp.) commonly occurs on point bars of newly deposited, coarsely textured, well-aerated substrates within the 2- to 10-year floodplain (McBride and Strahan 1984, Bradley and Smith 1986); high flows are needed to create these conditions. Seed dispersal and germination are timed to coincide with late-spring flows when water tables are high, and fresh alluvium has been deposited (Noble 1979). Successful establishment also may be limited to areas where the rate and extent of water table decline does not exceed the biological capacity of root growth (Mahoney and Rood 1992). At the lower limits of the floodplain, establishment is often not possible because high water in subsequent years destroys the young plants (Bradley and Smith 1986).

Saturated, finely textured soils associated with low-gradient riparian zones are often sites of anaerobic conditions; such sites are typically unsuitable for the establishment of cottonwoods or willows. Under these hydrologic and geomorphic conditions, the natural plant communities are dominated by sedges (*Carex* spp.), rushes (*Juncus* spp.), or hydrophytic grasses. At the opposite extreme, where coarse materials (cobbles and boulders) occur in elevated and excessively drained situations, riparian-obligate vegetation will not establish. These conditions rarely occur naturally in western riparian ecosystems. However, they may be found after extreme human perturbations (e.g., dredge mining, channelization, or other in-channel modifications) deposit spoils on streambanks and floodplains.

Ecological restoration begins with identification of those land use practices that are damaging ecosystems or preventing recovery, followed by implementation of land management strategies that allow for natural recovery to occur (National Research Council 1992, 1996; Jackson et al. 1995). Thus, ecological restoration aims to ensure the occurrence of (1) those physical and biotic processes facilitating persistence of species through natural recruitment and survival; (2) functioning food webs and systemwide patterns of consumer [illegible] relationships among plants, animals, and detritivores; and (3) the integrity of watersheds through linkages with the hydrologic, geomorphic, and climatic disturbance regimes that shape plant and animal communities (Jackson et al. 1995).

What Isn't Ecological Restoration?

Ecological restoration results in the reestablishment of linkages between organisms and their environment. Because an entire suite of organisms, physical features, and processes comprise an ecosystem, a species-only or single-process approach to restoration will likely fail (Beschta et al.

Photos by J. B. Kauffman

The influence of restoring streamflows and halting grazing on Rush Creek, California (1992–1996) is illustrated above. The small willow in the foreground in 1992 (left) is the same willow to the left of the third author in 1996. In 1992, a high density (50 m⁻²) of willow seedlings was established on the gravel bar the first year without livestock. By 1996, a dense willow community had formed, with many willows becoming more than 2 m in height.

1994; Jackson et al. 1995). For example, the reintroduction of an extirpated fish species or the installation of log weirs and large boulders into a degraded stream reach does not constitute restoration. While attempts to revive a single species are likely to target only a few of its more obvious habitat requirements, less-apparent needs and important processes and functions are [illegible] ignored. In the case of declining anadromous salmonids, a technological perspective has prevailed (Bottom 1997): first fish hatcheries, then fish ladders, and finally in-stream manipulations were looked on as solutions. However, increasingly apparent is that there is a remarkable complexity of environmental phenomena that affect salmon viability, and the cumulative losses of various biotic and physical components are what must be addressed (National Research Council 1996). By shifting the focus to the integrity of ecological processes and functions, we are more likely to successfully attain the restoration [illegible] species of interest.

Ecological restoration also [illegible] be distinguished from architectural and mechanical approaches to ecosystem management. Such "restoration" methodologies often call for the systematic reconstruction of a stream according to specific human perspectives of what the stream "should look like." More often than not, this will not achieve the goal of ecological restoration or species recovery. [illegible] without the function in an artificial configuration does not constitute restoration" (National Research Council 1992). A long-term perspective [illegible] is not inherent with [illegible]

[illegible] structures (boulders, rock gabions) does not replace many of the multiple functions of large woody debris, nor does it ensure or promote the future recruitment of woody debris into the stream system. Such structures are commonly engineered and constructed with the false assumption that they and the stream channel are static. High flows can be destructive when rigid structures are placed in degraded alluvial channels (Beschta et al. 1991; Gregory and Bisson 1997). The underlying failure of this approach rests in a lack of recognition regarding the natural dynamics of high-flow disturbances, bedload transport, local scour and fill, lateral channel movements, and particularly the interactions of streamside vegetation with fluvial disturbance regimes.

Fish hatcheries, fish ladders, and barging salmon downstream in dammed rivers are artificial means of maintaining anadromous fish in systems (functions with no natural [illegible]). These approaches seldom address fundamental problems associated with restoring the habitats of natural fish runs. Such activities could be construed to be mitigation or aquaculture but not restoration since they do nothing to restore habitat or reverse barriers to migration.

Preservation

Preservation is the maintenance of intact ecosystems; it is distinct from ecological restoration, which only addresses degraded ecosystems. Ecosystems that exist in a desired natural state warrant preservation (National Research Council 1992, 1996). The protection and preservation of intact ecosystems are of great importance, both environmentally and economically. Restoring the natural structure and function of riparian and stream ecosystems requires an understanding of the complex processes and linkages between the biotic and physical components of intact systems. Intact ecosystems are necessary as reference reaches from which to compare the efficacy of restoration programs (Case 1995; Beschta 1997). Furthermore, they are sources of natural genetic material for the reestablishment or reintroduction of the native biota to nearby areas in need of restoration.

Preservation is a management strategy that entails more [illegible] For example, management actions may be necessary to maintain natural functions and characteristics (e.g., prescribed fire, management of exotic species invasions, and large herbivore management). Measures to protect intact ecosystems (preservation) are important because they are often easier to implement, have greater rates of success, and are less expensive than restoration. Preserving intact ecosystems also may be less expensive than restoring them, just as preventative medicine is nearly always less expensive than corrective medicine (National Research Council 1992; Cairns 1993).

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Various other land management approaches seek to alter and improve riparian conditions or specific habitat features, yet they may not represent ecological restoration. Activities often confused with ecological restoration include creation, rehabilitation, reclamation, mitigation, replacement and enhancement. These activities typically emphasize altering ecosystem components for a particular human purpose (National Research Council 1992, 1996).

Creation

Creation is defined as establishing a new ecosystem that previously did not exist on a particular site. For example, developing a sustainable wetland in an area formerly occupied by upland plant communities would represent creation. Creation also includes attempts to create specific riparian features that previously did not exist on the treated site. Examples include the planting of willows or alders (*Alnus* spp.) on riparian wetland sites naturally occupied by sedges or rushes, placement of boulders in streams with floodplains comprised of fine sediment, and construction of secondary channels where none existed previously (Quammen 1986).

Reclamation

Reclamation is traditionally defined as the process of adapting wild or natural resources to serve a utilitarian human purpose (National Research Council 1992). Historically, this often included the conversion of riparian or wetland ecosystems to agricultural, industrial, or urban uses. More recently, however, *reclamation* has been defined as the process resulting in a stable, self-sustaining ecosystem that may or may not include some exotic species. Reclaimed sites may have similar, although not identical, structure and function of the original land (Jackson et al. 1995).

Rehabilitation

Rehabilitation implies making the land useful again after natural or anthropogenic disturbances. Restoration to predisturbance conditions and functions is not implied in the definition of *rehabilitation*. The creation of a crested wheatgrass (*Agropyron cristatum*) stand where sagebrush steppe (*Artemisia tridentata*) once existed or the planting of exotic grass species after a forest fire could be construed as rehabilitation but is not ecological restoration.

Replacement

Replacement is the substitution of a native species or ecosystem feature with an exotic species or foreign object, often it is considered another form of rehabilitation. Examples of replacement would include the planting of non-native trees or the placement of boulders, gabions, or weirs to substitute for natural features. The introduction of brook trout (*Salvelinus fontinalis*) or smallmouth bass (*Micropterus dolomieui*) in streams historically occupied by native salmonids is an example of ecological replacement.

Mitigation

Mitigation is an attempt to alleviate any or all of the detrimental effects or environmental damage that arise from anthropogenic actions. The construction of fish hatcheries or the allocation of headwater fish habitats to compensate for losses caused by dams is a mitigation approach. Wetland creation is often suggested as mitigation for the destruction of natural wetlands from construction, fill, or other human activities. However, these constructed wetlands seldom display the structural or functional attributes of the native wetlands they replaced (Quammen 1986; M. Kentula, U.S. Environmental Protection Agency, personal communication).

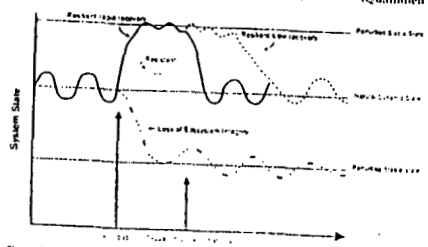

Figure 2 represents the conceptual responses of individual riparian plant communities to human perturbations and response pathways after cessation of perturbations. Resistant plant communities exhibit few deviations from natural equilibria when exposed to a perturbation. In contrast, nonresistant communities shift to a perturbed state unlike that of the natural dynamic state (i.e., changes in composition, structure, or productivity). After activities that caused ecosystem degradation (perturbations) stop, resilient communities will recover to natural system states. Nonresilient communities are those lacking potential for natural recovery and are characterized as having lost ecosystem integrity. In the absence of active restoration activities, they may remain indefinitely in an altered ecosystem state.

Enhancement

Enhancement is any improvement of a structural or functional attribute for a species or habitat. However, when enhancement activities are focused only on a single species or specific component of an ecosystem, they may create conditions outside the context of a natural riparian and stream system. For example, in-stream structures (e.g., rock jetties, gabions, pool excavations) are often used with the objective of fish habitat enhancement. However, these structures [illegible] time, sediment transport dynamics, and hydrologic connectivity with riparian vegetation, resulting in disruptions or losses of riparian-stream linkages. When in-stream spoils, rocks, or boulders are piled on a streambank, conditions may no longer be suitable for natural establishment of riparian vegetation nor for adjustments in channel morphology to natural variations in sediment transport and stream flow. Such physical

alterations may further limit the future recruitment potential of large, woody debris as well as degrade riparian wildlife habitat. The ecological costs and benefits to physical processes, biological diversity, and ecosystem functions should be considered before such actions are initiated.

Resistance and Resilience

In undertaking restoration, it is important to understand the response of riparian ecosystems to anthropogenic perturbations (resistance) as well as the capacity to recover after cessation or removal of the problem-causing activities (resilience). *Resistance* is the capacity of an ecosystem to maintain natural function and structure after a natural disturbance or an introduction of an anthropogenic perturbation. For example, some riparian meadow plants will maintain productivity with moderate levels of livestock grazing because of their adaptive capacities or tolerance to herbivory. These would be considered *resistant communities*. In contrast, even low levels of herbivory can retard community development on gravel bars dominated by young willow or cottonwoods (Case and Kaufman, in press; Green and Kauffman 1995); these are *nonresistant communities*.

Resilience is the capacity of species or ecosystems to recover after a natural disturbance or following the cessation of an anthropogenic perturbation. Because riparian species evolved in areas with frequent fluvial disturbances, they represent classic examples of a resilient biota. Not only do many riparian plants depend on natural disturbances for establishment, but rates of recovery or establishment following disturbances can be remarkably high (Busse 1989; Gecy and Wilson 1990; Case 1995). Paradoxically, while riparian ecosystems are often resilient to natural disturbance regimes, many rapidly degrade with the curtailment of these disturbances. For example, water impoundment and diversion projects have resulted in dramatic losses in riparian floodplain forests throughout North America (Bradley and Smith 1986; Rood and Mahoney 1990; Howe and Knopf 1991).

The conceptual pathways of riparian community response to the initiation and cessation of anthropogenic perturbations are illustrated in Figure 2. A severe anthropogenic perturbation (e.g., overgrazing, clear-cutting, channelization, dams, diversions) may sufficiently alter a riparian ecosystem such that it will attain a dynamic equilibrium different than what would occur under natural conditions. A *resistant ecosystem* is one that displays [illegible] perturbation. In [illegible] riparian zones or communities will change to a new system state or equilibrium typified by a different composition (e.g., dominance by exotics), different structure (e.g., losses of the woody component), altered productivity (e.g., shifts in above- and below-ground biomass), or a change in ecosystem functions (e.g., influences on water quality).

After cessation of perturbations, resilient riparian ecosystems usually show signs of recovery through measurable changes in composition, structure, or function (Figure 2). In these situations, cessation of those human perturbations that harm the riparian ecosystem may be all that is necessary to achieve restoration. Because some ecosystems recover more quickly than others, it is important to monitor changes before implementing other, often more costly, measures. Failure to wait minimally may result in wasting limited funds; at worst, it may exacerbate the extent of degradation.

When losses in ecosystem structure, composition, or function reach a sufficient magnitude, the simple cessation of perturbations may not be sufficient for ecosystem recovery (Figure 2). Factors that may diminish resilience and, hence, prevent recovery include species extinctions, introductions of exotics, excessive soil erosion, pollution, and severe changes in geomorphology or hydrology. In these

Rather than referring to a handbook, land managers should obtain the "blueprints" for the ultimate outcomes of planned restoration activities from intact streams.

situations, the ecosystem may remain degraded indefinitely even after the cessation of activities that caused degradation. In this scenario a concerted and active effort will be needed to accomplish restoration.

Conceptual Approaches to Restoration

The basic goal of riparian restoration is to facilitate a self-sustaining occurrence of natural processes and linkages among the terrestrial, riparian, and aquatic ecosystems. An important initial component of any restoration plan should be an evaluation of the ecological status of existing riparian and aquatic systems. Ideally, this assessment should be conducted at the watershed scale, while still being sufficiently detailed to depict specific reaches or channel units where particular restoration activities might ultimately occur. The objectives of the initial resource analysis should be to identify (1) those reaches that are relatively intact (few anthropogenic impacts evident) and worthy of protection or preservation management strategies; (2) those reaches where restoration is feasible with changes in current land use activities or without large expenditures of money; (3) those areas that could be restored but only at high costs and with a high probability of failure; and [illegible] alteration, degradation, or sociopolitical limitations.

When planning for ecosystem restoration, it may be useful from a strategic perspective to partition riparian zones into those capable of rapid recovery, those with a slow rate of natural recovery, and those with little or no resilience capacity (i.e., loss of ecosystem integrity; Figure 2). The greatest efforts should be initially focused on the former because of a greater potential for successful restoration with lowered risk or expenditures. Only after areas

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with a high-resilience capacity are improving or have been restored should restoration efforts focus on areas that have generally lost the capability of natural recovery, even after the cessation of human perturbations. However, special situations may exist in which degraded habitats of species near extinction can only be restored at high risk and cost; such areas assume a high priority for improvement.

Where possible, managers should emphasize preservation because preservation of intact ecosystems is typically less expensive than restoring degraded systems (Cairns 1993). Intact ecosystems are not only valuable sources of biological diversity, but they also provide important reference sites that land managers may seek to emulate in their restoration activities. Rather than referring to a handbook, land managers should obtain the "blueprints" for the ultimate outcomes of planned restoration activities in adjacent sites from intact streams. Because the failure rate of restoring degraded ecosystems is far greater than that of simply protecting fully functional sites, protecting and preserving intact ecosystems should represent the first priority of any watershed-scale restoration plan.

At the other extreme, many areas exist where ecological restoration in the strictest sense is neither economically, socially, nor technologically feasible (e.g., metropolitan reaches, dredged mine sites, etc.). If restoration practices are pursued in these situations, they may be costly. However, stream enhancement activities should not be ruled out in these scenarios, particularly if such activities would diminish harm to downstream or upstream riparian and aquatic ecosystems.

Reviews of instream habitat management projects throughout the western United States clearly indicate that passive restoration has been the critical first step in successful riparian restoration programs.

The domain of riparian and stream restoration lies between these two extremes (Figure 2). A successful riparian restoration program will result in the perpetuation of processes that determine ecosystem structure, function, and evolutionary trajectory. However, this operating principle is stated with the recognition that the intact wildlands of today and the future will exist in a fragmented landscape and will require specific preservation management activities such as prescribed fires, suppression of arson fires, control of biotic invasions, and maintenance of natural hydrologic disturbance regimes.

After identifying those degraded sites where restoration is deemed feasible, scientists must determine the causes of degradation and the activities preventing recovery (Beschta 1997). Also important is the identification of biotic components of the ecosystem that have been extirpated and the presence of biotic invaders that may prevent recovery. In addition to biotic considerations, scientists must determine the degree to which the hydrologic and geomorphic features of the ecosystem have been (or are being) altered. This includes determining the influences of past management activities on channel morphology, channel incision, hyporheic flows, water table dynamics, and water quality (i.e., the linkages between the terrestrial and aquatic system). From this initial analysis, not only can the extent and causes of ecosystem degradation be addressed, but potential restoration options may become evident. Obviously, *even at this stage, restoration is a multidisciplinary effort.*

The desired endpoints of restoration efforts are naturally dynamic and self-sustaining ecosystems (Figure 2). Given the fluctuating nature of environmental factors inherent to all natural systems, restoration managers should emphasize ecosystem processes and function rather than some preconceived landscape form. Fisheries professionals should recognize that because of the likely permanence of many exotic species, extinctions of native species, long-term changes in soil productivity due to erosion, and other severe environmental perturbations, complete recovery may not always be possible. *In such cases, goals of restoration are* to return a riparian system to a "potential natural community," whereby the ecosystem is naturally functioning in a manner as closely as possible to that in which it evolved.

Passive Restoration

Once professionals have decided where to [illegible] restoration activities, the first and most critical step is to halt activities causing degradation or preventing recovery, [illegible] (Kauffman [illegible]). Many riparian zones are capable of rapid recovery after human perturbations [illegible] biota has evolved [illegible] to survive and even reproduce despite [illegible] natural disturbance events [illegible] systems (Barnes 1983; Wilson 1970; Gecy and Wilson 1990).

In western riparian zones the two most common examples of successful passive ecological restoration are the rewatering of streams after years of withdrawal for agricultural or municipal purposes and the cessation of livestock grazing in riparian areas. Stream flow diversion, combined with heavy livestock grazing, can result in severe degradation of riparian and stream ecosystems. With the return of perennial instream flows and the halt of livestock grazing, the recovery of riparian vegetation can be dramatic. For example, in the Mono basin of California, 24% of the *area of riparian vegetation lost during a 50-yr period* of water diversion (1940–1989) had reestablished after only 4 years following rewatering (Jones and Stokes Associates, Inc., and Trihey Associates, personal communications). [illegible] willow and cottonwood seedling densities were often >50 m^{-2} with annual growth rates of 0.6 to 1.5 m high (B. Kauffman and R. Beschta, Oregon State University, personal communication). Now, vegetation establishment is beginning to influence channel diversity through the creation of narrower channels, bank undercuts, and pools. In contrast, while several million dollars has been spent on *engineering manipulations* in and around stream channels, the influence of those manipulations on trout densities was insignificant and actually hurt the natural restoration process of the riparian and stream ecosystem (Beschta et al. 1994; Inter-Fluve 1993; W. S. Platts, Don Chapman and Consultants, personal communications).

Livestock grazing has been perhaps the most prevalent cause of ecological degradation for many western riparian and stream ecosystems (Kauffman and Krueger 1984; Kauffman 1988; Fleischner 1994). After extensive field reviews of fish habitat improvement projects in eastern Oregon, Beschta et al. (1991) and Kauffman et al. (1993) concluded that the cessation of livestock *grazing in riparian zones* of eastern Oregon was the single most ecologically effective approach to restoring salmonid habitats.

While many reviews of grazing effects on riparian vegetation have been general in nature (e.g., Platts 1991; Elmore and Kauffman 1994), recent research is providing improved insights into the effects of grazing on woody riparian species. This research is important because willows, cottonwoods, and alders are significant features of terrestrial wildlife habitat, stream channel morphology, and aquatic habitat. In central Oregon, Busse (1989) found a lack of willow and cottonwood reproduction in grazed riparian zones of the Crooked River National Grassland. After constructing corridor fencing, she recorded a widespread and rapid rate of willow and cottonwood establishment. In northeast Oregon, similar rates of woody species recovery after cattle grazing stopped have been quantified (Green and Kauffman 1995; Case and Kauffman, in press). Three years after cattle grazing stopped on Meadow Creek (a tributary of the *Grande Ronde River*), Case and Kauffman (in press) reported that the average crown volume of willows increased nearly 300%. Average crown volume of black cottonwood and alder increased 800% and 200%, respectively. *Comparing 10 years of no grazing with light* to moderate late-season grazing use in northeast Oregon, Green and Kauffman (1995) reported significant increases in both the density and structural complexity of willows and cottonwoods in ungrazed exclosures. Although positive trends in willow density and height also occurred in the lightly to moderately grazed areas (three weeks annually late in the season), recovery rates were significantly less than those of the ungrazed areas.

...misinterpreting ecosystem needs is common with many instream rehabilitation and enhancement programs

Reviews of instream habitat management projects throughout the western United States clearly indicate that passive restoration has been the [illegible] (Beschta et al. 1991; Kauffman et al. 1993; Beschta et al. 1994). In many cases, this was all that was needed to initiate restoration of riparian ecosystems. Because of the high costs and potential for failure with active restoration and manipulation, we recommended that project managers monitor and observe the natural recovery process for an appropriate period of time (e.g., 10 years) after implementing passive restoration. Then, if managers ascertain that natural recovery is limited or not occurring, implementation of active restoration projects might begin.

Active Restoration

After implementing passive restoration, a site still may remain in an ecological state that is unlike what would occur naturally (Figures 2 and 3). These situations can occur when an ecosystem is sufficiently degraded such that the inherent capacity to recover has been lost. To achieve ecological restoration in such situations, active manipulations will be necessary.

Many factors may prevent a return to a natural dynamic system when using only passive restoration—species extinctions [particularly keystone species such as cottonwood or beaver (*Castor canadensis*)], exotic predators [smallmouth bass or bullfrogs (*Rana catesbeiana*)], exotic competitors [carp (*Cyprinus carpio*), reed canary grass (*Phalaris arundinacea*), or knapweeds (*Centaurea* spp.)], loss of hydrologic function and alteration of hydrologic disturbance regimes (e.g., diversions, regulated flows by dams, disruptions of groundwater flow patterns), and alteration of geomorphic features (e.g., channel incision, soil erosion, compaction). While some of these barriers to recovery might be easily ameliorated, others can be sufficiently severe in their magnitude and persistence that restoration may not be technologically feasible.

Biotic manipulations representing active ecological restoration include the reintroduction of beaver or plant species that have been extirpated from the area. Reintroductions are most successful when a feasibility analysis has confirmed that suitable habitat is present for the organism to be reintroduced. In the case of beaver, adequate habitat conditions include sufficient availability of forage and suitable structure of riparian plant communities. If introduced into degraded or recovering ecosystems before woody species have sufficiently reestablished, beaver can actually limit ecological recovery (Kauffman et al. 1982; Case 1995). Alternatively, when reintroduced in suitable riparian habitat conditions, the beaver can dramatically accelerate the restoration process through its influence on the hydrology, wetland extent, species composition, and quality of salmonid habitats (Naiman et al. 1988; Lowry 1993).

Vegetation plantings are a commonly proposed restoration technique. However, after passive restoration is implemented, [illegible] woody species on suitable sites often makes artificial plantings unnecessary (Busse 1989; Schulz and Leininger 1990; Case and Kauffman, in press). Where shrubs and other woody species have been eliminated and the potential for natural reinvasion no longer exists, active revegetation will be required. For example, where high-flow regimes have been significantly altered (e.g., below a

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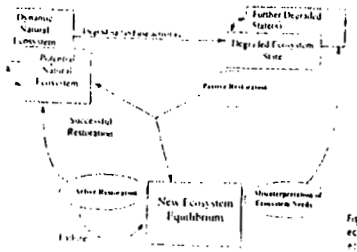

Figure 3 explores the conceptual pathways of ecosystem response to ecological restoration of western North American riparian and stream ecosystems

major dam), the natural regeneration of riparian-obligate trees and other woody species may be severely limited (Bradley and Smith 1986; Rood and Mahoney 1990). Without a recovery of high-flow regimes, artificial revegetation will likely be necessary to perpetuate forests within the historic floodplains. Gallery forests can be naturally perpetuated only if flow management allows high-water events to create conditions for regeneration.

By definition, ecological restoration of riparian vegetation entails the planting of only native species. The use of exotic plant species to "improve" riparian habitats associated with native fisheries is tantamount to introducing brook trout (*Salvelinus fontinalis*) or some other exotic fish as a substitute for extirpated native bull trout (*Salvelinus confluentus*) populations. In addition, revegetation with native species should focus on those areas of the riparian zone that contain appropriate substrates and microclimates. The planting of willows or conifers in native sedge meadows will likely result in failure or the creation of an unnatural, unsustainable plant community.

In addition to revegetation, a suite of silvicultural options to accelerate riparian forest development can be implemented. Creation of small canopy gaps, small clearings, and placement of coarse wood debris on the floodplain to serve as nurse logs can enhance growth rates of existing trees or provide conditions for establishment of desirable trees. Overstory manipulations should be done in a patchy, irregular manner to mimic natural disturbances and forest structure. In some instances, the products of thinning can be used as a source of instream wood or nurse logs. Prescribed burning also can be an important activity when used to mimic the disturbance regime of natural fires.

Appropriate livestock grazing management is of major importance for the proper functioning of many western riparian zones, particularly where grazing is deemed a primary use (e.g., private ranch lands). While some have suggested that livestock can be used as a "tool" in riparian enhancement, there is no ecological basis to indicate that livestock grazing, under any management strategy, can accelerate riparian recovery more rapidly than total exclusion (Platts 1991; Elmore and Kauffman 1994). The passive restoration approach of livestock exclusion demonstrably has resulted in a rapid recovery of riparian vegetation (U. S. General Accounting Office 1988; Beschta et al. 1991; Kauffman et al. 1993); however, less is known regarding rates of channel morphology recovery (P. McDowell, University of Oregon, personal communications). Although moderate levels of winter grazing, late-season (autumn) grazing, or early-season (spring) grazing have been demonstrated to reduce harm by livestock in some riparian zones (Platts 1991; Elmore and Kauffman 1994), any grazing practice must include close monitoring of woody use and bank conditions so that livestock can be promptly removed before significant damage occurs. The variety of approaches to active restoration is potentially large and beyond the scope of this document, but what is important regarding active restoration procedures is that any approach reestablish the disturbance regimes and conditions so natural hydrologic, geomorphic, and biotic processes can *occur. In some cases, active restoration may require* removing or altering artificial structures contributing to degradation or preventing natural ecosystem processes [illegible] occurring. These practices might include obliterating roads that are contributing excessive amounts of sediment, removing instream or streambank structures (e.g., rip-rap, gabions, and anchored structures) that limit channel dynamics, reconfiguring channelized reaches to increase their sinuosity and floodplain connectivity, and removing mainstem dams to eliminate barriers to fish migration.

Instream Structures

A general deficiency of large, woody debris within streams draining forested watersheds is common throughout much of the Pacific Northwest [illegible] historical practices of timber harvesting of riparian forests, splash damming, agricultural conversion, livestock grazing, and stream "cleaning" (i.e., the purposeful removal of wood debris). The natural recruitment of coarse, woody debris in such streams often requires much time (Gregory and Ashkenas 1990). As a result, managers often add large, woody debris. Where such practices are needed, the primary goal should be to provide natural amounts, types,

sizes, and spatial distributions of wood both in and along stream channels. During the inevitable high-water events that follow, added wood should function effectively in channel development and sediment and hydrologic routing (Gregory and Bisson 1997). Managers should place logs in or along channels so they resemble natural accumulations of debris, and should use complex wood debris (e.g., whole trees with branches and root wads if at all possible) to maximize habitat values and minimize potential for movement. The placement should enhance conditions that facilitate natural establishment of woody species (e.g., point-bar formation or nurse logs) so wood recruitment will become a self-perpetuating process. Anchoring or cabling complex pieces should be done sparingly, if at all, because it does not allow for the natural behavior of log accumulations during high-flow events. In this respect log length is critical; logs longer than the active channel width are not likely to move very far downstream (Lienkaemper and Swanson 1986).

Unfortunately, structural additions to channels (e.g., logs, boulders) are too often undertaken before anthropogenic impacts causing degradation have been eliminated or before significant natural recovery of riparian plant communities has occurred. In both situations, artificial structural additions are premature and can cause additional degradation to riparian and aquatic ecosystems. Of particular importance is the concern that placement activities should not diminish the natural regrowth capacity of riparian forests and should not severely curtail or accelerate natural channel dynamics such as channel migration, pool development, and streambank building. Riparian and stream ecosystems degraded from off-channel activities cannot be restored by focusing only on manipulations within a channel.

Throughout the western United States, inchannel placement of habitat structures has become one of the most common and widespread stream "enhancement" activities. Although instream structures have been commonly used in attempts to control channel erosion and rehabilitate fish habitat since the early twentieth century (Elmore and Kauffman 1994), systematic evaluation of their success has been limited. Furthermore, instream habitat handbooks (e.g., U.S. Forest Service 1952; Seehorn 1985, 1992) generally provide no ecological or geomorphic perspective as to where various habitat manipulations are appropriate (or inappropriate). A summary of instream enhancement projects throughout the region (Beschta et al. 1994) indicated little or no positive fisheries response to structural approaches. Clearly, the widespread practice of engineered structural modifications to streams with little or no scientific evidence of biological benefits represents a management paradox of immense proportions.

Misinterpretation of Ecosystem Needs

Active restoration should be undertaken to facilitate recovery of natural ecosystem processes (Kauffman et al. 1995). Riparian and instream activities that do not address ecosystem function and linkages are likely to fail or even exacerbate degradation of the ecosystem—a result of misinterpretation of ecosystem needs. Examples of such misinterpretation might include outplanting hatchery fish of nonindigenous genetic strains and introducing nonnative plant species. Implementation of riparian or inchannel activities that further degrade or prevent reestablishment of hydrologic, geomorphic, or biotic functions also represents a misinterpretation of ecosystem needs (Figure 3). Such activities may involve habitat manipulations such as blasting bedrock channels; adding logs and boulders in

> **Ecological restoration is a holistic approach not achieved through isolated manipulations of individual elements but through approaches ensuring that natural ecological processes occur...**

channels formed in floodplains of finely textured meadow systems; implementing in-channel engineering approaches *that are heavily anchored by cable, metal rods, or boulders* (structures that rely on geotextile fabrics to maintain their integrity); armoring streambanks with large boulders; and placing excavated sediments on streambanks and floodplains. Many of these approaches not only severely limit the capacity for streams to undergo natural adjustments in channel morphology and stream sinuosity through time, but they also may create conditions that suppress or stop the recovery of riparian vegetation.

Unfortunately, misinterpretating ecosystem needs is common with many instream rehabilitation and enhancement programs (Beschta et al. 1991; Kauffman et al. 1993). Stream manipulations targeted to fish habitat enhancement often exacerbate riparian and stream degradation for many reasons (Beschta et al. 1994):

- An inadequate understanding of riparian and stream ecology, particularly how stream-side vegetation and disturbance patterns shape both channels and habitat features;
- Sociopolitical pressures (e.g., it is socially or politically unacceptable to change ongoing land use practices that are causing degradation);
- Institutional limitations regarding the use of available funds (e.g., appropriations are designated only for mechanical or engineering approaches to stream manipulation with little or no appreciation of the effectiveness of improved stewardship);
- *Management philosophies that emphasize immediately* [illegible] the number of instream structures built during a fiscal year) rather than ecological improvement or improved stewardship;
- Emphasis on a "landscaping" approach (e.g., designing channels or building structures based on preconceived plans rather than addressing factors limiting the processes that create these habitat features);
- A presumption that engineering approaches (e.g., placement of boulders, woody debris, gabions,

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spawning gravels) are equivalent or superior to natural processes and structure:

- A presumption that inchannel structures can mitigate for riparian and aquatic degradation caused by land use practices (e.g., installing structures while allowing continued overgrazing, logging, or agricultural or industrial practices); and
- Current paradigms of land stewardship (e.g., a lack of a social or political land ethic that implicitly recognizes the value of natural or noncommodity products associated with naturally functioning and intact riparian ecosystems).

The rationale behind these reasons forms a common managerial paradigm: Stream, riparian, and fish habitat degradation brought about by anthropogenic activities, both locally and throughout a watershed, can be remedied solely through inchannel habitat manipulations. We suggest that the philosophy that natural habitat structure can be "improved" by engineering approaches misinterprets ecosystem needs and is an inadequate solution for fish habitat restoration. These approaches include activities that attempt to enhance fisheries habitat by eliminating natural barriers to fish passage, placing structures in intact ecosystems (old-growth forests), and putting spawning gravels or structural features such as logs or boulders in reaches where they would not naturally exist. Such activities not only carry a high risk of biological failure, but also risk a loss of capital resources, labor resources, and public credibility.

Sustainable and successful ecological restoration of degraded riparian systems is most likely to be achieved by considering the potential influences of proposed activities. Prior to the implementation of instream or riparian manipulations, the following questions should be addressed:

- Has passive restoration (e.g., changes in grazing, logging, etc.) been implemented, monitored, and evaluated prior to choosing structural manipulations?
- Will manipulations ultimately provide shade and thermally moderate stream temperature?
- Will they ultimately provide allochthonous inputs similar to that of stream-side vegetation?
- Will they ultimately provide the range of microhabitats typical of a particular stream?
- Will activities facilitate restoration of riparian vegetation that will restore natural channel morphology (e.g., overhanging banks, width-to-depth ratios, pool/riffle morphology)?
- Will they decrease time-rate dissipation of a stream's potential energy (i.e., stream power) by providing increased flow resistance from stream-side vegetation along a reach as compared with energy dissipation at localized points associated with inchannel structures?
- Will they allow for increased channel sinuosity from increased hydraulic roughness (as would occur with recovery of riparian vegetation)?
- Will biogeochemical and nutrient cycling influences on water chemistry—the results of the unique functional linkages between hydrologic and biotic features of intact riparian zones—be preserved or restored?
- Will the activities improve woody-debris recruitment and, hence, channel diversity because of enhanced vegetation establishment and growth?
- Are the restoration activities composed of naturally occurring materials? Are their characteristics and functions within the natural context of the riparian and stream reach to be treated?

Conclusions

Riparian zones are rich ecosystems in terms of biological diversity, unique biogeochemical processes, and productivity. For humans, riparian and stream ecosystems are a foci of commodity, recreational, and aesthetic values. The preservation and maintenance of intact riparian ecosystems and the restoration of degraded ones are important to local, regional, and global societies as well as to future generations.

While we recognize that ecological restoration sometimes comes at a high cost, we also note that ecological restoration is an investment in the natural capital of stream and aquatic systems and, hence, the environmental wealth of the nation. Healthy riparian ecosystems are a subsidy of nature. Conversely, degradation is the squandering of this natural wealth through the depletion of the productive capacity of ecosystems. Clearly, restoring once-productive riparian and aquatic ecosystems in the western United States is in the best long-term environmental and economic interests of the nation. Restored riparian and aquatic systems essentially will be self-maintaining and, therefore, useful in perpetuity (Cairns 1993). Because these ecosystems are a fundamental component of our life-support system, restoration should represent an important priority for both public and private landowners.

Complex ecosystems and associated habitat features cannot be created via simple and artificial construction of selected components. Ecological restoration is a holistic approach not achieved through isolated manipulations of individual elements but through approaches ensuring that natural ecological processes occur (National Research Council 1992). If society is to use, enjoy, and benefit from the wide range of values and products associated with western riparian and stream ecosystems, concerted efforts of ecological restoration should begin before their productive potential, diversity, and beauty are forever lost.

Acknowledgments

We wish to thank all of the biologists, hydrologists, landowners, and others dedicated to the restoration of the riparian and stream ecosystems of the world. Much of the research that generated the hypotheses and ideas presented in this paper was funded by the U.S.D.A. Pacific Northwest Research Station-Land and Water Interactions Team. We especially thank Peter Bisson, Nick Gerhardt, and Gordon Reeves for their helpful reviews of this paper.

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The National Watershed Assessment Program

By Sarah Lehman

To begin providing much-needed information on the condition of U.S. watersheds, the Environmental Protection Agency's (EPA) Office of Water, working with states, tribes, federal agencies (National Oceanic and Atmospheric Administration (NOAA), U.S. Geological Survey (USGS), and Natural Resources Conservation Service), and other partners (e.g., The Nature Conservancy) initiated the National Watershed Assessment Program (NWAP) in the summer of 1996. The NWAP is designed to collect, organize, and evaluate multiple sources of environmental information at the watershed level. The EPA defines watersheds using the USGS's eight-digit cataloging units. This divides the country into approximately 2,150 watersheds. This initiative will support and advance the EPA's watershed and community-based environmental protection efforts.

The objectives of the program are to:
- characterize the condition and vulnerability to pollution of 2,150 watersheds of the United States;
- empower citizens to learn more about their watersheds and work to protect them;
- provide the basis for dialogue among water quality managers; and
- measure progress toward the goal that all watersheds will be healthy places.

The National Watershed Assessment Project aims to move forward in various phases. In Phase I, EPA is the lead partner in aggregating aquatic resource information from different sources. The result of this work will be a set of 15 data layers combined to provide an overall view of aquatic system condition and vulnerability to future water quality problems in watersheds (Figure 1). The data layers selected for use in the NWAP characterization are based on a national set of water environmental indicators developed in five years by leaders of public and private water agencies and published in a report, "Environmental Indicators of Water Quality in the United States" (June 1996). The NWAP includes additional data sets for added clarity at the watershed level.

Even at this early stage in the process, the positive impacts of NWAP can be seen. For instance, NWAP has significantly improved some data sets supporting the characterization, and agencies are building closer relationships as they work to integrate these diverse data sets.

In Phase II of NWAP, states and tribes will be the lead partners, working with EPA regions and other partners, to use the data to decide where pollution prevention, remediation, or more data are needed. The NWAP characterization will be used in combination with other sources of information such as site-specific monitoring studies to make these decisions. Also in Phase II, EPA will continue to improve project's data and add six important missing elements: biological integrity, habitat, groundwater, coastal waters condition, air deposition, and downstream impacts of pollution exported beyond watershed boundaries.

Phase I is a good first step at aggregating diverse environmental data sets and producing a general characterization that can spotlight the need for additional work in particular watersheds. However, NWAP is not designed to provide the site-specific, detailed, and high-quality information on which individual activities such as issuing individual pollution discharge permits can be based. The project also is not the only or the final word on watershed conditions; there are additional, more-detailed data available at the state and local levels that watershed managers will want to use in designing watershed-specific action plans. Finally, NWAP is not designed as a template for a complete and detailed watershed monitoring plan; designing a monitoring plan should be undertaken as a follow-up step to the NWAP characterization in coordination with EPA regional, state, tribal, and local officials. The EPA has tools that can be used to set up such monitoring programs.

For more information about the project, contact Sarah Lehman, 202/260-7021.

NWAP Data Layers of Watershed Condition
1. Meeting designated uses set in state/tribal water quality standards
2. Fish consumption advisories
3. Source water quality indicators—community water systems
4. Contaminated sediments
5. Ambient water quality data—four toxic pollutants
6. Ambient water quality data—four conventional pollutants
7. Wetland loss index

NWAP Data Layers of Watershed Vulnerability
8. Aquatic/wetland species at risk
9. Discharge loads above permitted discharge limits—toxic pollutants
10. Discharge loads above permitted discharge limits—conventional pollutants
11. Urban runoff potential
12. Index of agricultural runoff impacts
13. Population change
14. Hydrological modification caused by dams
15. Estuarine pollution susceptibility index

Figure 1 lists the 15 data layers that define aquatic system condition and vulnerability to future water quality problems in watersheds used in the National Watershed Assessment Project.

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Environmental Scientists

[illegible] Society of Ecological Recovery and Restoration (SER), and [illegible] willing to assume a leadership role in [illegible] environmental [illegible] policy makers, and the private sector. Twenty Leopold Fellows per year will be chosen for the next three years. Those chosen will attend 14 days of training and [illegible] oriented workshops during their first year. Additional meetings will offer outreach and mentoring opportunities among a premier assemblage of environmental scientists. All expenses are paid. Program funding is provided by a grant from the David and Lucile Packard Foundation.

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For more information, contact Dr. Judith Vergun (541) 737-4684, vergunj@oce.orst.edu, or Dr. Jane Lubchenco (541) 737-5337, lubchenc@bcc.orst.edu, or visit the Aldo Leopold Leadership Program web site at http://www.leopold.orst.edu/.

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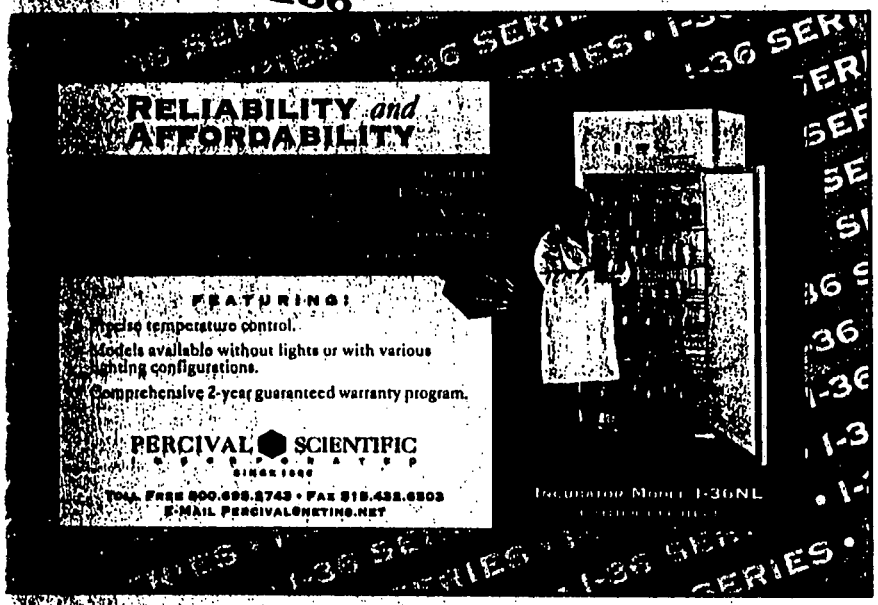

Managed Flooding for Riparian Ecosystem Restoration

Managed flooding reorganizes riparian forest ecosystems along the middle Rio Grande in New Mexico

Manuel C. Molles Jr., Clifford S. Crawford, Lisa M. Ellis, H. Maurice Valett, and Clifford N. Dahm

A centuries-old Indian pueblo named Isleta stands on a small rise of land west of the Rio Grande in central New Mexico. Its name, which means "island" in Spanish, reflects the fact that the pueblo was on an island in the middle of the Rio Grande when it was first seen by Spanish explorers (Pearce 1965). The name Isleta comes from the time before flood control on the Rio Grande, when spring flood waters roared down from the San Juan Mountains of Southern Colorado, flooding the middle Rio Grande Valley of central New Mexico (Figure 1). During some years, high spring runoff would extensively flood the middle Rio Grande Valley, sending most valley residents fleeing to surrounding high ground until the flood waters receded. However, these floods rarely touched Isleta Pueblo, only transforming it into the island its name suggests. While the residents of other settlements huddled in tent villages on the surrounding mesas, the life of Isleta's residents went on as usual. Today, dams and levees built on the Rio Grande have reduced the frequency and intensity of flooding; as a result, Isleta Pueblo is surrounded not by flood waters each spring but by alfalfa fields and suburban development.

> Out of this search for general ecological principles will come a better understanding of the structure and function of riparian ecosystems

The flood-pulse concept (Junk et al. 1989, Bayley 1995) emphasizes that water–land interactions create and maintain river–floodplain ecosystems as some of the most productive and diverse ecosystems in the world. However, river regulation has largely eliminated the flood pulse from most large rivers. Postel et al. (1996) estimated that humans now use a little over half of accessible river runoff worldwide. Fragmentation of river channels by dams, interbasin diversion, and irrigation strongly or moderately affect 77% of the total discharge of the 139 largest rivers in the northern third of the earth (Dynesius and Nilsson 1994). Benke (1990) noted that, except for the Yellowstone River in Montana, all large rivers in the 48 contiguous United States have been severely altered for flood control, hydropower, or navigation. He also estimated that of the 5,200,000 km of streams and rivers in the contiguous 48 states, only approximately 2% are classified as high quality. Moreover, only 42 free-flowing river segments longer than 200 km in length remain. There are currently 75,000 dams on the streams and rivers of the United States (Meyer 1996), and large dams are being completed at an estimated rate of 500 per year worldwide (Covich 1993). Thus, the extensive disconnection of rivers from their floodplains represents global-scale ecological change, the consequences of which we do not understand.

Studies of the effects of modified river flow on riparian ecosystem structure and function require long-term flow records. The flow record for the middle Rio Grande is exceptionally long. The first stream gauge established by the US Geological Survey was constructed on the Rio Grande at Embudo, New Mexico, in 1889. Since its construction, the Embudo gauge has been measuring the hydrologic regime of the Rio Grande. The most salient feature of that regime is a consistent annual peak in flow at the end of May or the beginning of June (Slack et al. 1993). Although flows still peak at the end of May, dams on the Rio Grande have eliminated most flooding. Historically, floods beginning in May would sometimes continue until late July. This spring flood pulse made the middle Rio Grande Valley a mosaic of river channels, marshes, wet meadows, and riparian forests of

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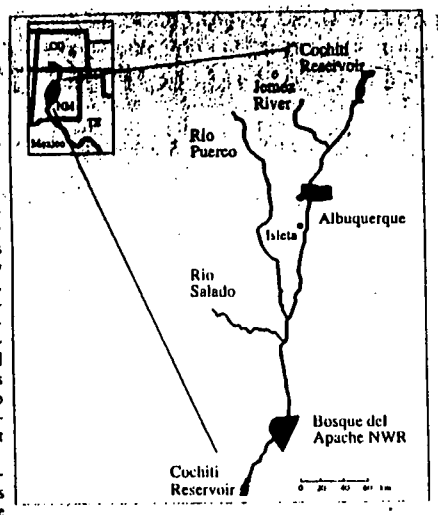

Figure 1. A map of the middle Rio Grande Valley in New Mexico showing the location of the study area at Bosque Del Apache National Wildlife Refuge.

various ages. Today, however, the middle Rio Grande no longer meanders freely across its valley but is constrained to flow within its levees. Most riparian forests are now confined to the area between the levees, and most of the wetlands in the middle Rio Grande have disappeared (Crawford et al. 1993, 1996a).

What are the ecological consequences of eliminating the annual flood pulse in the middle Rio Grande Valley? One of the most obvious consequences has been a dramatic reduction in the germination and establishment of native cottonwoods and willows (Howe and Knopf 1991). The riparian forest along the middle Rio Grande in central New Mexico is the most extensive cottonwood–willow forest left in the southwestern United States (Crawford et al. 1993). However, this extensive forest is largely an ecological legacy of past flooding. These stands may be rapidly senescing, and because of flood control, new stands of cottonwood are not being established. In addition, a stabilized river flow appears to favor invasion by non-native tree species, such as saltcedar, *Tamarix ramosissima*, and Russian olive, *Elaeagnus angustifolia* (Campbell and Dick-Peddie 1964, Crawford et al. 1996a).

Figure 2. A patch of riparian forest at Bosque Del Apache National Wildlife Refuge in 1991. This patch, which had not flooded for over 50 years, accumulated large amounts of woody debris. The absence of a flood pulse may contribute to such accumulations.

Students from the Department of Biology at the University of New Mexico have been monitoring several stands of riparian forest, or "bosque," as riparian forests along the Rio Grande are known, for approximately ten years. Monitoring of these riparian forests was prompted by the concern that without long-term data sets, these natural areas could not be managed properly. The riparian forest monitored by these students was established mainly during the last large flood on the middle Rio Grande, which took place in 1941–1942. Now, however, most of the forest along this reach no longer experiences overbank flooding. In the absence of flooding and with the invasion of non-native trees, these tracts of riparian forest have become tangled with woody debris (Figure 2). The organic matter that has accumulated on the floor of riparian forests along the middle Rio Grande now averages over 50×10^6 g/ha in some areas (Molles et al. 1996), which increases fire danger (Stuever 1997) and immobilizes substantial quantities of plant nutrients.

Monitoring has produced several data sets, including leaf fall, which has been used as an index of forest production. Autumn leaf fall has been measured in three sections of a 760 m long segment of riparian forest within the Rio Grande Nature Center in Albuquerque, New Mexico. From 1989 to 1996, leaf fall dropped steadily, declining by over 40% in just eight years. This record of leaf fall quantifies what had previously only been suspected: The bosque within Albuquerque is senescing rapidly (Figure 3). This finding gives a sense of urgency to research on riparian restoration along the middle Rio Grande.

Little is known about the potential importance of flooding for maintaining established riparian forest. To investigate how the absence of a flood pulse on the middle Rio Grande has affected the structure of microbial and animal populations on the forest floor and how the flood pulse affects the rates of ecosystem processes such as forest floor respiration and decomposition of plant litter, we created a series of managed floods in a riparian forest at Bosque del Apache National Wildlife Refuge near San Antonio, New Mexico. A major objective of our research is to evaluate the potential of managed floods as a tool for riparian restoration by measuring key population, community, and ecosystem responses to the reestablishment of flooding. In this article, we present some of our findings that bear on this approach to riparian restoration.

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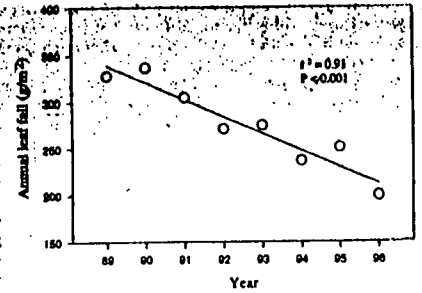

Figure 3. Annual leaf fall at the Rio Grande Nature Center in Albuquerque, New Mexico, from 1989 to 1996. Leaf fall declined by approximately 40% over that period. The absence of a flood pulse in the middle Rio Grande may reduce riparian forest leaf production.

Restoration and managed flooding

Figure 4 presents a conceptual model of the present status of and restoration efforts in the Rio Grande bosque. The present riparian ecosystem is a complex mosaic of forest patches dominated by either non-native vegetation, represented in Figure 4 by saltcedar, or native cottonwoods. These patches can be further subdivided into those that are disconnected from the river and are subject to long interflood intervals, and those that remain connected to the river and are subject to short interflood intervals. Current restoration efforts involve two main approaches. The first is aimed at converting non native forests to native forest by uprooting saltcedar and establishing cottonwood forests. This approach is indicated by the arrows labeled "1" in Figure 4. The second approach is to use managed flooding to reconnect disconnected riparian forests to the Rio Grande—that is, to reduce interflood intervals. It is this restoration approach (indicated by the arrow labeled "2" in Figure 4) that we explore in our studies.

Two study sites were established in 1991 in mixed cottonwood forest at Bosque del Apache National Wildlife Refuge, elevation 1400 m, approximately 5 km south of San Antonio, New Mexico. The two sites, which lie outside the river levee, have been isolated from flooding by the Rio Grande for more than 50 years. One site was designated as a control site and the other as the experimental flood site. Although we flooded approximately 10 ha of forest, ecological monitoring was organized around a 3.1 ha, 200 m diameter mammal-trapping web. In 1994, we established two additional study sites within the levees at Bosque del Apache. One of these additional sites seldom floods and so served as a second dry control site. The other site has continued to flood frequently because of its topography and position within the levees and was therefore designated as the natural flood site.

The canopy at all four study sites was dominated by Rio Grande cottonwood, *Populus deltoides* ssp. *wislizenii*, ranging from 8 to 15 m in height. The forest subcanopy consisted of Goodding willow, *Salix gooddingii*, and saltcedar. The dominant understory shrubs were seepwillow, *Baccharis glutinosa*, New Mexico olive, *Forestiera neomexicana*, and Russian olive.

We collected baseline data for two years and then flooded the experimental flood site for approximately one month during each of the following three years (Figure 5). These managed floods were designed to simulate the conditions of a low-energy flood near the edge or in the backwater of a major flood and to saturate riparian soils and soak organic matter on the forest floor. Floods, which took place from mid-May to mid-June of 1993, 1994, and 1995, were timed to coincide with the historic flood peak of May 31 at the US Geological Survey's Embudo gauging station on the upper Rio Grande (Slack et al. 1993). Floodwater was diverted from a nearby irrigation canal that carried a mixture of water diverted directly from the Rio Grande, irrigation return flows, and groundwater drainage accumulated in the nearby Rio Grande Low Flow Channel. The level of water diverted onto the experimental flood site was controlled by preexisting berms and by water-control gates constructed by personnel of the Bosque del Apache National Wildlife Refuge at the inflow and outflow of the experimental flood site. Because the topography is uneven, water depth during managed floods ranged from approximately 20 cm to over 200 cm, with an average floodwater depth of approximately 50 cm.

An ecosystem reorganization model for riparian restoration

Although Figure 4 depicts the reestablishment of the flood pulse to restore native forest as a direct process, reestablishing the flood pulse

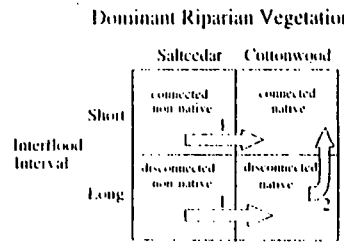

Figure 4. Riparian forest restoration in the middle Rio Grande Valley. Approach 1 converts non native forest into native cottonwood forest by uprooting saltcedar and establishing cottonwood through pole planting or wet-soils management to favor cottonwood seed germination. Approach 2 reestablishes the flood pulse, reconnecting riparian forest to the river and consequently reducing the interflood interval.

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to a riparian forest long disconnected from its river will initiate a distinctive ecological phase. Based on observations made during our research, we propose that flooding previously isolated riparian forests will initiate significant reorganization of the riparian ecosystem, a process much like that proposed by Bormann and Likens (1979) for hardwood forest ecosystems undergoing succession following clearcutting. We suggest that following reestablishment of flooding along the Rio Grande, this process of reorganization will eventually return the riparian forest to a position similar to its historic state (Crawford et al. 1996b). We propose that the ecological response to the restoration of flooding will involve three phases: the initial *disconnected phase*, represented in this study by the two dry control sites; a *reorganization phase* initiated by managed floods and represented in this study by the experimental flood site; and a *steady-state phase* that will approximate conditions prior to flood control, represented in this study by the natural flood site.

The structure and function of the riparian forest should differ substantially during the disconnected, reorganization, and steady-state phases. For instance, Figure 6 shows our model for changes in rates of forest-floor respiration during these phases. During the disconnected phase, forest-floor respiration will be limited by moisture availability. Indeed, as a consequence of moisture limitation in the arid climate of central New Mexico, forest-floor respiration should be orders of magnitude lower during the disconnected phase than during the other two phases. We predict that in mesic regions, forest-floor respiration should be more similar during the three phases.

The model predicts that forest-floor respiration will be highest during the initial stages of the reorganization phase, when organic matter pools are at their maximum and the pool of relatively labile organic matter is still large. As reorganization proceeds, annual flooding will continue to produce pulses of intense forest-floor respiration, but the height of the respiratory peak should be progressively damped as decomposition reduces the quantity and quality of organic matter on the forest floor. Eventually, when the pool of organic matter consists principally of the previous season's litterfall, the respiratory peaks will level off and the system will enter the steady-state phase.

Ecological responses to managed flooding

The first floodwaters diverted onto the experimental flood site crossed land that had not been subject to the flood pulse of the Rio Grande for over half a century. The rising waters of this managed flood induced immediate responses by forest-floor animals. The forest floor at the leading edge of the floodwaters came alive with hopping crickets and running spiders. However, our measurements revealed that some of the most dramatic responses to managed flooding involved unseen microbial populations and chemical and physical processes (Ellis et al. 1996). A broad range of ecological responses to the managed flooding conducted in this study is summarized in Table 1.

Population and community responses to flooding. Microbial populations and activity were generally increased by flooding (Table 1). Indications of increased microbial activity at the experimental flood site compared to the control site included increased abundance of soil bacteria, fungi, and cellulose decomposers. Both the root lengths colonized by mycorrhizal fungi and the mycorrhizal inoculum potential were also generally higher at the experimental flood site than at the control site. Dehydrogenase activity, which indicates soil biological activity, was more than twice as high at the experimental flood site.

Flooding also restructured the forest-floor arthropod community. During the course of the study, 120 species of forest-floor arthropods were collected at the control site and 116 species were collected at the experimental flood site. Managed flooding did not appear to affect the number of forest-floor arthropod species, but it did alter the relative abundance of species. Although flooding reduced both the species richness and the abundance of ants at the experimental flood site, at least one species of arboreal ant, *Crematogaster cerasi*, thrived in the presence of managed flooding. By contrast, floods reduced the abundance of ground-nesting ant species, such as *Monomorium minimum*. Flooding also reduced the abundance of two non-native terrestrial isopods, *Armadillidium vulgare* and *Porcellio laevis*. Meanwhile, populations of the native floodplain cricket, *Gryllus alogus*, increased with managed flooding.

In contrast to the responses by microbial and arthropod populations, three years of flooding had no measurable effect on small-mammal populations (Ellis et al. 1997). The dominant small mammal, the white-footed mouse, *Peromyscus leucopus*, was abundant at both the dry control sites and at the experimental and natural flood sites. Flooding did not affect the abundance of *P. leucopus* or its reproductive condition. Traps set in cottonwood trees during flooding showed that *P. leucopus* remained in the forest throughout the managed floods. This adaptability to managed flooding is not surprising because *P. leucopus* is common in floodplain forests throughout North America (Ruffer 1961, Blem and Blem 1975). This highly arboreal mouse escapes floodwaters simply by climbing trees.

Ecosystem responses to managed flooding. Large quantities of dissolved and particulate organic matter in the flooded forest created a very high biological oxygen demand, approaching that of raw sewage (Lieurance et al. 1994). The floodwaters entering the forest held approximately 8 mg/l. of dissolved oxygen (DO) but were rapidly depleted of DO by high oxygen demand. DO concentrations at 15 cm above the submerged litter layer fell to undetectable levels throughout the managed floods. By contrast, at the natural flood site, DO concentrations never fell below 4 mg/l within a few centimeters of the forest floor.

We used respiration chambers placed on the forest floor to measure forest-floor respiration during two managed floods and one natural flood. During the second managed flood, respiratory rates at the experimental flood site were 300 times higher than at the unflooded control site. During the third managed flood, forest-floor respiration was nearly 600 times higher at the experimental flood site than at the control site. The extremely high rates of respiration in the flooded forest appear to have involved many metabolic pathways, including sulfate reduction. During all three experimental floods, the flooded forest was filled with the smell of many sulfurous compounds. However, sulfurous smells were progressively reduced with each managed flood, which suggests ecosystem reorganization. Respiration rates measured at the natural flood site were approximately one-tenth the rates measured at the experimental flood site.

Flooding increased the rate of mass loss by leaves and logs (Molles et al. 1995, Ellis et al. 1996). By the second and third managed floods, mass loss by leaves at the experimental flood site was 125% higher than at the control site. However, the rates of leaf decomposition were almost identical at the experimental flood and natural flood sites. Flooding probably increases the rate of leaf mass loss through leaching of soluble substances and by increasing bacterial and fungal activity (Webster and Benfield 1986, Barlocher 1992).

Log decay rates were calculated using the exponential model $y_t = y_0 e^{-kt}$, where y_0 is the initial log mass, y_t is the log mass at time t, and k is the decay rate constant. At the experimental flood site, the average rate of log decay, k, was 0.065 y^{-1}, whereas at the control site it was 0.010 y^{-1}. These decay constants yield log half-lives of 10.6 years at the experimental flood site and 69.3 years at the control site. Although the three experimental floods did not significantly reduce the quantity of organic matter at the experimental flood site, the state of decay of woody debris was more advanced at this site than at the control site (Ellis et al. 1996, Molles et al. 1996).

Patterns of ecosystem reorganization

The population, community, and ecosystem responses we identified indicate that managed flooding initiated a process of ecosystem reorganization at the experimental flood site. Figure 7 pairs the conceptual model from Figure 6 with measurements of forest-floor respiration at the control, experimental, and natural flood sites. As predicted by the model, rates of respiration were two orders of magnitude higher during the experimental flood than on the dry forest floor. Contrary to the model, however, forest-floor respiration was 50% higher during the second experimental flood than it was during the first experimental flood. This increase may be the result of less anoxia during the second flood, which produced higher rates of organic matter processing. Also as predicted by the model, forest-floor respiration at the natural flood site was intermediate between the rates observed at the control and experimental flood sites.

The qualitative agreement between the ecosystem reorganization model and measured rates of forest-floor respiration indicates that restoration of flooding to disconnected riparian forests initiates a distinctive reorganization phase during the transition to full restoration. However, we predict that the amount of time required for reorganization will vary a great deal from one ecosystem component to another. As a consequence, some aspects of restoration will be delayed longer than others. Although long-term study and continued flooding of study sites will be necessary to document variation in the tempo of reorganization, it is possible to make some preliminary predictions.

The results of the three managed floods indicate that the time required for restoration of ecosystem components will range from less than one year to decades. For instance, the minimal response of small-mammal populations to the three managed floods suggests that restoration of flooding will not lead to a reorganization of these populations. By con-

Table 1. Several population, community, and ecosystem variables at control sites and experimental flood sites.

Response[a]	1993 C	1993 EF	1994 C	1994 EF	1995 C	1995 EF
Total soil bacteria (× 10^7 colonies/g soil)	43^{ab} (±6)	40^{a} (±4)	37^{a} (±6)	59^{a} (±4)	39^{a} (±4)	66^{a} (±6)
Total soil fungi (× 10^2/g soil)	67^{a} (±8)	34^{a} (±5)	45^{a} (±3)	69^{a} (±5)	$36^{a,b}$ (±4)	82^{b} (±9)
Cellulose decomposers (× 10^4 colonies/g soil)	20^{a} (±3)	52^{a} (±5)	48^{a} (±4)	93^{a} (±6)	46^{a} (±5)	94^{a} (±7)
Dehydrogenase (μg · g^{-1} · h^{-1})			4.19^{a} (±0.43)	9.26^{b} (±0.62)	3.75^{a} (±0.40)	9.4^{a} (±0.66)
Mycorrhizal colonization (% root length)	11^{a} (±4)	26^{a} (±2)	$48^{b,c}$ (±4)	$49^{c,b}$ (±7)	$40^{b,c}$ (±6)	56^{a} (±5)
Mycorrhizal inoculum potential (% root infection)	32^{a} (±4)	50^{a} (±4)	35^{a} (±4)	56^{a} (±9)	33^{a} (±9)	56^{a} (±5)
Ants (total in 30 traps in June and August)	348	18	192	9	95	10
Isopods (total in 30 traps in June and August)	970	320	407	49	2,335	405
Crickets (total in 30 traps in June and August)	2	5	2	84	4	9
Mice (individuals/ha in August)	22.02^{a} (±3.09)	25.98^{a} (±3.35)			16.74^{a} (±2.72)	13.66^{a} (±2.45)
Log decomposition (% mass remaining)			96.06^{a} (±1.48)	91.76^{a} (±2.11)	95.78^{a} (±1.29)	84.79^{b} (±5.07)
Leaf decomposition (g dry mass remaining)	2.78^{a} (±0.07)	2.18^{c} (±0.03)	3.32^{a} (±0.10)	1.78^{b} (±0.06)	3.27^{a} (±0.06)	1.98^{b} (±0.02)

[a]Statistical comparisons for microbial and fungal data are across all sites and years within each row; comparisons for mice and log and leaf decomposition are control versus experimental flood for each year only.
[b]Differently numbered superscripts indicate significant differences ($P < 0.01$).
[c]Values in parentheses are standard errors.
[d]$P = 0.061$

trast, populations of decomposer fungi, mycorrhizal fungi, and surface-active arthropods, such as ants and crickets, all showed substantial responses to the experimental floods and are therefore subject to reorganization. Both mycorrhizal and decomposer fungi doubled their activity during the course of each flood at the experimental flood site but returned to levels comparable to those at the control site within months. Thus, reorganization of fungal populations appears to take less than a year. Surface-active arthropods showed a greater response to flooding than fungi, but the response appears to have built up over the course of the three floods and not to have reached steady state. Consequently, reorganization of surface-active arthropod populations will likely take several additional years. By contrast, leaf decomposition was virtually identical at the experimental flood and natural flood sites by the third managed flood, indicating that reorganization of this process was complete.

Reorganization of forest-floor organic matter should take much longer. The orders-of-magnitude increase in forest-floor respiration in response to experimental flooding indicates a dramatic response by the forest-floor community. However, even with this high rate of respiration during flooding, three managed floods did not decrease the amount of forest-floor organic matter at the experimental flood site (Molles et al. 1996). The predicted half-life of 10.6 years for logs at the experimental flood site suggests that reorganization of forest-floor litter may take a decade or more.

Implications for management, policy, and research

The widespread modification of river and riparian ecosystems creates an urgent need to better understand the ecological effects of isolating riparian ecosystems from rivers and to develop methods to restore or better manage these threatened ecosystems. A growing scientific consensus identifies river and riparian restoration as priority areas for future research. Naiman et al. (1995) prioritized six research areas in freshwater ecology. The first priority was to develop principles to guide restoration of aquatic ecosystems and to develop methods to assess the success of restoration, the second was to determine principles for maintaining biodiversity, and the third was to explore the effects of modified hydrologic flow patterns on ecological processes. These three priorities are addressed by the effects of our managed floods on the composition of forest-floor communities and on rates of organic matter processing and by the ecosystem reorganization model for riparian restoration that we have proposed to explain these effects.

Restoration of river and riparian ecosystems has become a topic of intense interest worldwide. The managed flood on the Colorado River in the southwestern US in the spring of 1996 focused scientific and public attention on methods for managing and restoring river and riparian ecosystems through managed flooding (Collier et al. 1997; Schmidt et al. 1998). Reestablishing flooding on a river whose flow has been regulated for decades is now seen as a potential means to restore riverine fluvial geomorphology and to improve the chances for survival of threatened and endangered species in a riverine landscape. Another major restoration project is directed at the channelized and regulated Kissimmee River in South Florida. This project, which is scheduled to begin in 1998, is designed to restore 70 km of river channel and 11,000 ha of wetlands over the next 15 years (Dahm et al. 1995, Cummins and Dahm 1995, Toth et al. 1998).

Ambitious projects such as these represent historic initiatives in ecosystem restoration; however, they are a small part of the challenges that remain to restore degraded rivers and riparian zones throughout the world. Our research has yielded some of the first quantification of riparian ecosystem response to managed flooding. The observed rates of response and the ecosystem reorganization model for riparian restoration provide estimates of the potential trajectory and time required for riparian restoration with managed flooding.

Nowhere are anthropogenic impacts on river ecosystems greater than in the arid and semi-arid regions of the world. Water is the lifeblood of these regions, which constitute approximately 33% of the land surface worldwide. Increasing human demand for fresh water in arid regions leads to inevitable conflicts between the water needs of human populations and those of native ecosystems. The mismatch between water availability and water demand has placed most rivers and riparian zones of arid lands in peril. Based on historic habitat losses and increasing demands for water in the region, Christensen et al. (1996) describe all riparian forests in the United States as threatened ecosystems and the riparian forests of New Mexico, Arizona, and California as endangered.

Research to determine the basic principles for protecting and restoring these endangered ecosystems is, therefore, urgently needed. Our own studies have examined a broad spectrum of responses to managed flooding by a riparian ecosystem in a semi-arid region. Some of the results of this research have already been incorporated into policy and management recommendations for the Rio Grande (Crawford et al. 1993, 1996b). For instance, water managers along the Rio Grande are now considering a program of managed flooding, especially during years of higher water availability, to safeguard the health of the riparian forest. With this same goal in mind, academic scientists and water managers are conducting cooperative studies to quantify the potential water costs of managed flooding of riparian forests along the middle Rio Grande in New Mexico. The results of this work along the Rio Grande may have management implications for large, regulated rivers in other semi-arid regions.

There has been a growing understanding of the functional role of riparian zones (e.g. Gregory et al. 1991, Stanford and Ward 1993, Bayley 1995), which are now recognized as areas of high primary production, exceptional biodiversity, and rapid biogeochemical cycling. Our research applies an ecosystem perspective to riparian zones, similar to that emphasized by Gregory et al. (1991) and Bencala (1993), in which hydrologic exchange integrates river-

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Figure 5. The experimental flood site at Bosque Del Apache National Wildlife Refuge in 1994. Managed floods on this site flooded approximately 10 ha of riparian forest that had been disconnected from the Rio Grande for over 50 years.

ine and catchment systems and strongly influences biogeochemical processes and populations in riparian zones. Because flood control has limited the connections between rivers and riparian ecosystems, we are particularly interested in determining how variation in the interflood interval affects ecosystem structure and function. In most cases, reestablishing the full spectrum of historical river–riparian interactions is not a feasible management option (Crawford et al. 1996b). It appears, however, that managed floods can be used to partially restore riparian ecosystems.

It is essential to combine studies of ecosystem functional responses with community and population studies. By studying a broad spectrum of ecological responses to managed floods, we hope to resolve empirically the time course of ecosystem reorganization in response to hydrologic manipulation. Moreover, organizing experimental studies of restoration around conceptual models is likely to lead to general principles for ecosystem restoration. For instance, our proposed model of ecosystem reorganization led to two insights that should be considered during riparian restoration. First, *during restoration*, the ecosystem cannot proceed directly from the disconnected phase to the steady-state phase but must pass through a period of reorganization. Second, ecosystem components reorganize at different rates, and restoration projects must recognize and consider this variation in the tempo of reorganization. Out of this search for general ecological principles will come a better understanding of the structure and function of riparian ecosystems and more effective programs for their restoration.

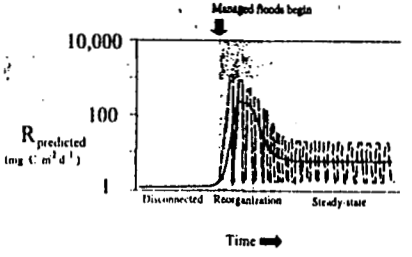

Figure 6. The reorganization model for riparian restoration. Restoration involves three phases: the disconnected phase, prior to the reestablishment of managed floods; the reorganization phase, induced by the reestablishment of the flood pulse; and the steady-state phase, which follows the reorganization phase. The predicted response to restoration plotted here is forest-floor respiration (R). Dotted line includes proposed within-year variation; solid line presents predicted average annual rates.

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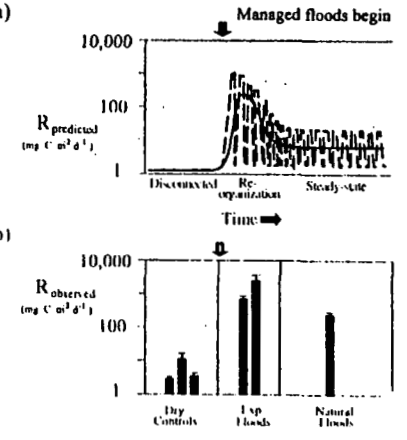

Figure 7. Predicted and observed rates of forest floor respiration. (a) Conceptual model (from Figure 6). (b) Observed rates of forest floor respiration at control sites, at the experimental flood site, and at the natural flood site.

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[illegible] undergraduate and graduate students at the University of New Mexico [illegible] insightful discussions with [illegible] Tidwell were much appreciated. This research was partially supported by Cooperative Agreement 14-16-0002-91-228 between The University of New Mexico and the US Fish and Wildlife Service, by NSF grant no. DEB-9414767, and by NASA Ecosystem Restoration Award NAGS-6999.

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Hydrologic Manipulations of the Channelized Kissimmee River

Implications for restoration

Louis A. Toth, Stefani L. Melvin, D. Albrey Arrington, and Joanne Chamberlain

Historically, much of south-central Florida was dominated by a contiguous wetland system that extended from the headwater lakes of the Kissimmee River basin to Florida Bay. During the past half century, this wetland landscape has been compartmentalized with a network of canals, levees, and water-control structures (gated spillways; Figure 1). This network is used to manage hydrologic regimes of the regional hydrosystem, primarily for flood-control purposes (Light and Dineen 1994, Toth and Aumen 1994).

Restoration of floodplain ecosystems requires the reestablishment of a broader range of hydrologic regimes than is possible through manipulations of managed hydrosystems

Modifications of the physical configuration and hydrology of the South Florida landscape have affected the Everglades, Lake Okeechobee, and the 7800 km² Kissimmee River basin, where an extensive flood-control project was constructed from 1962 to 1971. Lakes in the river's headwater basin were connected by canals and partitioned into flood-storage reservoirs; a 90 km long, 9 m deep, and 100 m wide drainage canal was excavated through the river–floodplain ecosystem; and the channelized river was transformed by levees and water-control structures into five pools with stabilized water levels.

The Kissimmee River flood-control project lowered both average and peak flood stages, reduced or eliminated water-level fluctuations, and drastically modified discharge regimes throughout the basin, but the hydrologic impacts were particularly severe within the channelized river–floodplain ecosystem. In contrast to the upper Mississippi River, in which maintenance of constant water levels upstream of navigation dams has increased open water and marsh habitats (Sparks 1995, Sparks et al. 1998), two-thirds (10,000 ha) of the Kissimmee's historic floodplain wetlands were drained by the lowering and stabilization of water levels (Toth et al. 1995). Even the most extreme post-channelization flood flows have been contained entirely within the banks of the constructed canal, and most of the floodplain wetlands that remain occur in the lower impounded portion of each pool and at the confluence of major tributary slough systems.

The modified hydrology and loss of wetland habitat have severely affected the structural and functional integrity of the floodplain (Toth 1993). Use of the river–floodplain system by wintering waterfowl has declined by 92% (Perrin et al. 1982). The naturalized cattle egret (*Bubulcus ibis*), a species that is primarily associated with cattle on pastures and other ruderal terrestrial habitats, has replaced the diverse complement of wading birds, including the endangered wood stork, that once used the floodplain wetlands (Toland 1990). A nationally renowned largemouth bass fishery and populations of other game fish species continue to decline, and the fish community is dominated by species tolerant of the altered habitat conditions of the channelized system (FGFWFC 1994). In addition to the loss of fish and wildlife habitat, drainage of floodplain wetlands has affected trophic resources that fueled the riverine food web (Toth 1990). Elimination of the nutrient-filtration function that was provided by the river's floodplain wetlands has exacerbated elevated nutrient loadings and transport to Lake Okeechobee, which is undergoing accelerated eutrophication due to intensive agricultural land uses (e.g., dairies) in contributing watersheds (Toth and Aumen 1994, Aumen 1995).

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QUANTIFYING IMPACTS TO RIPARIAN WETLANDS ASSOCIATED WITH REDUCED FLOWS ALONG THE GREYBULL RIVER, WYOMING

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Abstract: Reductions in river flows associated with hydrologic changes from diversions may reduce water elevations and impact hydrology of riparian wetlands. The U.S. Army Corps of Engineers and other federal agencies currently do not have appropriate tools to evaluate effects of hydrologic changes on wetlands. We describe use of HEC-RAS modeling to predict and quantify wetland impacts along 10 km of the Greybull River, Wyoming, USA following a proposed 28,313 L/sec diversion for a new off-channel reservoir. Riparian wetlands were delineated and mapped on aerial photographs and topographic maps. A water-surface-profile model of the river was developed using the HEC-RAS model. Floodplain boundaries with and without the diversion were plotted to the same scale and overlaid on the wetland maps to estimate area of wetlands that would not be flooded under the reduced flow model. The model predicted that total area flooded under the 28,313 L/sec diversion in the reach analyzed would be reduced from 167.2 to 149.7 ha and that approximately 0.47 ha of wetland would be impacted by the diversion. We believe that the procedure we used is a valid method to quantify effects of diversions on riparian wetlands and that this procedure should be further evaluated as a method to assess wetland impacts on similar projects.

Key Words: Greybull River, HEC-RAS modeling, riparian wetlands, Wyoming

INTRODUCTION

Many riparian wetlands are maintained by annual or semiannual flooding, especially those on the first terrace above the river channel. Reductions in river flows associated with hydrologic changes from diversions may alter wetland hydrology and eventually cause some wetlands to revert to uplands. A few studies have examined effects of reduced river flows on riparian communities, including wetlands, using historical gage data (e.g., Long and Nestler 1996) or historical and current aerial photography (e.g., Shoemaker et al. 1981). However, little research has been conducted that would allow for predicting and quantifying effects of reduced flows on riparian wetland area. The U.S. Army Corps of Engineers and other federal agencies involved with wetland preservation and management currently do not have appropriate tools to evaluate effects of hydrologic changes on wetlands (Long and Nestler 1996).

The Greybull Valley Irrigation District proposed the construction of a 36,948,700 m³ off-channel reservoir along the Greybull River in north-central Wyoming (Figure 1). The majority of water stored in the reservoir would be diverted during peak flows in the late spring and early summer. Wetlands along the Greybull River may potentially be impacted as a result of reduced flows of up to 28,313 L/sec in the river when active diversion of water to the reservoir is taking place. A method to estimate the area of wetland loss as a result of reduced flows was required to determine project-related impacts. Here, we describe use of HEC-RAS modeling to quantify impacts to wetlands resulting from reduced flows along the Greybull River.

STUDY AREA

The Greybull River is located in north-central Wyoming, USA in the Bighorn Basin. The upper end of the approximately 10-km stream reach potentially affected by reduced flows is located 24 km northeast of Meeteetse, Wyoming. That portion of the river within the project area is characterized as a highly braided stream (Zafft and Annear 1992). As is typical of streams fed by snowmelt, the majority of annual flow in the Greybull River occurs during the late spring and

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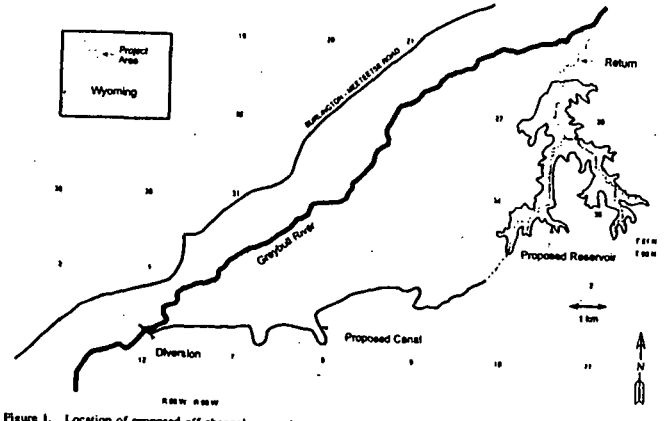

Figure 1. Location of proposed off-channel reservoir and analyzed reach of the Greybull River, Park County, Wyoming.

early summer months. Streamflow in the lower Greybull River currently fluctuates significantly on a daily basis due to variation in the rate of snowmelt in the high elevation headwaters of the river. The river has a riparian zone dominated by narrow-leaf cottonwood (*Populus angustifolia* James). Land adjacent to the river is predominantly irrigated agriculture; primary crops are malt barley, sugar beets, dry beans, and alfalfa. Average annual precipitation over the Greybull River drainage varies from less than 17.8 cm at the lower end of the basin to more than 152 cm at the upper end (Martner 1986). Average annual snowfall in the upper end of the drainage is more than 381 cm. The accumulated snowpack melts slowly in the spring, causing the peak flow in the Greybull River to occur in June, on average. Average annual runoff contributing to Greybull River flows is over 190,469 m^3/km^2 in the mountainous headwaters and declines to approximately 7143 m^3/km^2 in the desertic lower portions of the basin below Meeteetse.

METHODS

We delineated wetlands along the Greybull River riparian corridor using the U.S. Army Corps of Engineers (ACOE) wetland delineation manual (ACOE 1987) in 1996. We plotted delineated wetlands on aerial photographs with a scale of 1 cm = 48 m and enlarged 7.5' USGS topographic maps, and determined total area of each wetland polygon using a calibrated digitizer.

We developed a water-surface-profile model of the Greybull River using the HEC-RAS (Hydrologic Engineering Center—River Analysis System) model (U.S. Army Corps of Engineers 1995) to quantify potential effects on riparian wetlands of diversions to the proposed reservoir. The HEC-RAS model was developed by the U.S. Army Corps of Engineers and allows calculation of the water-surface profile through a river reach for a given flowrate or flowrates in the river. Input to the model includes the geometry of the river valley through the reach of interest as defined by cross-sections of the valley. Cross-sections are required at intervals short enough to allow hydraulic calculation of the water surface between cross-sections. Also input are the flowrate or flowrates for which profiles are to be calculated and the estimated hydraulic roughness of the river channel and overbank areas. Output from the model includes detailed calculated hydraulic data for each river reach between cross-sections and the calculated water-surface elevation at each cross-section for each flowrate. These calculated water-surface elevations can then be used to map the extent of inundation of the river valley that would be expected during each modeled flowrate in the river.

We used the HEC-RAS model to estimate extent of the flooded area during a 2-year flow event with and without the proposed 28,313 L/sec diversion. We assumed that potential effects of diversions would primarily be concentrated in the reach between the reservoir diversion point and the point where the reservoir released diverted water back to the river (Figure 1). We also assumed that the 2-year floodplain would be the outer limit of the wetland area potentially affected by the diversion because the peak flow that occurs every two years would provide inflow to depressions and low areas with enough frequency to potentially establish wetlands. The 2-year flood also should approximate the event that defines the lowest terrace adjacent to the incised channel of the river (Linsley et al. 1975). Diverting 28,313 L/sec from the 2-year peak flow and mapping the new floodplain allowed us to estimate the area of wetland that would no longer receive surface-water inflows with enough frequency to establish wetland hydrology under a proposed 28,313 L/sec diversion.

We developed geometry of the river reach using USGS 7 ½ minute quadrangle maps with 6.1 m contour intervals, and estimated the hydraulic roughness of the river channel and overbank areas using published data for similar rivers (Chow 1959, Henderson 1966). Contour lines on the quadrangle maps were digitized at elevation into a three-dimensional AutoCAD drawing. Because of the large contour interval, we estimated additional information by drawing three-dimensional polylines along the break points at the edge of each terrace and along the centerline of the stream. We prepared cross-sections at required points along the stream by draping a three-dimensional polyline over the contours and break lines along the cross-section alignment and then extracting the coordinates of the vertices into a digital file that was formatted for input into the HEC-RAS model.

We estimated the flowrate expected for the 2-year runoff event using flow data for the Greybull River at the Meeteetse gaging station, located approximately 24 km upstream of the diversion. Inflows below this station are generally the result of thunderstorms over the drainages of small tributaries to the Greybull River. These storms are relatively small and do not coincide with peak flows resulting from snowmelt in the upper basin. Results of conveyance loss modeling of the Greybull River also indicate that there is some conveyance loss between the Meeteetse station and the reach analyzed (Lewallen 1994); therefore, use of the 2-year runoff event based on flows at the Meeteetse gage station should result in a conservatively high estimate of the 2-year peak flow at the reach potentially affected by the project.

We analyzed peak flow data from the Greybull River at Meeteetse station for the period from 1921 through 1994 using the ACOE Flood Frequency Analysis (FFA) program (ACOE 1992) and a spreadsheet model we developed. The 2-year event was estimated using both the Log Pearson Type III distribution and the Extreme Value Type I distribution and different periods of record. Results of the analyses indicated that estimates of the 2-year flood ranged from 85,647 L/sec to 99,662 L/sec. Because the reach analyzed is located several km downstream of the gaging station, we used the number at the lower end of the range (85,647 L/sec) as the 2-year runoff event for the affected reach. Flowrates used to model floodplains associated with the 28,313 L/sec diversion were estimated by subtracting the respective canal capacity from the flow for the 2-year event.

To calibrate the model, we surveyed elevations at the intersection of the water surface with the side slopes of the valley at 22 selected cross-sections in the river reach. Budget constraints and the long river reaches involved made it economically infeasible to survey the entire cross-sections. Elevations were determined using a Geographical Positions System (GPS) satellite surveying unit during a relatively high flow period (25 June to 1 July 1996). Recorder charts were obtained from the Meeteetse gaging station for the same period so that flowrate in the river at the cross-section locations could be estimated for the times when the intersection points were surveyed.

Surveyed elevations were plotted against the river profile obtained from the topographic maps and appeared to be accurate. Because locations of the points in reference to the river profile could be identified, we used the surveyed elevations to calibrate the water-surface-profile model. A hydrograph of surface-water flow at the Meeteetse gaging station was prepared for the same period that water-surface elevations were determined (25 June through 1 July). We then used a conveyance loss study for the Greybull River (Lewallen 1994) to simulate hydrographs at the locations of the surveyed points on the cross sections. The conveyance loss study contained estimates of travel times and conveyance losses between the gaging station at Meeteetse and the study-area reach for various flowrates in the river. We used a spreadsheet to apply these travel times and conveyance losses to the hydrograph at the Meeteetse gage to simulate hydrographs at the cross sections along the reach analyzed. All travel times and conveyance losses were proportionally adjusted for the distance from the Meeteetse gage to the reach analyzed as well as for the magnitude of the flow. Hydrographs for the Meeteetse gaging station

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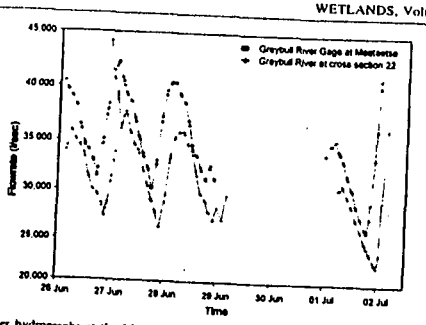

Figure 2. Greybull River hydrographs at the Meeteetse gage and survey point 22 during the period when surveying was conducted.

Table 1. Comparison of surveyed and modeled water-surface elevations (m) at survey locations along the Greybull River.

Point No.	Surveyed Elevation	Modeled Elevation	Difference
1	1582.9	1582.9	0.0
2	1576.7	1576.8	0.1
3	1574.2	1574.7	0.0
4	1570.2	1570.3	0.1
5	1565.5	1565.2	−0.3
6	1558.2	1558.4	0.2
7	1555.9	1556.1	0.2
8	1554.2	1554.0	−0.2
9	1547.1	1547.1	0.0
10	1540.7	1540.7	0.0
11	1535.4	1535.3	−0.1
12	1533.0	1532.9	−0.1
13	1531.5	1531.1	−0.4
14	1526.5	1526.5	0.0
15	1521.9	1521.9	0.0
16	1502.5	1502.4	−0.1
17	1499.1	1499.1	0.0
18	1490.1	1490.0	−0.1
19S*	1478.6	1478.6	0.0
19N	1478.7	1478.6	−0.1
20S	1474.8	1475.0	0.2
20N	1474.8	1475.0	0.2
21S	1468.2	1467.0	−1.2
21N	1467.1	1467.0	−0.1
22S	1434.7	1434.7	0.0
22N	1434.5	1434.7	0.2

* S = south side of river, N = north side of river at same cross section.

and an example survey point at a cross section show effects of travel time and conveyance losses on flow in the river between these two points (Figure 2).

Using the simulated hydrographs, we estimated the flowrate at a surveyed point at the time of the surveyed elevation measurement. Estimated flowrates at the points generally fell into a pattern where the flowrates in the upper reaches were all approximately 31,144 L/sec; flowrates in the middle portion of the analyzed reaches were approximately 35,391 L/sec, and flowrates in the lower portion of the analyzed reach were approximately 28,596 L/sec. These estimated flowrates were then used to calibrate the model. Water-surface elevations obtained from the first HEC-RAS model run were generally lower than the surveyed elevations. To calibrate the model, we adjusted elevations of the HEC-RAS cross-sections to match the surveyed data by raising or lowering the portions of the cross-section nearest the river while retaining the original data for portions of the cross-section away from the river (Table 1). The general shape of the adjusted cross-sections was maintained while adjusting the height of the terraces along the river.

We calibrated the model by adjusting cross-sections as described above because there is a band of shrubs and trees immediately adjacent to both banks of the river in the reach analyzed. Outside this band, the upper terraces along the river are usually cultivated fields or open pasture. In general, we expected the elevations of the cross-sections obtained from the quadrangle maps to be more accurate in the open fields where the ground surface could be seen in aerial photographs and less accurate adjacent to the river where vegetative

cover obscured the ground surface. The general shapes of the cross-sections were assumed to be accurate because they were based on features observable in aerial photographs.

Results of the calibration process indicated that our assumptions regarding accuracy of the cross-sections were correct. The first HEC-RAS model run, based on data taken directly from the quadrangle maps, had several breaks in slope along the profile of the river channel in the analyzed reach. These breaks in slope made it difficult to obtain convergence in the HEC-RAS model. However, after we adjusted the cross-sections using the surveyed elevations, most of these breaks in slope were eliminated, and the model was able to converge relatively easily. Since we would not generally expect to see numerous changes in the slope of a river channel through a wide alluvial valley such as the Greybull River valley in the reach analyzed, we assumed that the cross-section elevations along the river taken from the quadrangle maps were in error.

Our options for calibration of the HEC-RAS model were limited because of a shortage of usable data. The only topographic data available were from the quadrangle maps, and the only flow data were from a station located 24 km upstream. This lack of data is typical of most streams in Wyoming due to the rural and isolated nature of the state. In most cases, a HEC-RAS model of a stream reach in Wyoming is calibrated using a single measured or estimated flood elevation for a measured or estimated runoff event at a single point along the river reach to be analyzed. In this case, we were able to calibrate to 22 measured flood elevations at 22 points along the river reach in question, and the results of the calibration process indicated that the calibration was reasonable. A sensitivity analysis of the calibration process was not conducted due to the lack of data with which to calibrate.

We used the calibrated model to estimate floodplain boundaries for the 2-year runoff event of 85,647 L/sec. The 2-year peak flow was entered into the HEC-RAS model and coordinates of the intersections of the water-surface profile with the cross-sections were output into a table. The table was used to plot the boundary points in the AutoCAD drawing, and the floodplain boundary was drawn between the cross-sections. Once we established the 2-year floodplain boundary, we ran the HEC-RAS model again assuming that 28,313 L/sec was diverted from the river. The same procedure described above was used to prepare a map of the floodplain boundary for the 2-year event minus 28,313 L/sec (Figure 3).

We then used the plotted floodplain boundaries to estimate total area between the floodplain boundaries from the reservoir diversion point to the return point. Floodplain boundaries were plotted to the same scale and overlaid on the wetland maps to estimate area of wetland that might be affected. We conservatively assumed that if the reduced flow model resulted in loss of flow to the wetland, then the entire wetland was affected, even if the wetland extended beyond the limits of the HEC-RAS flooded area prediction. Likewise, we assumed that if any part of the wetland fell within the flooded area of the reduced flow model, the wetland would remain flooded.

RESULTS AND DISCUSSION

There are approximately 10 linear km of the Greybull River between the diversion structure and the return flow point (Figure 1). Total area of all wetlands in this stretch of river was 68.6 ha. Many wetlands along the river were associated with islands, gravel/sand bars, secondary channels, and low areas adjacent to the river that are frequently flooded. Additional wetlands form as a result of irrigation return flows and drainage from non-irrigated uplands adjacent to the river. Based on observations made during the field delineation, we estimated that 64% of wetlands along the river corridor have river-induced hydrology, 30% are created by irrigation return flows, and 6% receive water from both the river and irrigation return flows. Based on U.S. Fish and Wildlife Service National Wetland Inventory map classifications, 40% are classified as palustrine emergent seasonally flooded wetlands, 30% are classified as riverine lower perennial unconsolidated shore seasonally flooded wetlands, 25% are classified as palustrine scrub-shrub temporarily flooded wetlands, 3% are classified as palustrine emergent temporarily flooded wetlands, and 2% are classified as riverine lower perennial unconsolidated bottom intermittently flooded wetlands.

Based on the HEC-RAS model, approximately 167.2 ha are flooded during a 2-year flood event between the diversion point and return flow point for the proposed reservoir. With a 28,313 L/sec diversion, approximately 149.7 ha would be flooded, a reduction of 17.5 ha (10.5%). HEC-RAS model overlays indicated that approximately 0.47 ha of wetland could be impacted by reduced flows in the Greybull River of up to 28,313 L/sec; these wetlands were all classified as palustrine emergent wetlands.

In view of the large area of riparian wetlands, predicted wetland impacts were minimal, primarily because the modeled floodplain boundaries with and without the 28,313 L/sec diversion were very close together (Figure 3). It appeared that the 2-year flood filled the channel and covered the first terrace above the river. Even a 28,313 L/sec reduction in flow did not result in a significantly different floodplain boundary because of the width of the floodplain at these

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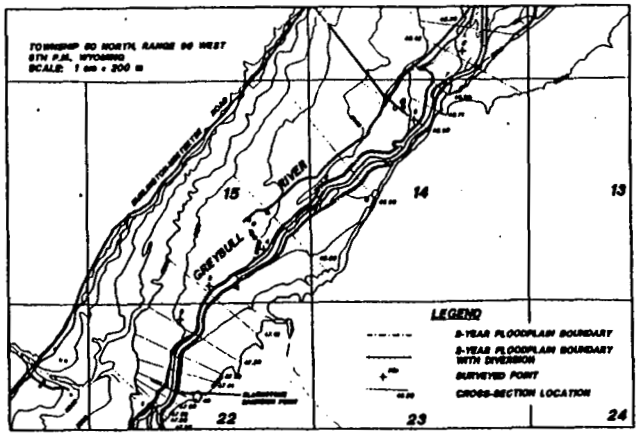

Figure 3. Results of HEC-RAS modeling showing two-year flood event boundaries with and without a 28,313 L/sec diversion for example portion of stream reach analyzed.

flowrates. The wide floodplain in combination with the steep slopes at the periphery of the first terrace in most of the reach allow large variations in flowrate with small differences in water surface elevations.

The accuracy of the results obtained with this procedure is directly related to the accuracy of the input data. In this case, the length of the river reach we investigated precluded use of surveyed cross-sections to define the river valley geometry and collection of extensive water-surface-elevation data for model calibration. The steepness of the Greybull River valley and the braided geomorphology of the stream channel were additional complicating factors because each condition increases the number of cross-sections required to define the geometry of the river valley. Identification of impacted wetlands would likely have been more accurate if it had been economically feasible to obtain more accurate model input data for river-valley geometry.

The estimated flowrate for the 2-year event as well as the estimated flowrates used during the model calibration process were probably as accurate as could be expected for most river reaches for which this procedure might be used. The gaging station used in this study was a significant distance above the river reach being investigated; however, there were no significant inflows below the gage and above the reach in question. A recent conveyance loss and time-of-travel study also was available for the Greybull River between the gage and the reach investigated, which increased the reliability of the estimates. We believe that the procedure we used is a valid method to measure effects of a diversion on riparian wetlands and that this procedure should be further evaluated as a method to assess wetland impacts on similar projects.

ACKNOWLEDGMENTS

This research was supported by the Wyoming Water Development Commission and the Greybull Valley Irrigation District. C. Peter of the ACOE Cheyenne, Wyoming regulatory office provided helpful input on study design. P. Reid of AVI, p.c., Cheyenne, Wyoming surveyed cross-section points along the river. Numerous landowners along the Greybull River kindly allowed access for the study. We greatly appreciate the helpful review of this manuscript by R. Dahlgren of States West Water Resources, Cheyenne, Wyoming.

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Manuscript received 13 February 1998; revision received 7 August 1998; accepted 10 August 1998.

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SEPTEMBER 29, 1995

Riparian Zone Workshop Focuses on Natural Water Pollution Prevention

GRAND FORKS, N.D. - The establishment of riparian zones-areas of trees, shrubs and vegetation that line the banks of streams and rivers-is one of the best methods for preventing surface water and groundwater pollution.

To assist in the restoration of riparian zones in the Red River basin, a workshop will be held Oct. 3 4 at the University of North Dakota (UND), Grand Forks. Participants will be updated on the Red River Basin Riparian Demonstration project which is aimed at restoring riparian areas and improving surface water and groundwater in eastern North Dakota.

"Riparian zones are vital because they provide natural buffers that reduce the amount of contaminants and soil sediments flowing into waterways," says Linda Kingery, riparian project coordinator for the Red River Regional Planning Council. "They also provide bank stabilization and wildlife habitat."

The workshop will include discussions on issues and techniques for managing forested riparian areas; a bioengineering workshop on stream bank stabilization conducted by the Michigan State Natural Resources Conservation Service Riparian Team; and a field demonstration of stream bank stabilization using bioengineering practices.

"Only two percent of the length of all rivers in the United States is adequately protected by riparian buffers," says Kingery. "If nutrient loading occurs, the average family will pay $10-15 a month to remove contaminants from water, which is very expensive compared to the one-time cost of establishing riparian zones."

Kingery says that working with landowners and educating them about the value and benefits of riparian zones has led many farmers and ranchers to voluntarily restore riparian areas on their land. Changes in farming and ranching practices, along with the replanting of grasses and woody vegetation along stream and river banks, can help reverse damage to riparian areas.

The riparian workshop is being organized by the UND Energy & Environmental Research Center (EERC) in cooperation with the Red River Conservation and Development Committee, the Red River Regional Council, the North Dakota Society of American Foresters, the North Dakota Forest Service and the Glacial Lake Agassiz Interbeach Committee.

For More Information Contact:

- Linda Kingery, riparian project coordinator, Red River Regional Council, (701) 352-3550
- Gale Mayer, Senior Research Manager/gmayer@eerc.und.nodak.edu, (701)777-5108

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Restoring prairie wetlands : an ecological approach / Susan M. Galatowitsch and Arnold van der Valk.

Galatowitsch, Susan M.

Personal author:	**Galatowitsch, Susan M.**
Title:	**Restoring prairie wetlands : an ecological approach / Susan M. Galatowitsch and Arnold van der Valk.**
Edition:	**1st ed.**
Publication info:	**Ames : Iowa State University Press, 1994.**
Physical description:	**x, 246 p. : ill. ; 24 cm.**
General note:	**"A special publication of Ducks Unlimited's Institute for Wetland and Waterfowl Research."**
Bibliography note:	**Includes bibliographical references and index.**
Subject:	**Wetland conservation.**
Subject:	**Wetland conservation--Prairie Pothole Region.**
Subject:	**Restoration ecology.**
Subject:	**Restoration ecology--Prairie Pothole Region.**
Subject:	**Wetland ecology.**
Subject:	**Wetland ecology--Prairie Pothole Region.**
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cooperation with the Florida Department of Environmental Regulation.
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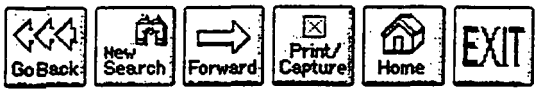

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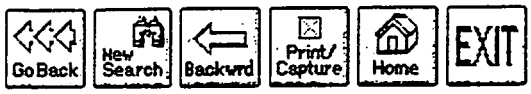

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TITLE The western San Juan Mountains : their geology, ecology, and human history / managing editor, Rob Blair ; technical editors, Tom Ann Casey, William H. Romme, Richard N. Ellis.

PUBLISHER Niwot, Colo. : University Press of Colorado : Fort Lewis College Foundation, c1996.

DESCRIPTION xiii, 406 p. : ill., maps ; 23 cm.

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CONTENTS Origin of landscapes / Rob Blair -- Paleotectonic history / Douglas C. Brew -- Precambrian rocks / Jack A. Ellingson -- Paleozoic history / John A. Campbell -- Mesozoic and early Cenozoic history / Jack Campbell and Doug Brew -- Volcanic rocks / Jack A. Ellingson -- Ore deposits and minerals / Scott Fetchenhier -- Energy resources / T.L. Britt and J.M. Hornbeck -- Weather and climate / Richard A. Keen -- Ecological patterns / Albert W. Spencer and William H. Romme -- Biotic communities of the semiarid foothills and valleys / Lisa Floyd-Hanna, Albert W. Spencer and William H. Romme -- Biotic communities of the cool mountains / David W. Jamieson, William H. Romme and Preston Somers -- Wetlands, riparian habitats, and rivers / Preston Somers and Lisa Floyd-Hanna -- The foragers of the forest / Philip Duke -- The Anasazi : prehistoric farmers / Gary Matlock -- The Spanish / Richard N. Ellis -- The Utes / Richard N. Ellis -- The miners : they builded better than they knew / Duane Smith -- Points of interest along the San Juan Skyway / Rob Blair and Preston Somers -- Points of interest along the Durango-to-Silverton narrow-gauge railroad / Rob Blair -- Points of interest along the Alpine Loop / Barb Byron.

NAME ED AUTH Blair, Rob, 1943-

ISBN 0870813781 (alk. paper)
0870813773.

OCLC # 33440779.

LC CONTROL # 95041819.

LOCATION	CALL #	STATUS
1 > ANDERSON/GENERAL COLL	F782.S18 W47 1996	IN LIBRARY

AUTHOR	Galatowitsch, Susan M.
TITLE	Restoring prairie wetlands : an ecological approach / Susan M. Galatowitsch and Arnold van der Valk.
EDITION	1st ed.
PUBLISHER	Ames : Iowa State University Press, 1994.
DESCRIPTION	x, 246 p. : ill. ; 24 cm.
SUBJECT HDNG	Wetland conservation. Wetland conservation -- Prairie Pothole Region. Restoration ecology. Restoration ecology -- Prairie Pothole Region. Wetland ecology. Wetland ecology -- Prairie Pothole Region.
NOTE	"A special publication of Ducks Unlimited's Institute for Wetland and Waterfowl Research." Includes bibliographical references and index.
ADDED AUTH	Valk, Arnoud van der.
CORP AUTHOR	Institute for Wetland and Waterfowl Research.
ISBN	0813824990 (alk. paper)
OCLC #	29755979.
LC CONTROL #	93027825.

LOCATION	CALL #	STATUS
1 > ANDERSON/GENERAL COLL	QH75.G35 1994	IN LIBRARY

3610

TITLE Plant life in aquatic and amphibious habitats / edited by R.M.M. Crawford.
PUBLISHER Oxford [Oxfordshire] ; Boston Mass., U.S.A. : Blackwell Scientific Publications ; Palo Alto, Calif. : Distributors, U.S.A. and Canada, Blackwell Scientific Publications, 1987.
DESCRIPTION xii, 452 p. : ill. ; 26 cm.
SUBJECT HDNG Aquatic plants.
Aquatic ecology.
Plants, Effect of floods on.
Wetland plants.
Wetland ecology.
SERIES Special publication ... of the British Ecological Society ; no. 5.
NOTE "Produced as a tribute to D.H.N. Spence."
Includes bibliographies and index.
ADDED AUTH Crawford, R. M. M.
Spence, David Hugh Neven, 1925-1985.
ISBN 0632016280.
OCLC # 14097311.
LC CONTROL # 86020752.

LOCATION	CALL #	STATUS
1 > ANDERSON/GENERAL COLL	QK930.P57 1987	IN LIBRARY

TITLE Trends and status of wetland and aquatic habitats in the Galveston Bay System, Texas / William A. White ... [et al.]. ; principal investigators, E.G. Wermund, Jr. and L.R. Handley.
JBLISHER [Galveston, Tex.] : Galveston Bay National Estuary Program, [1993]
DESCRIPTION 225 p. : ill., maps ; 28 cm. + 3 leaves of plates.
SUBJECT HDNG Wetland ecology -- Texas -- Galveston Bay.
Aquatic ecology -- Texas -- Galveston Bay.
SERIES Publication GBNEP ; 31.
NOTE "This project has been funded in part by the United States Environmental Protection Agency under assistance agreement # CE-006550-01 to the Texas Water Commission"--P. iv.
Plates folded in back pocket.
Includes bibliographical references (p. 129-135)
ADDED AUTH White, William Allen, 1939-
Wermund, E. G.
Handley, Lawrence R.
CORP AUTHOR United States. Environmental Protection Agency.
Texas Water Commission.
Galveston Bay National Estuary Program.
OCLC # 29748553.
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PUBLISHER [Galveston, Tex.] : Galveston Bay National Estuary Program, [1993]
ESCRIPTION 225 p. : ill., maps ; 28 cm. + 3 leaves of plates.
JBJECT HDNG Wetland ecology -- Texas -- Galveston Bay.
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SERIES Publication GBNEP ; 31.
NOTE "This project has been funded in part by the United States Environmental Protection Agency under assistance agreement # CE-006550-01 to the Texas Water Commission"--P. iv.
Plates folded in back pocket.
Includes bibliographical references (p. 129-135)
ADDED AUTH White, William Allen, 1939-
Wermund, E. G.
Handley, Lawrence R.
CORP AUTHOR United States. Environmental Protection Agency.
Texas Water Commission.
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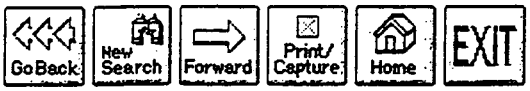

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Urbanska, K. M. (Krystyna M.)

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GE42 .E45 1997
Faking nature : the ethics of environmental restoration / Robert Elliot.
Elliot, Robert, 1950-
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#9 ☐ View
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Illinois wetland restoration and creation guide / Alicia Nugteren Admiraal ... [et al.].
Admiraal, Alicia Nugteren.
copies: 1 (STACKS)
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Hammer, Donald A.
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Restoring diversity : strategies for reintroduction of endangered plants / edited by Donald A. Falk, Constance I. Millar, Margaret Olwell ; foreword by Reed F. Noss.
Falk, Donald A.
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pubyear: 1996

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Land restoration and reclamation : principles and practice / James A. Harris, Paul Birch and John P. Palmer.
Harris, James A.
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Restoration of temperate wetlands / edited by Bryan D. Wheeler ... [et al.].
Wheeler, Bryan D.
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Rehabilitating damaged ecosystems / edited by John Cairns, Jr.
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United States. Dept. of Energy.
copies: 1 (GOV-MICRO)
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Restoration of endangered species : conceptual issues, planning, and implementation / edited by Marlin L. Bowles and Christopher J. Whelan.
Bowles, Martin L.
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#18 ☐ **QH105.F6 E94 1994**
Everglades : the ecosystem and its restoration / editors, Steven M. Davis, John C. Ogden ; associate editor Winifred A. Park.
Davis, Steven M.
copies: 1 (STACKS)
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#19 ☐ **QH541.5 .S3 R47 1994**
Restoring and protecting marine habitat : the role of engineering and technology / Committee on the Role of Technology in Marine Habitat Protection and Enhancement, Marine Board, Commission of Engineering and Technical Systems, National Research Council.
National Research Council (U.S.). Committee on the Role of Technology in Marine Habitat Protection and Enhancement.
copies: 1 (STACKS)
at: FONDREN
pubyear: 1994

#20 ☐ **QH75 .G35 1994**
Restoring prairie wetlands : an ecological approach / Susan M. Galatowitsch and Arnold van der Valk.
Galatowitsch, Susan M.
copies: 1 (STACKS)
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Geological Survey (U.S.)

Corporate author:	Geological Survey (U.S.)
Title:	Wetlands of modern and ancestral lakes Erie and St. Clair, Michigan, Ohio, Indiana, Pennsylvania, and New York, U.S.A., and Ontario, Canada / U.S. Department of the Interior, U.S. Geological Survey ; by Eleanora I. Robbins ... [et al.].
Map data:	Scale 1:500,000 (W 85°30*--W 78°00*/N 43°00*--N 41°00*
Publication info:	Reston, VA : The Survey ; Denver, CO : For sale by Map Distribution, 1994.
Physical description:	1 map : col. ; 61 x 124 cm. on sheet 76 x 132 cm., folded in envelope 30 x 24 cm.
Series:	Miscellaneous investigations series ; map I-2451
General note:	Relief shown by spot heights.
General note:	Depths shown by isolines and soundings.
General note:	Includes text, bibliography, and location map.
Subject:	Wetlands--Erie, Lake, Region--Maps.
Subject:	Wetlands--Saint Clair, Lake, Region (Mich. and Ont.)--Maps.
Personal author:	Robbins, Eleanora I. (Eleanora Iberall), 1942-
Series:	Miscellaneous investigations series (Geological Survey (U.S.)) ; I-2451.
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Aquatic and wetland plants of southwestern United States, by Donovan S. Correll and Helen B. Correll.

Correll, Donovan Stewart, 1908-

Personal author:	**Correll, Donovan Stewart, 1908-**
Title:	**Aquatic and wetland plants of southwestern United States, by Donovan S. Correll and Helen B. Correll.**
Publication info:	**[Washington] Environmental Protection Agency; [For sale by the Supt. of Docs., U.S. Govt. Print. Off.] 1972.**
Physical description:	**xv, 1777 p. illus. 24 cm.**
Series:	**Water pollution control research series**
Bibliography note:	**Bibliography: p. 1737-1738.**
Subject:	**Aquatic plants--Southwestern States.**
Subject:	**Wetland plants--Southwestern States.**
Personal author:	**Correll, Helen B., joint author.**
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Ecological restoration [microform] : a tool to manage stream quality.
United States. Environmental Protection Agency. Office of Water.
copies: 1 (GOV-MICRO)
at: FONDREN
pubyear: 1995

#2 ☐ View
QH75.A1 R58 1992
River conservation and management / edited by P.J. Boon, P. Calow, and G.E. Petts.
Boon, P. J.
copies: 1 (STACKS)
at: FONDREN
pubyear: 1992

#3 ☐ View
SH157.8 .H86 1991
Better trout habitat : a guide to stream restoration and management / Christopher J. Hunter ; edited by Tom Palmer ; illustrated by Ellen Meloy ; foreword by Nick Lyons.
Hunter, Chris (Christopher J.)
copies: 1 (STACKS)
at: FONDREN
pubyear: 1991

#4 ☐ View
QH75 .R47 1985
The Restoration of rivers and streams : theories and experience / edited by James A. Gore.
Gore, James A.
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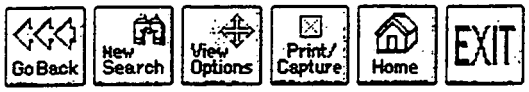

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QK604.2 .E28 B75 1996

Fungi and environmental change : symposium of the British Mycological Society, held at Cranfield University, March 1994 / edited by J.C. Frankland, N. Magan & G.M. Gadd.

British Mycological Society. Symposium (1994 : Cranfield University)

Corporate author: British Mycological Society. Symposium (1994 : Cranfield University)

Title: Fungi and environmental change : symposium of the British Mycological Society, held at Cranfield University, March 1994 / edited by J.C. Frankland, N. Magan & G.M. Gadd.

Publication info: **Cambridge [England] ; New York : Published for the British Mycological Society [by] Cambridge University Press, 1996.**

Physical description: **xvi, 351 p. : ill., maps ; 24 cm.**

General note: **Includes indexes.**

Contents: **Effects of climate change on fungal diseases of trees / D. Lonsdale and J.N. Gibbs -- Effects of climate change on fusarium foot rot of winter wheat in the United Kingdom / T.R. Pettitt and D.W. Parry -- Effects of UV-B radiation (280-320 nm) on foliar saprotrophs and pathogens / P.G. Ayres ... [et al.] -- Implications of global warming and rising sea-levels for macrofungi in UK dune systems / M. Rotheroe -- Red Data Lists and decline in fruiting of macromycetes in relation to pollution and loss of habitat / B. Ing -- Effects of dry-deposited SO2 and sulphite on saprotrophic fungi and decomposition of tree leaf litter / L. Boddy ... [et al.] -- Effects of atmospheric pollutants on phyllosphere and endophytic fungi / N. Magan, M.K. Smith and I.A. Kirkwood -- Influences of acid mist and ozone on the fluorescein diacetate activity of leaf litter / P.J.A. Shaw -- Mycorrhizas and environmental stress / J.V. Colpaert and K.K. Van Tichelen -- Myccorhizas, succession, and the rehabilitation of deforested lands in the humid tropics / D.P. Janos -- Potential effects on the soil mycoflora of changes in the UK agricultural policy for upland grasslands / R.D. Bardgett -- Uptake and immobilization of caesium in UK grassland and forest soils by fungi, following the Chernobyl accident / J. Dighton and G. Terry -- Effects of pollutants on aquatic hyphomycetes colonizing leaf material in freshwaters / S. Bermingham -- Fungi and salt stress / L. Adler -- Fungal sequestration, mobilization and transformation of metals and metalloids / G.F. Morley ... [et al.] -- Urban, industrial and agricultural effects on lichens / D.H. Brown -- Fungal interactions with metals and radionuclides for environmental bioremediation / I. Singleton and J.M. Tobin -- Impact of genetically-modified**

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microorganisms on the terrestrial microbiota including fungi / J.M. Whipps -- Has chaos theory a place in environmental mycology? / A.D.M. Rayner.

Subject: **Fungi--Ecophysiology--Congresses.**

Personal author: **Frankland, Juliet C.**

Personal author: **Magan, N. (Naresh)**

Personal author: **Gadd, Geoffrey M.**

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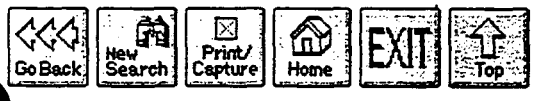
EP 1.23/5:620/R-97/002
Pilot test of wetland condition indicators in the prairie pothole region of the Unites States [microform] / prepared by the U.S. Geological Survey, Biological Resources Division, Northern Prairie Science Center, Jamestown, North Dakota for the U.S. Environmental Protection Agency, Office of Research and Development, National Health and Environmental Effects Research Laboratory, Western Ecology Division, Corvallis, Oregon ; Spencer A. Peterson ... [et al.], editors.
Peterson, Spencer A.

copies: 1 (GOV-MICRO)
at: FONDREN
pubyear: 1997

#2 ☐

QH75 .G35 1994
Restoring prairie wetlands : an ecological approach / Susan M. Galatowitsch and Arnold van der Valk.
Galatowitsch, Susan M.

copies: 1 (STACKS)
at: FONDREN
pubyear: 1994



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Winter, T. C., and M. K. Woo. 1990. Hydrology of lakes and wetlands. Pages 159–187 *in* M. G. Wolman and H. C. Riggs, editors. The geology of North America, Vol. O-1. Surface water hydrology. The Geological Society of America, Boulder, Colorado, USA.

Zedler, J. B. 1996. Coastal mitigation in southern California: the need for a regional restoration strategy. Ecological Applications 6:84–93.

Zedler, J. B., and M. W. Weller. 1990. Overview and future directions. Pages 405–414 *in* J. A. Kusler and M. E. Kentula, editors. Wetland creation and restoration: the status of the science. Island Press, Washington, D.C., USA.

Ecological Applications, 6(1), 1996, pp. 65–76
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THE ROLE OF REFERENCE WETLANDS IN FUNCTIONAL ASSESSMENT AND MITIGATION[1,2]

MARK M. BRINSON AND RICHARD REHNHARDT
Biology Department, East Carolina University, Greenville, North Carolina 27858 USA

Abstract. Compensatory mitigation for damages to wetlands in the United States occurs largely without explicit analysis and replacement of wetland functions. We offer an approach to standardize such analyses and strengthen the connection between ecological principles and policies for wetland resources. By establishing standards from reference wetlands chosen for their high level of sustainable functioning, gains and losses of functions can be quantified for wetlands used in compensatory mitigation. Advantages of a reference wetland approach include (1) making explicit the goals of compensatory mitigation through identification of reference standards from data that typify sustainable conditions in a region, (2) providing templates to which restored and created wetlands can be designed, and (3) establishing a framework whereby a decline in functions resulting from adverse impacts or a recovery of functions following restoration can be estimated both for a single project and over a larger area accumulated over time.

To establish reference standards, conditions inherent to highly functioning sites must be identified for classes of wetlands that share similar geomorphic settings. Ecological functions are then identified, and variables used to model the functions are employed in developing reference standards. Variables range from the highest levels of sustainable functioning to the complete absence of functions when a wetland ecosystem is displaced. An example given for wet pine flats in the North Carolina coastal plain illustrates how to determine the loss of a given function for an impacted wetland, how to calculate recovery (gains) in function through compensatory mitigation, and how to use the relationships between the two (loss vs. gain in function) to set minimum replacement ratios of restored to impacted area. In all cases, data from reference wetlands provide the benchmarks for making these estimates and for directing restoration or creation of wetlands toward the standards established for the wetland class. Programs to implement the use of reference wetlands require regional efforts that build upon the knowledge base of existing wetlands and their functioning.

Key words: assessment, compensatory mitigation, creation; functioning; hydrogeomorphic classification of wetlands, North Carolina wet pine flats; reference standards; reference wetlands; restoration; wetland.

INTRODUCTION

Design and performance standards are used in engineering and manufacturing to ensure that products meet specified levels of quality. With increasing emphasis on ecosystem sustainability, restoration, and adaptive management (Holling 1978, Lubchenco et al. 1991), the development of "performance" standards for ecosystems could provide the basis for judging the quality of restoration efforts and their effectiveness in offsetting unavoidable impacts. Restoration and creation of wetland ecosystems have been the focus of symposia and reviews to address progress and to discuss techniques for replacing lost area and functions (Josselyn 1982, Kusler and Kentula 1990, National Research Council 1992). We argue that reference wetlands should be central to the development of standards against which impacts to wetlands and restoration efforts are evaluated. Before we describe how reference wetlands can be used, we must first identify goals of mitigation, explain how assessment of wetland ecosystem functioning is conducted, and provide guidance on how reference wetlands are chosen.

Goals of mitigation

Regulatory programs that deal with mitigation of damages to or losses of wetlands operate within a combination of federal, state, and local regulatory programs. The most prevalent of these programs is §404 of the Federal Clean Water Act (CWA)[3] which has the goal of maintaining and improving the chemical, physical, and biological integrity of the Nation's waters (40 CFR Part 230.1).[4] Before a wetland can be filled, drained, or otherwise degraded, the landowner or pro-

[1] Manuscript received 20 March 1994; revised 18 April 1995; accepted 21 April 1995; final version received 30 May 1995.

[2] For reprints of this group of papers on wetland mitigation, see footnote 2, page 33.

[3] United States Code: Title 33.

[4] CFR = Code of Federal Regulations, the official compilation of all agency regulations that implement U.S. (federal) law.

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must obtain a permit from the U.S. Army Corps of Engineers (Corps), the lead federal agency for the CWA §404 program. The permit review sequence is outlined in the Corps Regulatory Program Regulations (33 CFR Parts 320–330) (see footnote 4), Environmental Protection Agency (EPA) §404(b)(1) Guidelines (40 CFR Part 230), and several Memoranda of Agreement between the Corps and EPA.

If a permit is issued, project approval may be contingent on restoring, enhancing, or creating wetlands to compensate for any unavoidable loss in wetland area and function. In theory, compensatory mitigation is dealt with only after an application to fill wetlands has passed an "alternatives test" that demonstrates that the project is water dependent, that there are no practicable alternatives, and that efforts have been taken to avoid and minimize impacts to wetlands. Reference wetlands can be used as standards to compare impacts among proposed alternatives, and to determine whether the level or severity of the preferred alternative is significant, whether a proposed mitigation would effectively compensate for the impact, and whether the mitigation, once in place, has actually compensated for the impact. In addition to the more general goals of the Clean Water Act, policy goals specific to wetlands, such as "no net loss," have been articulated (National Wetlands Policy Forum 1988). While the Forum's intent was no loss in both surface area and ecosystem function, debate continues on how the goal might be achieved.

Replacement of unavoidable loss of wetland ecosystem area and functioning may be achieved by restoring and creating wetlands. Restoration of wetlands is the return of a site to its pre-existing wetland condition. Creation of wetlands is the conversion of nonwetland (upland) to jurisdictional wetland status, usually by excavating a depression that intercepts the surficial groundwater table or by connecting the site hydraulically to a source of surface water.

Results from evaluations of compensatory mitigation have itemized causes of failure to achieve functional replacement (National Research Council 1992). Certain classes of wetlands are particularly difficult to create. River floodplain wetlands cannot be constructed without either creating a river to support them or increasing the flood storage capacity and width of an existing floodplain. The former is virtually impossible while the latter has the undesirable consequence of impacting toe-slope seeps and adjacent riparian and upland vegetation. Peat-based wetlands cannot be created without either removing peat from existing wetlands or waiting the decades to millennia for sufficient peat to accumulate. Of the creation projects that have been evaluated, many have not been successful (Kusler and Kenula 1990).

Functions and functional assessment

Ecosystem functions can be defined as the activities or processes that characterize an ecosystem. Four general categories have been used for wetlands: hydrologic, biogeochemical, plant community maintenance, and animal community maintenance (Brinson et al. 1994). Other functions, such as maintaining site water balance, facilitating energy flow, supporting nutrient cycling, and maintaining species diversity could be used, depending on the goals of functional assessment. Functions, then, are useful in compensatory mitigation because they allow expression of the multifaceted nature of ecosystems and provide perspectives around which performance standards can be designed.

Assessment methods to determine levels of functioning may use absolute measurements (e.g., rates of nutrient cycling, etc.) or measurements relative to some reference standard (e.g., 75% of expected species richness). The most widely used method currently is the Wetland Evaluation Technique (WET) which assesses 41 functions (Adamus et al. 1991). The Habitat Evaluation Procedure of the U.S. Fish and Wildlife Service is another method that evaluates the quality of habitat for a single species or groups of species that share habitat requirements. In each of these cases, a given function or habitat is compared to some reference or ideal condition, and usually is expressed as an index relative to the high or established maximum. Aggregate indices, such as the index of biotic integrity (IBI) for streams (Karr 1991), have been used as standards for ecosystem condition. Such indices rely on the assumption that the relative abundance of several key species populations (i.e., fish for the IBI) are reflective of an ecosystem that is relatively intact and functioning at an optimal level. Consequently, the presence and relative abundance of key species populations become the performance standard rather than the ecosystem itself.

As applied here, functions are expressed as indices relative to some reference condition that is the performance standard of a wetland class. Just as the relative abundance of fish species characterizes a stream's IBI, so the relative levels of functioning characterize a wetland ecosystem's condition.

Choosing reference wetlands

Reference wetlands are defined as sites within a specified geographic region that are chosen, for the purposes of functional assessment, to encompass the known variation of a group or class of wetlands, including both natural and disturbance mediated variations. Examples of classes include bottomland hardwoods of the southeastern U.S., prairie potholes of the northern plains states, and steep riparian wetlands of the northern Rocky Mountains. Properties of reference wetlands, ranging from those with highest levels of functioning to those that are highly disturbed, correspond to the ranges within a defined class at which various functions occur. *Reference standards* would represent the conditions exhibited by the subset of reference wetlands that correspond to the highest level of functioning of the ecosystem across a suite of functions.

Reference wetlands and functional assessment are used hand-in-hand. To understand how they are related, it is first necessary to consider how reference wetlands can be established and their functioning identified. The first step is to classify wetlands according to similarities in their landscape settings, water sources, and hydrodynamics (Brinson 1993*a*), following the general hydrogeomorphic approach used for mangroves by Lugo and Snedaker (1974). A number of other classification systems based on similar properties have been described (Gosselink and Turner 1978, Novitzki 1979, Hollands 1987, Gilvear et al. 1989). Experience in stream restoration and assessment also provides some guidelines that could be applied in the choice of reference wetlands (Hughes et al. 1986).

The hydrogeomorphic classification step is critical because it provides the resolution to distinguish between a wetland that has lost a certain function through alteration or degradation and a wetland that would never support the function due to properties inherent to its class. For example, wetland classes that excel in improving water quality, such as headwater riparian zones (Brinson 1993*b*), would not provide as favorable a habitat for waterfowl as shallow ponds in coastal marshes (Smith et al. 1989). Judgement must be used in deciding on the balance between subclassifying, thereby reducing the variation in reference standards while improving resolution of differences, and using broader classifications, thereby losing resolution due to more widely varying reference standards.

After specifying the wetland class for determining reference standards, functions must be identified for the next class. Next, information on ecosystem structure would be obtained for a number of wetlands within the class. A reference data set for a wetland class should include sites ranging in ecological integrity from highly degraded to highly functioning, and from early successional to mature. Reference standards are then determined using information obtained on the least degraded members of the class. The presumption is that the least degraded wetlands function optimally, i.e., they support a multiplicity of functions inherent to their class. This is in contrast to other wetlands in the class that may be deficient in one or more functions or wetlands that maximize the level of one function either in an insustainable manner or at the expense of others.

For forested wetlands, reference standards may include flooding to a certain depth on an annual basis, a range of tree basal areas and densities, and a species composition within a specified similarity to reference standards. Natural disturbances such as the effects of fire, storms, and droughts must be recognized as natural variation within reference standards. The choice of sites that represents acceptable variation requires the application of "best professional judgement" by experienced practitioners familiar with the ecosystem class and knowledge of pertinent scientific literature. The validity of this judgement depends upon two assumptions: (1) that structure (biomass, species composition, soil/sediment type, etc.) reliably indicates corresponding functions and (2) that the structure of highly functioning wetlands corresponds to a suite of functions that are sustainable within the constraints of the existing landscape or watershed condition. Stated another way, each function should be assessed relative to conditions determined in fully functioning, self-sustaining ecosystems, rather than some maximum level of functioning.

How Are Reference Wetlands Used in Mitigation?

We provide a brief treatment of wet pine flats on the coastal plain of North Carolina to illustrate how impact assessment can apply reference standards to measure loss in functions, to measure gain toward established mitigation goals, and to determine replacement ratios based on losses and gains in functioning (Tables 1 and 2). Wet pine flats occur on predominantly mineral soils and are dependent on frequent fire to maintain their characteristic species composition (Fig. 1). In contrast to other wetlands that receive groundwater or overland flow as water sources, wet pine flats receive only precipitation. Consequently, wet conditions result from their poor drainage rather than from supplementary water sources. As such, wet pine flats do not perform all of the same functions that riverine wetlands perform, such as energy dissipation of floodwaters or moderation of groundwater discharge.

Once fully functioning conditions were identified for wet pine flats, functional models were developed for each of eight functions, which roughly followed the format of Brinson et al. (1995) for riverine wetlands. One function, Recycles Nutrients and Other Elements, consists of combinations of eight variables, represented by estimates of living biomass (canopy and subcanopy tree biomass, forb and graminoid biomass, and woody seedling biomass) and various measures of non-living biomass (litter, standing dead stems, and coarse woody debris) (Table 1). We reasoned that nutrient cycling could be inferred from the nutrient pools presumed to exist in living and non-living biomass. The first column of data shows directly measured data for wet pine flats in a highly functioning condition that we designate as "reference standards." Each of the functions, and the variables that logically or empirically have been shown to contribute to each function, were then scaled from 1.0 (the level achieved in fully functioning conditions of reference wetlands, or reference standards) to zero (absence of the function when the ecosystem is totally displaced).

The sequences for assessing the project site before and after impact and the mitigation site before and after restoration are illustrated in Fig. 2. The figure also shows the central role of reference standards as a basis

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TABLE 1. Models and indices of ecological functioning attributed to the function "Recycles Nutrients and Other Elements"* for wet pine flats in eastern North Carolina. See *How are reference wetlands used in mitigation?* for explanation.

Variables†	Reference standards		Project site			
			Before impact		After impact	
	Data	Index	Data	Index	Data	Index
V_{can}	15.7	1.0	14.6	0.93	0.0	0.0
V_{sub}	12 225	1.0	13 314‡	1.00	0.0	0.0
V_{frb}	33.4	1.0	4.7	0.14	0.0	0.0
V_{sdg}	19.6	1.0	0.0	0.00	0.0	0.0
V_{grm}	55.8	1.0	43.6	0.78	0.0	0.0
V_{lit}	6.0	1.0	5.9	0.98	0.0	0.0
V_{snag}	21.2	1.0	0.0	0.00	0.0	0.0
V_{cwd}	1.03	1.0	0.0	0.00	0.0	0.0
Computation of index:		1.0		0.51		0.0

* Definition: Biotic and abiotic processes that convert elements from one form to another; primarily recycling processes.

† V_{can} = Canopy biomass, measured as absolute basal area of trees (m²/ha); V_{sub} = Subcanopy biomass, measured as absolute density of subcanopy shrubs and understory trees (no./ha); V_{frb} = Forb biomass, measured as percentage cover; V_{grm} = Graminoid biomass, measured as percentage cover; V_{sdg} = Seedling biomass, measured as percentage woody seedling cover; V_{lit} = Litter biomass, measured as thickness of litter layer (cm); V_{snag} = Biomass of standing dead stems, density (no./ha) of snags >10 cm dbh; and V_{CWD} = Biomass (in m³/ha) of downed coarse woody debris (CWD) >10 cm diameter and >1m in length.

Computation of function:

$$\{[(V_{can} + V_{sub} + [(V_{frb} + V_{grm})/2] + V_{sdg})/4] + [(V_{lit} + V_{snag} + V_{cwd})/3]\}/2.$$

‡ Even if a datum for the project site exceeds that of reference standards (e.g., V_{sub}), the index cannot exceed 1.0 because the condition would not be considered sustainable.

for comparison at each step in the assessment process. Consequently, the differences determined from the project and mitigation sites use the same standard of comparison, that of reference standards for pine flats.

When the Project Site Before Impact (Data column) is displaced by a project, all variables become zero (Project Site After Impact, Data column) (Table 1). Then the data for the project site before and after the impact are normalized to the reference standards. For V_{can} the index is set as 1.0 for the reference standard, is calculated for the project site before impact as 0.93 (14.6 divided by 15.7), and is set at 0.0 at the project site after impact indicating complete loss of the variable. This last calculation is repeated for the remaining seven variables. Finally, the index for the function is computed from the equation for Recycles Nutrients and Other Elements. The score is set at 1.0 for reference standards, calculated as 0.51 for the project site before the impact, and calculated at 0.0 after the impact.

An additional example is given for the function, Supports Characteristic Vegetation (Table 2). Similarity coefficients for composition or cover of the four vegetation strata are used to compare reference standards with sites being assessed. In this case, the function score of the Project Site Before Impact is only 0.28 because of a low similarity in plant species composition between the proposed project site (a loblolly pine plantation) and forest stands used to develop reference standards (i.e., fire-maintained savanna dominated by longleaf and pond pine).

Function scores are similarly calculated for a site slated for restoration and chosen to compensate for the impacts calculated above. This is done to determine how much area of degraded wetland (degraded relative

TABLE 2. Models and indices of ecological functioning attributed to the function "Supports Characteristics Vegetation"* for wet pine flats in eastern North Carolina. See *How are reference wetlands used in mitigation?* for explanation.

Variables†	Reference standards		Project site			
			Before impact		After impact	
	Data	Index	Data	Index	Data	Index
V_{comp}	100.0	1.0	29.0	0.29	0.0	0.0
V_{comp}	100.0	1.0	48.9	0.49	0.0	0.0
V_{comp}	100.0	1.0	0.0	0.00	0.0	0.0
V_{grm}	33.3	1.0	4.7	0.14	0.0	0.0
Computation of index:		1.0		0.28		0.0

* Definition: Capacity to support floral and compositional attributes of characteristic natural plant community (all strata).

† Potential variables (as similarity coefficients between assessment site and the highly functioning condition): V_{comp} = Canopy composition; V_{comp} = Subcanopy composition; V_{comp} = Vine composition; and V_{grm} = Graminoid cover.

Computation of function:

$$\{[V_{comp} + [V_{comp} + (V_{comp} + V_{grm})/2]/2\}/2$$

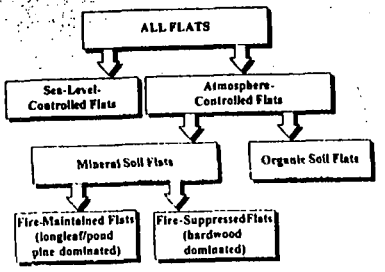

FIG. 1. Classes of wet pine flats on the North Carolina coastal plain showing principal features of separation that include dominant water source, soil properties, and presence of fire. Models for indices of functioning were developed only for fire-maintained flats (Table 1).

to a wetland meeting reference standards) would be needed, through restoration, to recover individual functions. For the Recycles Nutrients and Other Elements function in the hypothetical project, the 0.51 amount of loss expected to be caused by the project could be recovered by restoring a degraded wetland that has a score for this function of 1.0. For a degraded wetland with an index score of 0.25 for Recycles Nutrients and Other Elements, an equivalent area of wetland would have to be restored to a level of 0.76 to replace the expected loss in function (0.51 plus 0.25). The ratio between the amount lost (0.51) and the amount recovered (0.51) is equivalent to a 2:1 replacement ratio. However, if a wetland chosen for restoration was less degraded and began with a score of 0.75, only 0.25 credits would be possible because the function score cannot exceed 1.0 for restoration to reference standard. If this were done, two units of land would be needed for restoration to offset one unit of function lost in the hypothetical project (a 2:1 replacement ratio).

In this simple example, we have not accounted for functions lost between the time the project site was impacted and the time at which the mitigation site would achieve the reference standards (1.0). Further, compensatory mitigation that restores a function to a level of 0.76 raises two other issues. First, it would be difficult to restore Recycles Nutrients and Other Elements to a level of function at exactly 0.76. Second, even if this were possible, it is inadvisable to restore a site to less than a fully functioning condition. Restoration should proceed with the goal that all functions can eventually achieve reference standards if the potential exists on the site.

As it turns out, not all functions are affected equally by impacts (unless they all decline from 1.0 to 0.0), nor are all functions recoverable at the same rate and to the same degree over similar periods of time (Golet 1986, Larson and Neill 1987, PERL 1990). For wet pine flats, we specified eight functions, and although all declined to zero with the hypothetical project, they were initially operating at different levels relative to reference standards. For mitigation wetlands slated for restoration of functions, the function-by-function assessment provides enough detail to determine which variables need to be restored.

Once replacement ratios are determined for individual functions, one still must decide how much area to restore for a given impact. While gains and losses of individual functions can be quantified, it is not obvious how replacement ratios for whole ecosystems should be determined. This is the point at which policy must be developed to provide guidance (Fig. 2). Some logical alternatives are to (1) give priority to hydrologic variables when possible because they are fundamental

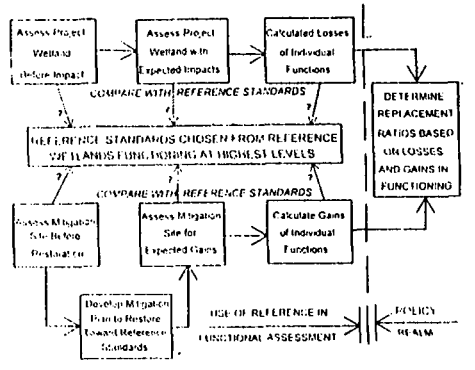

FIG. 2. The central role of reference standards in assessing project wetlands before and after impact, and assessing compensatory mitigation sites before and after restoration. Level of functioning at each point in the process (indicated by "?") are compared to reference standards for calculating gains and losses. Functional assessment procedures are described in Smith et al. (1995).

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[illegible] (2) base ratios on functional [illegible] region and (3) use the individual [illegible] with the highest ratio to establish overall re[illegible] ratios. The latter alternative may often ex[illegible] a 1:1 functional replacement overall. However, this could be applied toward deficits in functions that develop between the time of the impact and the achievement of a fully functioning condition in the compensation wetland.

Comparison of Common Mitigation Options and the Reference Approach

Three broad options dominate the execution of compensatory mitigation for damages to wetlands (Kruczynski 1990). One is in-kind vs. out-of-kind compensation in which the former restores or creates the same class of wetland (and corresponding functions) that are lost by impacts, and the latter restores or creates alternative wetland classes. In some cases, out-of-kind compensation is the only option. In other quite rare cases, compensation is extended to restoring or protecting upland sites valued as exceptionally rare (or as habitat for an endangered species) rather than creating a wetland class that may be already common in the geographic region. For example, a permit was approved to fill a wetland swale on a barrier island with the condition that protection be provided for rapidly disappearing upland maritime forest (Clean Water Act §401 Certification Files, 1991, North Carolina Division of Environmental Management, Raleigh, North Carolina, USA). While such decisions may have long-lasting socioeconomic benefits, a reference wetland approach to functional assessment cannot compare functions across wetland classes because each class has different reference standards.

A second option is on-site vs. off-site compensation, the former requiring that compensation activities occur adjacent to the permitted project, or at least located within the same embayment, stream reach, or local watershed (Kruczynski 1990). Off-site compensation implies that restoration or creation can take place in a different and perhaps distant watershed. If a reference wetland approach is used, on-site restoration within the same local watershed seems justified, especially for wetlands that are physically or functionally connected to one another in the landscape.

A third option is to vary the credit given to restored vs. created wetlands by adjusting replacement ratios (restored or created area divided by area impacted by a project). High replacement ratios usually are required in cases (1) where the risk of failure is perceived as being high (e.g., creation might require more area than restoration of a degraded system), (2) when a long time is required for a fully functioning wetland to develop (e.g., creation of forested wetlands), or (3) when mitigation consists of preservation alone (Kruczynski 1990).

While these three options have not exclusively dominated past mitigation practices in the U.S., there is a prevailing philosophy among the wetland management community that in-kind and on-site restoration is more desirable than its alternatives (i.e., the functioning of damaged wetlands is more likely to be replaced). As such, we contend that this philosophy is reacting to a higher risk of failure that accompanies creation and off-site alternatives (as described by Kruczynski 1990) than an explicit determination of whether or not functions are being replaced. This clearly differs from a philosophy based on assessments of ecological functions standardized to fully functioning reference wetlands and restoration designed to attain the least degraded condition for the wetland class. While the two approaches may arrive at the same requirements for a particular project (e.g., 2 ha of marsh creation required for 1 ha of marsh filled), the reference wetland approach evaluates the potential functional effectiveness of the proposed mitigation wetland relative to losses in the project wetland. The same procedure may be continued to evaluate progress with post-project monitoring. The point of this comparison is not to suggest that the three mitigation options mentioned above entirely disregard function, but rather to illustrate that the use of reference forces one to constantly revisit and calibrate on reference standards. In so doing, reference standards and reference wetlands take the lead in guiding mitigation, and all parties involved in mitigation are fully informed of the process. This potentially leads to greater consistency and efficiency in achieving goals of Clean Water Act §404.

Additional policy guidelines would still be needed for the framework of reference wetlands. Thresholds for permit compliance would have to be established or negotiated for forested wetlands that require many decades to reach reference standards indicative of a relatively mature condition. Further, an endpoint of highly degraded conditions for the mitigation wetland should not be acceptable even if the project wetland was originally degraded. If this were acceptable, degraded wetlands would continue to accumulate through mitigation practices, a situation inconsistent with restoration goals of the Clean Water Act and the National Wetlands Policy Forum. Additional policy guidance would be needed on what to do if appropriate landscape conditions are lacking for the creation of fully functioning wetlands (e.g., urbanizing landscapes), if opportunities for restoration are lacking, and if there are conditions where creation is favored over restoration. Such policies may be needed if consistent progress is to be made toward a no net loss goal.

Potential Misuses of the Approach

While it appears that reference wetlands could improve consistency and accuracy in measuring changes in the functioning of wetlands, they are also vulnerable to misuse in the following ways.

The choice of reference wetlands for determining reference standards.—Because highly functioning conditions of reference wetlands would serve as both design templates for restoration and standards to evaluate compensatory mitigation projects, the choice of reference wetlands is critical, as illustrated in Fig. 2. The most obvious misuse would be to accept reference standards from sites that are degraded. This would be counterproductive to goals of restoring and creating wetlands that will function at high levels.

Setting reference standards higher than can be sustained in the landscape.—It would be unrealistic to expect that similar levels of sustained functioning be met for wetlands in highly urbanized settings as in forested, rural watersheds. For example, highest levels of functioning would be low for wetlands in some locations in New Jersey where urbanization has affected plant species composition and water quality (Ehrenfeld and Schneider 1993). Just as stream quality is tightly linked to land use activities in watersheds (Hughes et al. 1986), so are many wetlands constrained by activities in their surrounding uplands.

Giving primacy to individual functions at the expense of other functions or the wetland ecosystem.—While functional assessments allow one to determine changes in individual functions, the fundamental unit of assessment is the wetland ecosystem. This principle has two consequences. First, functions can be compared only between wetlands of the same class because they have the same reference standards. If functions were the only basis for compensatory mitigation, the logic could lead to the substitution with wetlands of a different class or with non-wetlands that have overlapping functions. For example, surface water storage is a wetland function, but it is maximized by storm detention basins that are normally dry and generally lack attributes of wetlands. Second, individual functions should not be altered to maximize one function at the expense of others, a process known as enhancement (Kruczynski 1990).

The concept of reference wetlands and its application to each step in the mitigation process (Fig. 2) helps to avoid these pitfalls. Functional assessment and mitigation policies that rely on wetland ecosystems as fundamental units of the landscape can be made consistent and stable. For areas in which reference standards cannot be achieved because of urbanization or other land use changes, adaptive management may require alternative pathways for restoration. The use of reference wetlands, however, clarifies the threshold at which scientific information must yield to policy guidelines on mitigation.

Conclusions

The use of reference wetlands offers a way to standardize components of compensatory mitigation that is consistent with broad policy goals. Advantages of a reference wetland approach include (1) making explicit the goals of compensatory mitigation through identification of reference standards from data that typify sustainable conditions in a region; (2) providing templates to which restored and created wetlands can be designed; and (3) establishing a framework whereby a decline in functions resulting from adverse impacts or a recovery of functions following restoration can be estimated, both for a single project and over a larger area accumulated over time. While individual wetland scientists, regulators, and consultants may have their own perceptions of what constitutes fully functioning wetlands, the proper use of reference wetlands removes potential bias and provides the foundation for more objective functional-assessment procedures. Projects for restoration and creation should be designed around existing ecosystems and data that characterize them, and not around lists of design standards and development goals with criteria that do not specify a particular existing class of wetland. If consistently applied, the use of reference wetlands can facilitate the development of realistic goals for mitigation projects and provide a mechanism for evaluating progress toward meeting those goals.

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CORP AUTHOR United States. Congress. House. Committee on Transportation and Infrastructure. Subcommittee on Water Resources and Environment.

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AUTHOR	Dennison, Mark S.
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CORP AUTHOR United States. Congress. House. Committee on Transportation and Infrastructure. Subcommittee on Water Resources and Environment.

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were more effective than Reglone A in reducing phytoplankton biomass in the poorly buffered stormwater retention lakes in the City of Edmonton (Babin et al. 1992).

In addition, laboratory experiments indicate that lake sediments did not sorb microcystin from lake water, thus the persistence of exo-MCYST concentrations after Reglone A addition is likely to increase chronic health risks in drinking water. A suitable withholding period (≥7 days), together with exo-MCYST monitoring is required after Reglone A addition, or after the addition of any other chemical that lyses cells, before the water can be used as a drinking water supply or for contact recreation.

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Patterns in fish assemblages from coastal wetland and beach habitats in Green Bay, Lake Michigan: a multivariate analysis of abiotic and biotic forcing factors

John C. Brazner and Edward W. Beals

Abstract: From May to September in 1990 and 1991, 24 coastal wetland and beach sites in Green Bay, Lake Michigan, were sampled to investigate abiotic and biotic factors influencing fish assemblages; half the sites were modified by human developments, and half were relatively undeveloped. The greatest assemblage differences were observed among regions, but there also were strong differences among assemblages from different habitats. Degree of development had less of an effect on site differences, although assemblages at undeveloped wetlands were unique, and those from developed and undeveloped sites in the upper bay were relatively distinct. The most influential abiotic factors were turbidity, reflecting the trophic gradient in the bay, and a suite of variables associated with macrophyte coverage and diversity, which were critical components of nursery habitats for the primarily immature fishes we captured. The volatile and unpredictable nature of shoreline habitats in the Great Lakes apparently precluded competition and predation from having a strong organizing role. This study demonstrates that undeveloped wetlands are a valuable and intensely utilized fish habitat, particularly as nursery areas, that should receive special consideration in ecosystem management plans for the Great Lakes.

Résumé : De mai à septembre, en 1990 et 1991, 24 sites riverains constitués de terres marécageuses et de plages ont été échantillonnés dans la baie Green, lac Michigan, pour étudier les facteurs abiotiques et biotiques influant sur les assemblages de poissons; la moitié des sites ont été modifiés par l'activité humaine et la moitié étaient relativement peu développés. Les plus grandes différences d'assemblage ont été observées entre les régions, mais il y avait également des différences prononcées entre les assemblages des différents habitats. Le degré de développement avait un effet moins grand sur les différences entre les sites, bien que les assemblages dans les terres marécageuses non développées aient été uniques et que les assemblages caractéristiques des sites développés et non développés dans la partie supérieure de la Baie aient été relativement distincts. Les facteurs abiotiques ayant l'effet le plus grand étaient la turbidité, qui reflète le gradient trophique dans la baie, et une série de variables liées à la superficie couverte par les macrophytes et à leur diversité, qui étaient des constituants déterminants des habitats d'alevinage pour les poissons principalement immatures que nous avons capturés. La nature volatile et imprévisible des habitats riverains dans les Grands Lacs a apparemment empêché la compétition et la prédation d'exercer un rôle important au niveau de l'organisation. Cette étude démontre que les terres humides non développées constituent un habitat précieux et intensément utilisé par le poisson, particulièrement comme aire d'alevinage, qui mérite une attention spéciale dans les plans de gestion de l'écosystème des Grands Lacs.

[Traduit par la Rédaction]

Introduction

Comparative studies of north temperate lakes indicate that fish assemblages are structured by a variety of abiotic and biotic factors. Two principal abiotic factors implicated in structuring fish assemblages are low pH (Rahel 1986) and low dissolved oxygen in winter (Tonn and Magnuson 1982; Magnuson et al. 1989). Predation has been identified as the principal biotic factor involved in structuring fish communities, although competition for food also appears to play a role (Keast 1978; Tonn 1985). Typically, small or soft-rayed forage species are reduced or absent from lakes where large piscivores are abundant (Robinson and Tonn 1989; He and Wright 1992). Other factors, such as lake area (Johnson et al. 1977; Matuszek and Beggs 1988), habitat heterogeneity (Eadie and Keast 1984; Benson and Magnuson 1992), productivity (Gascon and Leggett 1977; Kelso 1988), and biogeography (Eadie et al. 1986; Jackson and Harvey 1989) may also influence structural patterns. Distinct patterns in fish communities have even been shown to correspond to broad patterns in topography, land use, vegetation, and soils within a watershed (Whittier et al. 1988). Although fish assemblage patterns in relation to biotic and abiotic factors within lakes have been documented (e.g., Werner et al. 1977; Keast and Harker 1977), most conclusions have been derived from comparisons among lakes.

Numerous studies in streams have related fish community structure to human induced stresses (Reeves et al. 1993; Weaver and Garman 1994; Wichert 1995), but relatively few

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have been done in lakes. However, the effects of eutrophication (Schindler et al. 1971; Persson et al. 1991); heavy metals (Somers and Harvey 1984), acid deposition (Schindler et al. 1985; Tremblay and Richard 1993), and elevated turbidity (Hayes et al. 1992) on lake fish communities have been examined. With the exception of this study and a few others from around the Great Lakes basin (for review see Jude and Pappas 1992; Brazner 1994), lake-edge wetland and littoral fish assemblages have largely been ignored.

Because the ecology of coastal wetland fishes is not well understood in the Great Lakes, and because degradation of coastal wetlands due to shoreline development and other stressors continues to be a problem (Bosley 1978; Whillans 1982; Krieger et al. 1992), further study of fish assemblages from these habitats seemed warranted. Indications are that a high percentage (>75%) of Great lakes fishes depend upon coastal wetlands for some part of their life cycle (Stephenson 1990; Whillans 1992). Using a univariate, demographic approach, Brazner (1997) found that there were differences in the composition and abundance of fish assemblages related to regions, habitats, and human development intensity in Green Bay coastal habitats. However, the specific factors driving these differences were not identified. Here, our goals were to identify abiotic and biotic factors producing differences in assemblage patterns, using a community-based approach to characterize differences among types of sites and their species structure.

We expected variables associated with trophic status to have an important influence on fish assemblage patterns because a strong trophic gradient is a predominant feature in Green Bay (Sager and Richman 1991), and a similar production gradient had a key role in structuring littoral zone fish communities in Lake Memphremagog (Nakashima et al. 1977; Gascon and Leggett 1977). We also expected that variables associated with site-specific differences in habitat complexity would lead to differences in fish assemblages based on observations made in littoral zones of other freshwater (Guillory et al. 1979, Benson and Magnuson 1992) and coastal marine environments (Heck et al. 1989, Lenanton and Caputi 1989). Although we were unsure what the relative influence of human development might be in this study, we expected the effects of development to be readily apparent because of the high degree of shoreline modification in various parts of Green Bay (Bosley 1978; Harris et al. 1988). Differences in the physical stability of wetland and beach habitats led us to believe that biotic interactions would be more important at wetland sites. High environmental instability, such as the high degree of exposure to wind and waves at beach sites, was expected to decrease the importance of interactions like competion and predation (Menge and Sutherland 1987; Winemiller and Rose 1992) and increase the influence of abiotic factors (Wiens 1984; Jennings and Philipp 1994).

Methods

The study sites, experimental design, and fish sampling methods were described in detail elsewhere (Brazner 1997). Fish assemblages from 24 sites (12 wetland, 12 beach), primarily along the western shoreline of Green Bay, Lake Michigan (Fig. 1), were sampled five times from May to September during 1990 and 1991 with small-meshed (≤5 mm) fyke nets, seines, and minnow traps. Sites spanned the 193 km length of the bay, from the city of Green Bay in the south to the northern end of Little Bay de Noc in the north. Eight sites were selected in each of three geographic regions (lower, middle, and upper bay) to encompass the trophic gradient that is present (Sager and Richman 1991). Half of the sites were among the least developed within each region; the other half were modified by human developments (e.g., residential and (or) industrial development). Sites were 100-m wide, bounded by the shoreline on the inshore edge, and the 1-m depth contour offshore. Coastal wetlands were defined as contiguous, lacustrine habitats less than 2 m deep that had free exchange with the bay and emergent, floating, and (or) submergent vegetation. Beaches were more open, unprotected sites defined by the predominance of fine-textured sand substrates; most had little or no macrophyte cover.

Environmental measurements

Physicochemical variables

Environmental variables expected to influence the littoral fish assemblages in Green Bay were measured concurrently with fish sampling. Water temperature, conductivity, dissolved oxygen and pH were measured at mid-depth along the 1-m depth contour with a Hydrolab 4041 multiprobe sensing unit (Hydrolab Corp., Austin, Tex.) calibrated weekly. Wind speed and direction were determined with a hand held anemometer (Wind Wizard, Davis Instruments, Hayward, Calif.) and wave height was recorded as the mean of the three largest waves measured at the 0.5-m depth contour during a 2-min observation period. Turbidity was estimated in the field from a surface water sample at the 0.5-m depth contour using a model TTM turbidity test kit (LaMotte Chemical, Chestertown, Md.) as Jackson Turbidity Units (JTU). Bottom slope was estimated by averaging the distance from shore to the 1-m depth contour at the two ends and center of each 100-m site transect. Sites were assigned geographic positions (latitude and longitude; Brazner 1997) using a portable Global Positioning System unit (Trimble Transpak, Sunnyvale, Calif.) with a reported accuracy of 33 m. Because of the primarily north–south orientation of the shoreline (i.e., limited longitudinal variability) only latitude was included in statistical analyses. Length of continuous habitat along the shoreline surrounding each site was estimated to the nearest 100 m using a mechanical range finder (Rangematic 1200, Ranging Inc., Rochester, N.Y.).

Substrate variables

Predominant substrate types (comprising ≥25% of total sample) were subjectively determined for each site from three, randomly selected, 1.0-L grab samples taken during August–September in 1990 and 1991. Samples were scored on a seven-point scale (1, sand; 2, sand with muck or silt; 3, sand with cobble or gravel; 4, muck with woody debris; 5, gravel with cobble; 6, sand with silt and muck; 7, sand with muck and cobble or wood, or silt with gravel and cobble or wood) to provide a scale of increasing substrate diversity similar to those calculated by Tonn and Magnuson (1982) and Benson and Magnuson (1992). Substrate samples were frozen and analyzed later for organic carbon using a combustion method (Dean 1974). Sediment diversity and organic carbon estimates are means of values from the 2 years of study. Sediment diversity was rounded to the nearest integer.

Macrophyte community variables

The number of macrophyte species and the percentage of area covered by macrophytes were estimated. Any species observed during a 15-min wading survey between the 1-m depth contour and the daily seiche line was counted. Percentage cover (recorded to the nearest 10%) was a subjective estimate of total areal coverage by all macrophyte species in the designated study areas. A diversity index of macrophyte growth forms (Fassett 1930) similar to the ones described by Tonn and Magnuson (1982) and Benson and Magnuson (1992) was calculated. Macrophyte growth form diversity ranged from 1 to 7 (1, no macrophytes; 2, flexuous forms only; 3, rosette forms only; 4, emergent and flexuous forms; 5, emergent, flexuous, and rosette forms; 6, emergent, floating and flexuous forms; 7, emergent, floating, flexuous, and rosette forms); assigning the highest scores to sites with the greatest number of growth forms.

Overall macrophyte diversity was calculated from percentage cover, the number of species and growth form diversity:

$$MD = C(S/MS)(F/7)$$

where MD is macrophyte diversity, C is percent cover, S is number of species, MS is maximum number of species found at any site, and F is growth form diversity. This index of macrophyte diversity potentially ranged from 0 to 1; sites with no macrophytes received a score of 0 and sites with 100% cover, the maximum number of species observed and a growth form diversity of 7 receiving a score of 1. The highest macrophyte diversity actually calculated for any site was 0.74.

Human development variables

Three measures were utilized to characterize human development adjacent to a site. These were (*i*) distance to the nearest city (Green Bay, Oconto, Peshtigo, and Marinette Wis., and Menominee, Escanaba, and Gladstone, Mich.); (*ii*) distance to the nearest federal or state highway measured from 1 : 30 000 scale NOAA navigation maps for

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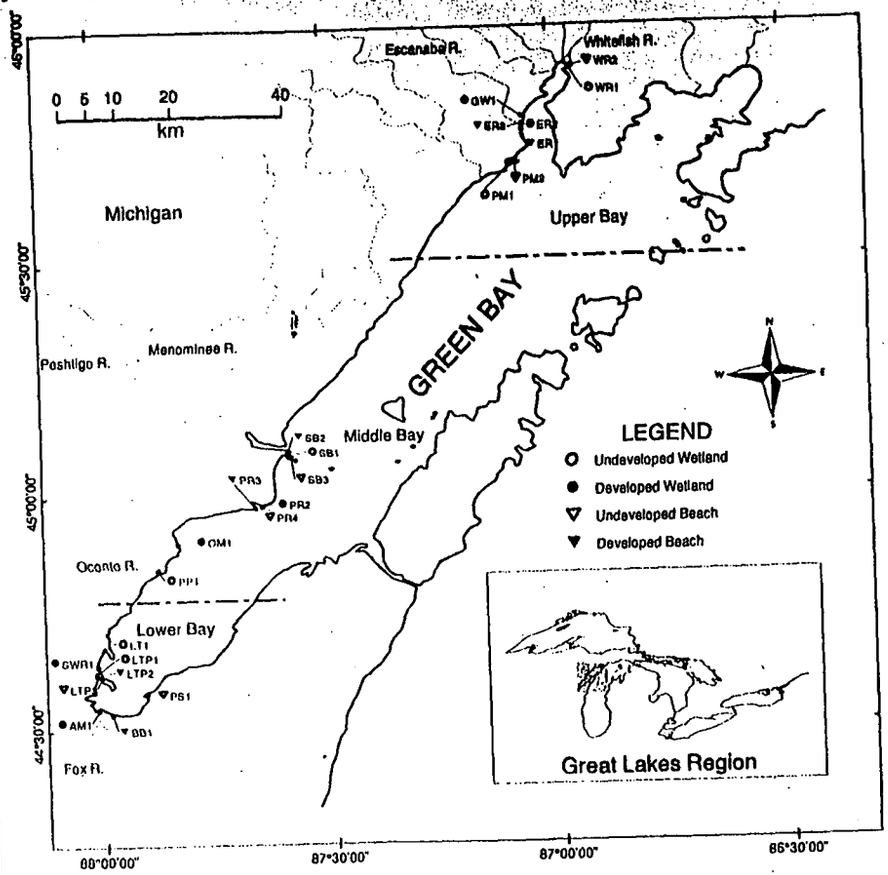
Fig. 1. Map of Green Bay showing its relative position in the Great Lakes region and Lake Michigan, as well as locations of 24 sites sampled during the study (undeveloped wetland sites, O; developed wetlands, ●; undeveloped beaches, ▽; developed beaches, ▼; more site details are given in the Appendix).



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the Great Lakes printed in 1984, and (*ii*) a relative index of human development within 1.0 km of the center each site. The index ranged from 1 to 4 (1, little or no human development; 4, extreme development) and was estimated from the area and intensity of physical alteration (e.g., landfilling, road building, home and industrial development, cottage use).

Data analysis and summary

Environmental distinctness

To evaluate the differences in environmental conditions at different types of sites, values for each variable averaged over all sampling dates were analyzed with three-way ANOVA using region (lower, middle, upper), habitat type (wetland, beach) and development status (developed, undeveloped) as main factors and a habitat-by-development status interaction term. Fisher's least squared difference (LSD) was used for multiple mean comparisons. All environmental variables were $\log(n + 1)$ transformed to increase variance homogeneity except for latitude, pH, and those based on an index or percent scale.

Fish assemblage structure

We used classification and ordination methods to examine patterns in littoral fish assemblages. Because of their complementary nature, classification and ordination together provide a powerful tool for identifying pattern in the structure of community data (Gauch 1982; Pielou 1984; Ludwig and Reynolds 1988). Several different classification and ordination methods, distance measures, and transformations were tested using data from 1990. These preliminary analyses examined sites in species space, and species in site space matrices to determine which of these analyses would be most suitable. Those techniques that produced the most ecologically meaningful and interpretable patterns were selected for the full data set.

Ward's method was selected as a clustering technique (Lance and Williams 1967; Pielou 1984). The relative euclidean distance measure used with this technique is Wishart's (1969) objective function, which measures information loss as agglomeration proceeds (McCune 1991). A modified version of the Bray–Curtis ordination technique (Bray and Curtis 1957) that incorporates a variance-regression approach for endpoint selection (Beals 1984) provided clearer site separation and greater ecological interpretability than detrended correspondence analysis or nonmetric multidimensional scaling. Sørensen's (1948) coefficient as a distance measure and a $\log(n + 1)$ transformation of abundances provided the best results with this technique. By eliminating species that were rarely captured (fewer than five individuals captured or two or fewer sites of capture) the analytical problems associated with many zeros in the data matrix were reduced (Legendre and Legendre 1983; Tonn et al. 1990). The influence of rare species on ordination analysis of the data set as a whole (Gauch 1982), and rare species are usually the least adequately sampled. Although finding an appropriate reduction in the species data matrix can be problematic and bias results (Rahel et al. 1984; Yant et al. 1984), a reduced matrix (54 species) that omitted rare species was selected because it produced a more ecologically meaningful and workable representation of the data than when all 54 species were included.

Three forms of the data matrix were used for the cluster and ordination analyses to explore patterns in the data set and generate hypotheses about the patterns. A matrix of sites in species space was used to examine similarities and discontinuities among groups of sites based on fish species composition and abundance. To help interpret patterns in the ordinations, product–moment correlations were calculated between positions of sites along each ordination axis and species abundances and environmental characteristics at those sites. Strength of the groupings were estimated with multiple discriminant analysis (Wilkinson 1990). Abundances of the eight fishes most closely correlated with the first three ordination axes were inputs to a discriminant analyses; the number of misclassifications in the site-classification matrices estimated the strength of relationships hypothesized from the ordinations. We limited the number of input variables to eight because the number of samples to be grouped with discriminant analyses should be three to four times greater than the number of predictor variables to assure stability of the discriminant function loadings (Williams and Titus 1988) and that canonical correlations reflect actual underlying relationships (Smith 1981). A matrix of species abundances in site space (the transpose of the first matrix) was used in a cluster analysis to identify which species were associated with particular types of sites.

A third form of the data matrix was used to ordinate species directly in environmental space and determine which abiotic factors were most important to the distribution of individual species. The original site by species matrix was transposed (A′) and postmultiplied by the environmental matrix (E) to produce a matrix (A′E) of species scores for each environmental variable (McCune 1991). The A′ and E matrices were first standardized by the mean and standard deviate for each variable. This third matrix provides a direct and efficient way to investigate relationships between species and environment, but like all ordination comparisons with environmental variables, it is constrained by the presumption that the important environmental variables have been measured (Beals 1984; McCune 1991).

Species scores for each environmental variable were overlayed onto the ordination plot to identify which environmental variables contributed most. Ordination points for each species were sized in proportion to their standardized score for each environmental variable (McCune 1991). Contour lines based on these proportionally sized points and judged to correspond with major breaks in the species scores were drawn to provide three or four groups of species. Overlays were plotted for the six environmental variables that were highly correlated with ordination axes and provided clear separation between contours.

Species distributions

The utility of different abiotic factors as predictors of species abundances and community structure was evaluated with multiple regression. The interactive stepwise procedure included both forward selection and backward elimination (Wilkinson 1990) to select the two best models with less than five predictor variables based on the highest overall significance and r^2 values, the lowest residual variance, and normality of residual plots. Simpler models were selected over more complex models when the amount of explained variance was not significantly less with the reduced model based on an F-test comparison of the residual variances associated with the two models (Neter et al. 1983).

The importance of species interactions was estimated using contingency and correlation analysis to examine the distribution of species co-occurrences among sites. Contingency analysis was based on a two by two contingency table approach and was therefore limited to presence–absence data; correlations were based on log-transformed abundances. For both analyses, the number of statistically significant positive and negative co-occurrences were recorded for all pairwise combinations of species ($n = 496$) captured at more than five sites to avoid bias in test statistics (Zar 1974). Fisher's exact test ($p < 0.01$) and product–moment correlations ($p < 0.10$, Bonferroni corrected) were calculated to measure statistical significance. Basing the overall importance of species interactions on the total number of co-occurrences that were positive, negative, or neutral (Tonn et al. 1990) was deemed more appropriate than strict hypothesis tests for each species pair because statistical independence assumptions are violated with the latter approach (Bowers and Brown 1982).

Results

Environmental conditions

Differences in environmental conditions between sites from different regions and habitat types were larger and more

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Table 1. Environmental differences between site types that had significant differences ($p \leq 0.05$) between means in ANOVA.

(A) Habitat differences.

	Wetlands		Beaches		
Variable	Mean	Range	Mean	Range	p
Macrophyte cover (%)	36.3	0–76	5.1	0–39	<0.001
Substrate diversity (1–7)	5.3	3–7	2.0	1–5	<0.001
No. of macrophyte species	10.5	0–18	1.6	0–8	<0.001
Macrophyte diversity (0–1)	0.23	0.00–0.74	0.02	0.00–0.17	0.002
Macrophyte GFD (1–7)*	5.5	1–7	2.6	1–7	0.006
Waves (cm)	3.2	1–7	7.4	1–16	0.008
Organic carbon (%)	2.7	0.7–10.1	0.9	0.4–1.7	0.041

(B) Development differences.

	Undeveloped		Developed		
Variable	Mean	Range	Mean	Range	p
Development index (1–4)	1.5	1–2	3.2	2–4	<0.001
Macrophyte cover (%)	26.8	0–76	14.6	0–66	0.025
Conductivity (µS/cm)	273	220–374	297	248–386	0.042

(C) Regional differences.

	Lower Bay		Middle Bay		Upper Bay		
	Variable	Mean	Range	Mean	Range	Mean	p**
Latitude	44.6*a*	44.5–44.7	45.0*b*	44.8–45.1	45.8*c*	45.7–45.9	<0.001
Turbidity (JTU)	104*a*	86–137	32*b*	20–72	16*c*	9–26	<0.001
Conductivity	336*a*	292–386	257*b*	242–290	262*b*	220–316	<0.001
Nearest highway (km)	2.7*ab*	0.8–4.4	6.4*a*	2.4–12.3	1.4*b*	0.1–2.2	0.002
Macrophyte cover (%)	14*a*	0–42	12*a*	0–31	32*b*	0–76	0.003
Substrate diversity	4.3*a*	1–7	2.4*b*	1–6	4.3*a*	1–7	0.018
Macrophyte diversity	0.06*a*	0.00–0.26	0.07*a*	0.00–0.18	0.25*b*	0.00–0.74	0.020
pH	8.0*a*	7.6–8.4	7.7*b*	7.4–8.2	7.6*b*	7.2–8.0	0.027

(D) Habitat × development differences.

	Undeveloped wetlands		Developed wetlands		Undeveloped beaches		Developed beaches		
Variable	Mean	Range	Mean	Range	Mean	Range	Mean	Range	p**
Development index	1.7*a*	1–2	3.2*b*	3–4	1.3*a*	1–2	3.2*b*	2–4	0.001
Substrate diversity	5.0*a*	3.0–6.0	5.5*a*	3.0–7.0	2.0*b*	1.0–5.0	2.0*b*	1.0–3.0	0.003
Macrophyte GFD (1–7)*	6.0*a*	5.0–7.0	5.0*ab*	1.0–7.0	2.8*b*	1.0–7.0	2.4*b*	1.0–5.0	0.020
Macrophyte cover (%)	45.5*a*	24–76	27.2*b*	0–66	8.2*c*	0.39	2.0*c*	0–11	0.020
No. of macrophyte species	13.7*a*	10.0–18.0	7.3*a*	0.0–15.0	2.2*b*	0.0–8.8	1.0*b*	0.0–4.0	0.030
Waves (cm)	3.3*a*	1.0–7.0	3.0*ab*	1.0–6.0	8.0*bc*	1.0–16.0	6.8*c*	4.0–15.0	0.046
Macrophyte diversity	0.32*a*	0.14–0.74	0.15*b*	0.00–0.58	0.03*b*	0.00–0.17	0.00*b*	0.00–0.02	0.048

Note: Means followed by different letters are significantly different ($p \leq 0.05$); *GFD, growth form diversity; ** maximum significance value from ANOVA associated with differences between means.

statistically significant than between undeveloped and developed sites (Table 1). Physicochemical conditions differed greatly between regions; turbidity decreased from south to north (Table 1C) reflecting the strong trophic gradient and phytoplankton-induced turbidity in the highly eutrophic southern part of the bay (Richman et al. 1984; Sager and Richman 1991). Conductivity, pH, and water temperature exhibited similar but weaker gradients and were positively correlated with each other and turbidity ($r \geq 0.5$ for all combinations except water temperature with conductivity, $r = 0.2$). Macrophyte cover and diversity were highest in the north where mesotrophic conditions result in greater water clarity (Harris et al. 1991). Compared with beaches, wetlands generally had more diverse macrophyte communities, more areal coverage in macrophytes, more diverse substrates, higher sediment organic carbon, and smaller waves (Table 1A). These differences result from the more protected nature of wetland sites. Wetlands develop in locations less influenced by storms and currents (Geis 1979; Herdendorf 1990). Compared with developed sites, undeveloped sites tended to have more macrophyte cover and lower conductivity (Table 1B). Undeveloped wetlands had the highest macrophyte diversity and cover, while developed beaches had the lowest Table 1D).

Patterns among sites in species space

Over 40 000, primarily immature (>90%), fish from 54 species

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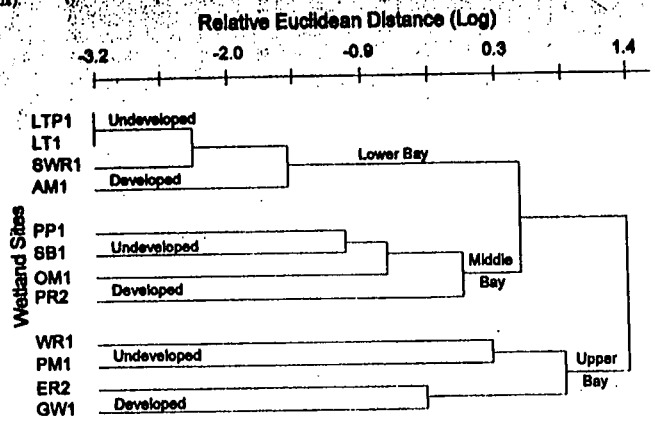
Fig. 2. Cluster analysis (Ward's method) of wetland sites in species space (text annotations included to aid in cluster interpretations; site codes detailed in Appendix).



and 20 families were captured during the study (see Brazner 1994, 1997 for details); thus, data reflect primarily the ecology of young individuals. To simplify the process of discerning patterns, initial analyses were conducted for wetland sites only. Cluster analysis of these data revealed distinct clusters among sites from different regions and sharp differentiation associated with development status (Fig. 2). Ordination also revealed strong separation between regions along axis 1, with some separation between developed and undeveloped sites along axis 2 (Fig. 3). These two axes accounted for 88% of the original distances calculated among sites. In addition, some of the variation along axes 1 and 3 apparently was related to exposure of the sites; wave height was one of the most highly correlated abiotic factors with these axes ($r_{axis\ 1} = -0.80$, $r_{axis\ 3} = -0.66$). Sites that scored lowest along axes 1 and 3 tended to be the more exposed wetland sites (e.g., AM1, SWR1, OM1; see Table 2 for site codes) while those that scored higher on these axes were among the most protected sites (e.g., PM1, PR2, WR1).

Differentiating patterns became more complicated when all sites were included, but some of the same trends were apparent. A strong regional signal was still discernable in the ordination of these data (Fig. 4). Regional separation occurred primarily along axis 1. This axis accounted for 50% of the original distances among sites of the 83% accounted for by the first three axes together. Gizzard shad (*Dorosoma cepedianum*), emerald shiners (*Notropis atherinoides*), spotfin shiners (*N. spilopterus*), white bass (*Morone chrysops*), and yellow perch (*Perca flavescens*) were the fish species that were most closely correlated with axis 1 (Table 3). Except for yellow perch, which was caught consistently throughout the bay (especially at wetland sites), these species were nearly always most abundant in the lower bay and could be characterized as lower bay species. The environmental variables that were most highly correlated with axis 1 were turbidity, latitude, water temperature, conductivity, and pH (Table 3).

Separation among sites based on habitat differences was also apparent but weaker than the regional differentiation. Middle and upper bay sites had the most distinct separation between beaches and wetlands (Fig. 4). Separation among the different types of sites was the weakest in the lower bay. Habitat separation among sites was primarily along the third axis with most sites (9 of 11) scoring less than 0.4 as wetlands and most sites (10 of 13) with scores greater than 0.4 as beaches. This axis accounted for 23% of the original distances calculated between sites and was most closely correlated with pumpkinseeds (*Lepomis gibbosus*), largemouth bass (*Micropterus salmoides*), golden shiners (*Notemigonus chrysoleucas*), johnny darters (*Etheostoma nigrum*), and bowfin (*Amia calva*) (Table 3). These fishes are indicative of wetlands except for johnny darters, which had a significant beach component to their catch (Table 2). However, 84% of johnny darters from beaches came from the upper bay beach site (WR2) that ordinated closest to wetland sites. The environmental variables that correlated most closely to axis 3 were the four macrophyte-related variables and wave height (Table 3). This suggests that the diversity and physical structure of the macrophyte community influenced the fish assemblages. The negative correlation with wave height is consistent with the positive correlation with macrophytes (Geis 1979, 1985; Keddy 1983).

Separation between sites based on development was weaker than separation between habitat or region. However, some separation was apparent along axis 2 which accounted for 10% of the original distances between sites (Fig. 4). Separation associated with development was more nonlinear than regional or habitat associated separation, but within regional clusters of sites, development-associated separation was fairly clear. The fish species that were most closely correlated with axis 2 were smallmouth bass, common shiner (*Luxilus cornutus*), alewife (*Alosa pseudoharengus*), rock bass (*Ambloplites rupestris*), and spotfin shiner (Table 3). The positively correlated smallmouth bass were more prevalent (76% of all captured) at

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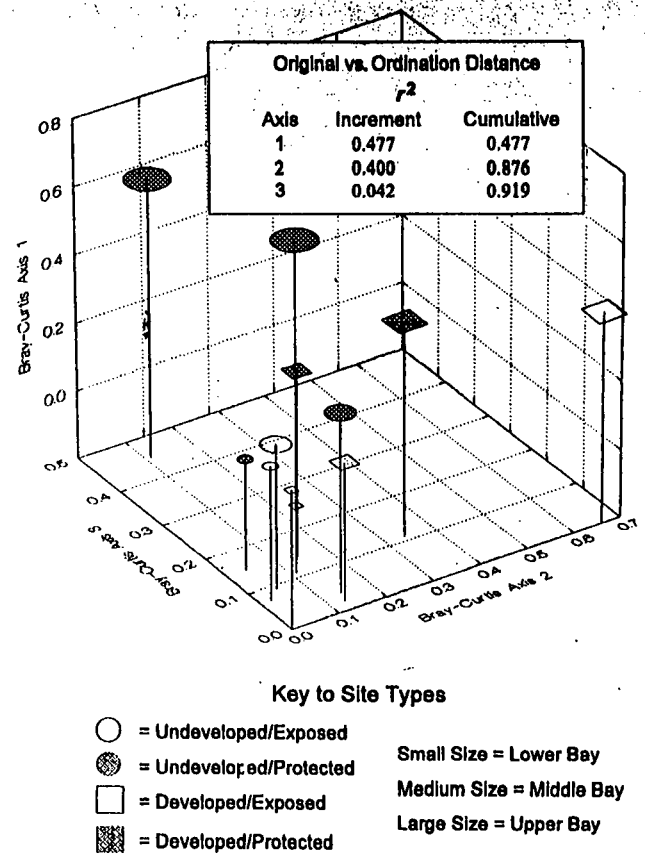
Fig. 3. Bray–Curtis ordination (variance-regression endpoint selection) on wetland sites in species space (correlations between site distances along each of the ordination axes and distances in the original n-dimensional data matrix space tabled in inset box).



developed sites, while the negatively correlated spotfin shiners were more prevalent (70% of all captured) at undeveloped sites. Environmental factors most closely correlated with axis 2 were distance to the nearest highway, turbidity, latitude, water temperature, and wind speed (Table 3). This suggests that a combination of regional and development-related factors influenced patterns along this axis.

Discriminant analyses helped quantify the statistical distinctness of the ordination patterns. Using the eight species with the strongest regional signals (e.g., highest correlations with axis 1) in the ordinations (Table 3), discriminant analysis classified 23 of 24 sites correctly (Table 4). Only one middle bay site (SB2), was misclassified as an upper bay site. This misclassification is consistent with ordination results where SB2 clustered closely with developed sites from the upper bay (Fig. 4). Discriminant analysis using species with strong habitat affiliations in the ordinations classified only 18 of 24 sites correctly (Table 4). All but 1 (92%) of the wetland sites and 7 of 12 (58%) beach sites were classified correctly. The middle bay wetland, PP1, was the only wetland misclassified, but all lower bay beaches and the upper bay beach, WR2, were misclassified as wetlands. WR2 also mapped closest to wetlands in the ordination (Fig. 4). These results suggest that wetland fish assemblages were more distinctive than beach assemblages

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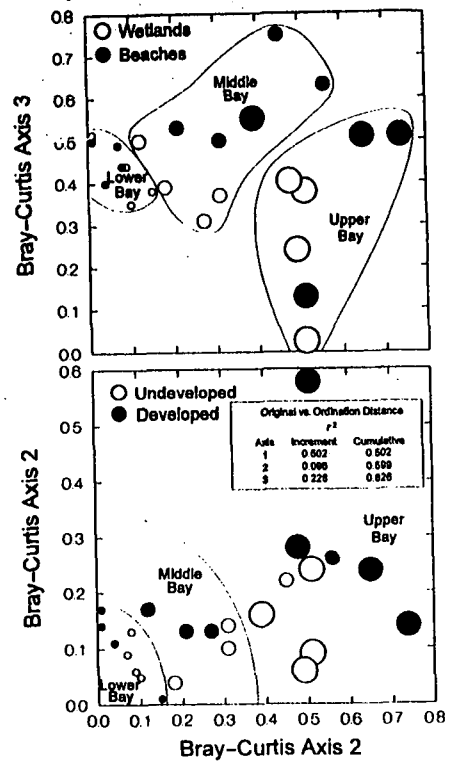
Table 4. Fish species and environmental variables most closely correlated (r) with Bray–Curtis ordination axes 1–3.

	Axis 1	Axis 2	Axis 3
Fish species			
Gizard shad	−0.854		
Emerald shiner	−0.812		
Spotfin shiner	−0.807	−0.537	
White bass	−0.798		
Yellow perch	−0.742		
Smallmouth bass		0.672	
Common shiner		−0.565	
Alewife		−0.539	
Rock bass		0.521	
Pumpkinseed			−0.806
Largemouth bass			−0.732
Golden shiner			−0.708
Johnny darter			0.704
Bowfin			−0.680
Environmental variables			
Turbidity	−0.915	−0.558	
Latitude	0.893	0.482	
Water temperature	−0.609	−0.445	
Conductivity	−0.601		
pH	−0.577		
Highway distance		−0.596	
Wind speed		−0.273	
% Macrophyte cover			−0.793
Macrophyte growth form diversity			−0.714
Macrophyte diversity			−0.710
Macrophyte species richness			−0.691
Waves			0.670

across the regional and developmental range of sites sampled in the bay. The discriminant analysis using species most closely associated with development-related axes in the ordinations classified only 16 of 24 (67%) of the sites correctly. Differences in fish assemblages resulting from development were apparently weak, at least when considered irrespective of habitat. However, discriminant analysis using species most closely correlated with both habitat and development-related axes (axes 2 and 3) provided additional insight. Here, the overall correct classification rate was poor (58%), but all undeveloped wetland sites were classified correctly.

Cluster analysis of species in site space resulted in seven main groups that were separated by overall abundance and particular site affinities (Fig. 5). Species highest on the dendogram were among the most abundant (e.g., spottail shiners, *N. hudsonius*, yellow perch) while those near the bottom were rarer. Distinct groups of species were abundant in the lower bay (e.g., emerald shiner, gizzard shad, white bass), or common in the upper bay (e.g., sand shiner, *N. stramineus*, white sucker, *Catostomus commersoni*, smallmouth bass). Species typical of undeveloped wetlands in the upper bay clustered into two groups, differing in abundance: commonly captured fishes (e.g., golden shiners, pumpkinseeds, and largemouth bass) and less common species (bowfin and walleye, *Stizostedion vitreum*). Several species typically captured at developed sites also clustered together but were separated by lower bay (e.g., freshwater drum, *Aplodinotus grunniens*, quillback, *Carpiodes cyprinus*, channel catfish, *Ictalurus punctatus*) or

Fig. 4. Bray–Curtis ordination (variance-regression endpoint selection) on all sites in species space (smallest circles, lower bay sites; medium-sized circles, middle bay sites, largest circles, upper bay sites; lines surrounding and separating groups are aids for pattern interpretation but not statistically based; correlations between distances along each of the ordination axes and distances in the original *n*-dimensional data matrix space appear as inset box in lower plot).



middle bay (e.g., yellow bullhead, *Ictalurus natalis*, trout-perch, *Percopsis omiscomaycus*, rainbow smelt, *Osmerus mordax*) affiliations.

Species co-occurrence analyses suggested that biotic interactions, such as competition and predation, were unimportant. The summary of species co-occurrences obtained from both contingency and correlation analysis revealed that approximately 95% of the 496 possible species co-occurrence distributions were neutral (Table 5). Both analyses produced similar and nearly equal numbers of positive co-occurrences (17 for contingency and 18 for correlation analysis) and fewer and

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different numbers of negative co-occurrences (10 for contingency and 2 for correlation analysis). Species with significant positive co-occurrences all had strong affinities for a particular region, usually the lower bay. Nearly all negative correlations could be explained by the strong differences in regional distributions. One exception might be the rock bass – alewife relationship identified with correlation analysis. Rock bass and alewife occurred in the same types of sites in both the middle and upper bay, but their abundances were negatively related ($r = -0.78$), indicating the possibility of a competitive or predator–prey relationship.

The influence of several abiotic factors on species distribution patterns was evident through ordinations of species directly in environmental space. The first three axes accounted for 99% of the original distance calculated among sites; 83% with axis 1, 13% with axis 2, and 3% with axis 3. Based on the correlations of environmental variables with each ordination axis, species locations along axis 1 were driven by regional factors, along axis 2 by habitat, and along axis 3 by development. Latitude, turbidity, and pH were most closely correlated with axis 1 ($r > 0.95$); macrophyte diversity, substrate diversity, and wave height were most highly correlated with axis 2 ($r > 0.80$); and the development index, conductivity, and macrophyte growth form diversity were most closely correlated with axis 3 ($r \geq 0.60$).

Six of the environmental variables closely correlated with ordination axes of species in environmental space had particularly clear gradients. Contour overlays revealed marked separation primarily along axis 1 among three species groups corresponding to their scores (for details see Brazner 1994) for latitude and turbidity (Figs. 6E and 6F). Species positioned low along axis 1 were usually from lower bay sites with high turbidity, while species positioned high along axis 1 were usually from upper bay sites with low turbidity. Thus, the three species groups were typical of lower, middle, and upper bay assemblages. Contour overlays for other factors that varied on a regional scale, such as conductivity, pH, and water temperature, were similar to those for turbidity and latitude, but separation among species groups was less distinct.

Contour overlays also revealed clear separation primarily along axis 2 among three species groups corresponding to their scores for substrate diversity (Fig. 6D). Species positioned highest along axis 2 were usually from sites of low substrate diversity (beaches) while species positioned lowest along this axis included typical wetland fishes. The response to sediment organic carbon was similar but not as clear as the response to substrate diversity. Another important gradient related to habitat was the macrophyte gradient. Contour overlays for number of macrophyte species, growth form diversity, and areal coverage all revealed clear separation among fish along both axes 1 and 2. The clearest response was apparent for the combined macrophyte diversity index, which divided fishes into four groups (Fig. 6C). Fish from sites with the highest macrophyte diversity (undeveloped wetlands) were positioned in the lower right hand corner of the plot, while those in the upper left hand corner were usually from sites with little or no macrophyte cover (developed beaches). Contours for wave height were similar to those for macrophyte diversity in that there was separation along axes 1 and 2 (Fig. 6B). However, separation along axis 3 also was observed when plotted against axis 2 suggesting that wave height is related to a variety of factors

Table 5. Site classification matrices based on discriminant analyses with eight fishes that were most closely correlated (the four highest positive and four highest negative r values) with Bray–Curtis ordination.

(A) Axis 1 (regional discrimination).

	Predicted region				
Actual region	Lower	Middle	Upper	% Correct	Species
Lower	8	0	0	100	GZ, ES, WB
Middle	0	7	1	88	SF, RB, SB
Upper	0	0	8	100	LP, SS
Total	8	7	9		

(B) Axis 2 (development discrimination).

	Predicted development			
Actual development	Undeveloped	Developed	% Correct	Species
Undeveloped	8	4	67	AW, SF, GZ, CS
Developed	4	8	67	SB, RB, SS, TP
Total	12	12		

(C) Axis 3 (habitat discrimination).

	Predicted habitat			
Actual habitat	Wetland	Beach	% Correct	Species
Wetland	11	1	92	GS, PS, JD, BF
Beach	5	7	58	AW, RS, TP, ST
Total	16	8		

(D) Axes 2 and 3 (habitat × development discrimination).

	Predicted site type					
Actual site type	UW	DW	UB	DB	% Correct	Species
UW	6	0	0	0	100	GS, PS, AW
DW	1	2	1	2	33	TP, SB, RB
UB	1	2	2	1	33	SF, CS
DB	0	1	1	4	67	...
Total	8	5	4	7		

Note: Two-letter species codes are given in the Appendix.
UW, undeveloped wetland; DW, developed wetland; UB, undeveloped beach; DB, developed beach.

(e.g., regional, habitat, development). A gradient in fish response was clearly apparent for one development-related variable, the development index. Contours of species scores for the development index were most clearly separated along axes 1 and 3 (Fig. 6A). Species usually from sites with the highest development index (e.g., channel catfish, quillback, green sunfish) were in the upper left hand corner of this plot, while those typifying undeveloped sites (e.g., johnny darter, bowfin, largemouth bass) were in the lower right portion of the plot. Contours of conductivity and slope along these same axes provided similar but less distinct separation.

Regression analysis provided a more predictive and quantitative approach for understanding which abiotic factors were driving a limited number of species distributions (the five most abundant fishes and five other species of special ecological interest in Green Bay), as well as patterns in species richness and overall fish abundance. The two best models for each fish or community structure variable (Table 6) were used to evaluate which environmental factors were most predictive of fish species abundance and assemblage structure. Only two models

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Table 4. Summary of species co-occurrences based on 2 × 2 contingency analysis of presence–absence data and correlation analysis of total abundance data for all species captured at more than five sites.

Analytical technique	Positive co-occurrences	Negative co-occurrences	Neutral
Contingency analysis (χ^2, $p \leq 0.01$)	17 3.4% White bass (SF, GZ, GR, CP, FD, QB) Green sunfish (GZ, SF, CS, WB, FD) Gizzard shad (WB, GR, CP, FD) Freshwater drum (GZ, WB, GR, CP) Common carp (GZ, WB, FM, FD)	10 2.0% Sand shiner (GR, GZ, CP, FD) Golden shiner (TP, RS) Rock bass (CS, GR) Smallmouth bass (CP, GZ) Gizzard shad (SS, SB) Common carp (SS, SB) Green sunfish (SS, RB)	469 94.6%
Correlation analysis (r, $p \leq 0.10$, Bonferroni corrected)	18 3.6% Gizzard shad (YP, ES, WB, CP, FD) White bass (GZ, ES, CP, FD) Freshwater drum (GZ, ES, WB) Emerald shiner (GZ, WB, FD) Golden shiner (PS, BC) Logperch (JD, LB)	2 0.4% Rock bass (AW, SF)	476 96.0%

Note: Species with the greatest number of significant co-occurrences have specific pairwise combinations listed separately. Two-letter species codes are given in the Appendix.

were single factor regressions; macrophyte cover was highly predictive of bluegill abundance and macrophyte diversity was highly predictive of golden shiner abundance. Of the remaining 22 models, 13 required only 2 input variables, while 7 required 3 input variables, and 2 had 4 input variables. The most predictive variables included both regional and habitat related factors. Turbidity, latitude, or water temperature was the most explanatory variable in half of the 24 models, while one of the macrophyte variables was most explanatory in 10 of the remaining 12 models. Development variables had high predictive power in only three models: one white sucker model and the two models of overall abundance.

Discussion

Distinct fish assemblages were present in the shallow inshore habitats of Green Bay. The greatest differentiation among assemblages was observed at a regional scale, but there also were differences among assemblages from different habitats. Differences due to development were least apparent, although assemblages at undeveloped wetlands were unique from those at other habitat-by-development site combinations. In addition, assemblages from developed and undeveloped sites in the upper bay were relatively distinct, as were differences between very highly developed sites (e.g., AM1, BB1) and all other sites.

Regional patterns

Site separation within regions was the smallest in the lower bay and largest in the upper bay. This may reflect the general level of degradation and mixing in each region. The lower bay is an Area of Concern (IJC 1987) with a large contaminant load, hypereutrophic nutrient status, high turbidity, and intense development on the shoreline throughout much of the area. The upper bay has lower population density, lower trophic status, clearer water, and less human development (Bertrand et al. 1976). The lower bay is also well mixed because of its shallow, open morphometry; approximately 70% of the water inside of Long Tail Point and Point Sable is comprised of Fox River water (Epstein et al. 1974). This results in a high degree of physical and chemical similarity throughout the lower bay and may be the reason fish assemblages are most similar there. In the upper bay, where turbidity is low and mixing is presumably less because of the protected nature of Little Bay de Noc, there was greater differentiation among sites and the influence of development was more apparent. These results are also consistent with the finding that infertile wetlands are more sensitive to human disturbance and have greater variation in vegetation than wetlands in fertile areas (Moore et al. 1989).

Environmental influences

Of all environmental factors, turbidity had the most influence on fish assemblage structure. Turbidity varied primarily on a regional scale and reflected the trophic gradient. About half of the turbidity is biotic, while the other half results from erosion, runoff, and resuspension of sediments in the shallow lower bay (Harris et al. 1991; Millard and Sager 1994). Other factors that covary with turbidity also reflect (e.g., conductivity, pH) or contribute to (e.g., water temperature) the trophic gradient. They each may have independently influenced fish assemblage structure, but turbidity was correlated most consistently with the major axes of variation in the sites in species space ordinations, was most predictive in the regression equations, and had clearly separated contours in ordinations of species in environmental space.

Turbidity has also been implicated as a primary factor limiting macrophyte communities in the Great Lakes (Phillips et al. 1978; Stuckey 1989; Crowder and Painter 1991) and in the lower and middle sections of Green Bay (Harris et al. 1991; McAllister 1991). This is especially relevant to this study because, after turbidity, macrophytes were the next most important factor structuring the fish assemblages. Macrophyte cover was correlated with assemblage differences between wetlands

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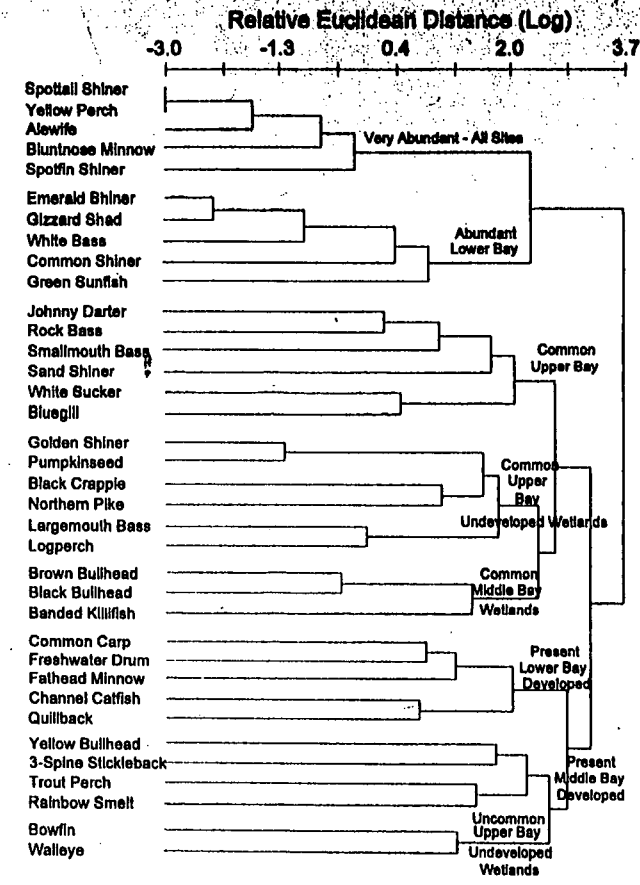
Fig. 5. Cluster analysis (Ward's method) of species in site space using all sites (text annotations included to aid in cluster interpretations).



and beaches and between undeveloped and developed wetlands. Where macrophyte cover and richness was high, fish species richness and abundance also tended to be high. This same pattern was apparent in other Great Lakes littoral habitats (Minns et al. 1994) and in more inland lakes (Keast et al. 1978; Benson and Magnuson 1992); it is driven by the fact that fish are attracted to the increased habitat heterogeneity that macrophytes provide (Tonn and Magnison 1982; Eadie and Keast 1984; Robinson and Tonn 1989) and the invertebrate prey species that utilize macrophytes for substrates and food (Keast and Harker 1977; Keast 1978; Wiley et al. 1984). However, extremely high densities of macrophytes (>70–80% cover) can limit their utility to fish and result in lower overall fish species richness than in moderately vegetated habitats (Crowder and Cooper 1982; Killgore et al. 1989; Lillie and Budd 1992). Macrophytes rarely reached high densities during this study, but heavy macrophyte cover is not uncommon in other Great Lakes coastal wetlands and may become more common in Green Bay as the zebra mussel (*Dreissena polymorpha*) invasion advances and leads to greater water clarity and better growing conditions for macrophytes (Skubinna et al. 1995). A better characterization of the relationship between fish distribution and macrophyte community structure would be useful, since a relationship between areal coverage of vegetated

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Table 5. Regression relationships between environmental variables and individual fish species or community structure variables measured at each site.

Species or community component	Best models	r	p
Yellow perch	**44.03** – 0.94(latitude) + **0.18**(substrate diversity)	0.80	<0.001
	–0.63 + 1.47 log(turbidity) + 0.14(macrophyte GFD)	0.78	<0.001
Spottail shiner	29.31 – 0.86(latitude) + 8.53 log(water temperature)	0.70	0.001
	–12.48 + 9.59 log(water temperature) + 0.97 log(turbidity)	0.66	0.002
Alewife	**29.62** + 2.39 log(turbidity) – 0.03(% macrophyte cover) – 12.81log(conductivity) + 0.23(% sed. OC)	0.83	<0.001
	18.67 + 1.77 log(turbidity) – 0.02(% macrophyte cover) – 7.89 log(conductivity)	0.76	0.001
Spotfin shiner	**45.73** – 1.32(latitude) + 10.88 log(water temperature) + 0.06(city distance)	0.93	<0.001
	47.80 – 1.39(latitude) + 12.13 log(water temperature)	0.91	<0.001
Bluntnose minnow	**37.48** + 0.49(macrophyte GFD) – 0.83(latitude) – 0.97(no. of macrophyte species)	0.85	<0.001
	32.95 + 0.28(macrophyte GFD) – 0.72 log(latitude)	0.81	<0.001
Bluegill	–0.10 + 0.02(% macrophyte cover) + 0.11(% slope)	0.76	<0.001
	0.19 + 0.02(% macrophyte cover)	0.71	<0.001
Northern pike	0.30 + 2.15(macrophyte diversity) – 0.12(% sed. OC) – 0.05(% slope)	0.81	<0.001
	0.16 + 1.76(macrophyte diversity) – 0.11(% sed. OC)	0.76	<0.001
Golden shiner	0.11 + 3.43(macrophyte diversity) – 0.11(% sed. OC)	0.87	<0.001
	0.01 + 2.59(macrophyte diversity)	0.83	<0.001
White sucker	**–32.85** + 2.24 log(wind speed) + 0.73(latitude) + 0.07 log (city distance)	0.75	0.001
	0.15 + 1.96 log(wind speed) + 0.15(% slope)	0.64	0.004
Sand shiner	–42.09 – 2.01 log(no. of macrophyte species) + 0.94(latitude) + 0.42(macrophyte GFD) – 0.17(% slope)	0.85	<0.001
	–40.07 – 0.49 log(no. of macrophyte species) + 0.91(latitude)	0.64	0.004
No. of species	2.06 + 8.65 log(turbidity) + 1.05(macrophyte GFD)	0.79	<0.001
	5.71 + 7.66 log(turbidity) + 4.06 log(no. of macrophyte species)	0.77	<0.001
Log total abundance	–4.39 + 5.17 log(water temperature) + 0.54 log(turbidity) – 0.17(development index)	0.82	<0.001
	1.81 + 0.85 log(turbidity) – 0.14(development index) + 0.06(macrophyte GFD)	0.78	<0.001

Note: The two best models with less than four variables and all coefficients significantly different from zero, $p \leq 0.10$, are presented. Models were selected through interactive stepwise regression procedure; those with the highest r, overall significance values, lowest residual variance, and normal residual plots were deemed "best." Simpler models were always selected over more complex models when all else was equal. Constants given in boldface are significantly different from zero. GFD, growth form diversity; sed. OC, sediment organic carbon.

wetland habitat and open lake fisheries would be important to quantify. This sort of relationship has been observed in coastal marine ecosystems (Turner 1977; Boesch and Turner 1984; Deegan 1993) but is not well established in Great Lakes coastal systems even though recent studies suggest a wetland–fisheries connection may exist. (Whillans 1989; Keough et al. 1996). Studies designed to further examine macrophyte – littoral fish – open lake fish community interactions are currently in progress on both Lake Superior and Lake Michigan (D.A. Wilcox, National Biological Service, Ann Arbor, Mich., personal communication; J.C. Brazner, unpublished data). Indications are that there may be a significant relationship that is dependent upon the morphometry and configuration of littoral habitats in a particular area (e.g., coastal wetland hydrogeomorphic type).

Macrophyte communities in the Great Lakes are structured by a variety of factors in addition to turbidity (Stuckey 1989). Water level fluctuation is clearly one of the most important (Keddy and Reznicek 1985; Keough 1992; Wilcox and Meeker 1992), and exposure to wind and wave energy is another (Keddy 1982). Exposure also is one of the more obvious physical differences between wetlands and beaches and may be the underlying reason why substrate diversity and sediment organic carbon were closely related to differences in fish assemblage structure between these site types. Organic carbon and particle diversity in sediments reflect differences in exposure (Cole and Weigmann 1983; Wilson and Keddy 1985) and can affect macrophyte community structure, colonization, and growth (Keddy 1983; Wilson and Keddy 1985). More protected sites, less subject to storm, current, and wave action, have more organic carbon and higher percent silt and clay in their sediments. It appears that intermediate exposure levels result in the highest macrophyte species richness (Keddy 1983) and, based on this study, also the highest fish species richness.

Quantifying development

Although some differences in the fish assemblages were attributed to human development, particularly when only wetland site data were included in the analysis, effects of development were surprisingly weak. The semiquantitative index of development was the most useful, while distance to the nearest city and highway were poorer predictors. A better index of disturbance from different types of development is needed. Because much of the Great Lakes shoreline is fringed with roads and cities, distances to roads and cities may have been too similar among sites to represent development effectively. Population density, road density, or percentages of land in various uses near a site quantified using a geographic information system approach (e.g., Detenbeck et al. 1993; Weaver and Garman 1994) might have been more effective. This approach has been used particularly effectively to compare differences in the fish community-based Index of Biotic Integrity with varying watershed conditions in Ontario streams (Steedman 1988).

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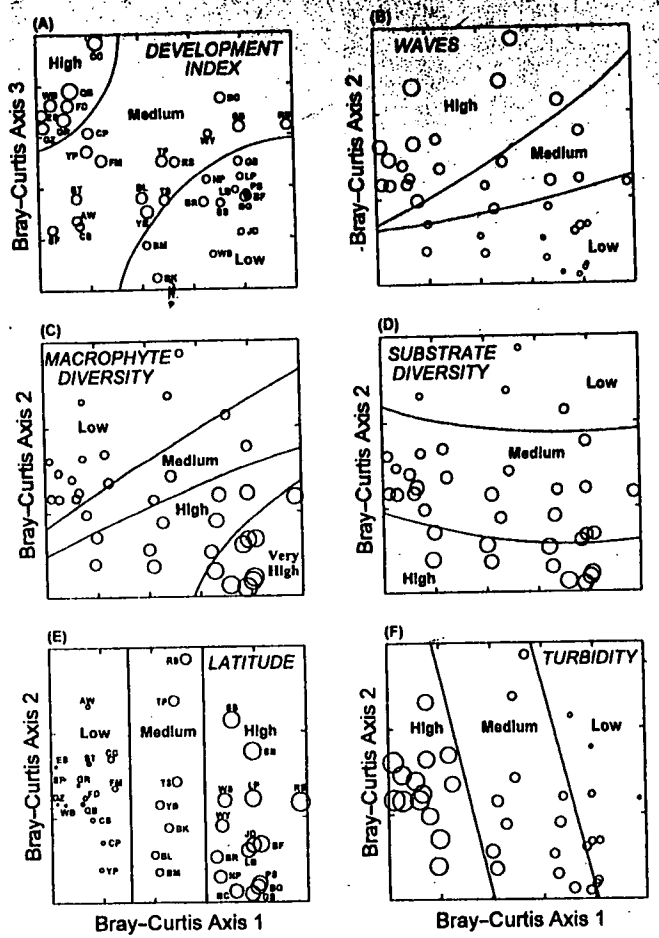
Fig. 6. Bray–Curtis ordination (variance-regression endpoint selection) of species in the transformed space using all sites; contours for abiotic variables overlayed (point size based on species scores for each variable; contours are lowess fit lines that separate species into three or four response levels for each variable based on species scores for that variable (details in Brazner 1994). The two-letter species codes are defined in the Appendix. Note that all axis 2 versus axis 1 codes are detailed in the panel for latitude, and upper left panel is the only plot of axis 3 versus axis 1.



Biotic interactions

Despite the possible exception noted for rock bass and alewives and limitations inherent to the kinds of analyses we used (Bowers and Brown 1982; Tonn et al. 1990), strong species interactions appeared to be rare, and their direct influence on the structure and patterns in the fish assemblages was probably minimal. The apparent unimportance of biotic interactions to these fish assemblages may be related to high variability in physical conditions typical of nearshore habitats in the Great Lakes. Hourly, daily, seasonal, and annual fluctuations in

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water level along with strong storm surges, pronounced wave activity, wide daily temperature fluctuations, ice scours, and other harsh environmental conditions are associated with these habitats in Green Bay (Heaps et al. 1982; Miller and Saylor 1985; Lathrop et al. 1990). This variability may preclude competition and predation from becoming strong organizing forces (Wiens 1984; Menge and Sutherland 1987; Winemiller and Rose 1992). Other studies of intertidal communities (Sousa 1979), coral reef fishes (Sale 1980), birds (Tramer 1969; Rotenberry 1978), and phytoplankton (Tramer 1969) from unpredictable environments support this hypothesis. The fact that >90% of the fish captured during this study were immature probably also reduced the likelihood of detecting predator–prey interactions and reinforces the idea that coastal wetlands have a primary role as nursery habitats for fish (Stephenson 1990; Brazner 1997).

Overall, it appears that a combination of regional and site-specific factors were important in structuring fish assemblages in Green Bay's coastal wetland and beach habitats. Tonn et al. (1990) refer to this as the "balance between local and regional processes" in their study of patterns in fish assemblages from small North American and Finnish lakes. Although assemblages in a particular location may be primarily the result of local processes, factors that vary across larger spatial scales, such as geomorphic conditions or climatic factors, may also have a significant influence (Ricklefs 1987). Understanding scale of analysis in the interpretation of patterns may be especially important for littoral zone organisms. It has been suggested that the high complexity of littoral environments, compared with more homogeneous pelagic habitats, requires the ecology of littoral organisms be studied across a hierarchy of influences that encompass both regional and site-specific scales (Duarte and Kalff 1990). After completing this sort of analysis in Green Bay, it appears that regionally varying factors (e.g., turbidity) had the most influence on littoral fish assemblages, and undeveloped wetlands provide the most valuable and intensely utilized fish habitat, particularly as nursery areas. These results and studies of fishes associated with vegetated and beach habitats in smaller inland lakes (Guillory et al. 1979; Bryan 1992) and altered and unaltered littoral habitats from the Great Lakes (Poe et al. 1986; Johnson 1989) support the idea that a broad geographic perspective is important and that wetland habitats should be given special consideration in ecosystem management plans for the Great Lakes.

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Appendix. Number of individuals of each species captured by site (reduced data matrix only, which includes the 36 most abundant species of 54 captured).

Site, code, and development*	YP	ST	AW	SF	BM	GZ	WS	ES	CS	BG	WB	SS	GR	GS
Wetlands														
Lower Bay														
Long Tail Point Wetland, LTP1, U	3525	789	265	194	285	384	14	113	105	18	52	0	3	1
Little Tail Point Wetland, LT1, U	942	207	142	227	116	264	10	31	34	3	226	0	5	0
Atkinson Marsh, AM1, D	333	224	92	45	15	160	1	251	6	0	106	0	2	0
Sensiba Wildlife Refuge, SWR1, D	1108	241	124	220	259	137	103	224	81	6	9	0	2	3
Middle Bay														
Pecor Point Marsh, PP1, U	170	316	151	436	23	13	297	24	174	4	9	0	5	1
Seagull Bar Wetland, SB1, U	267	513	193	82	607	1	53	4	7	42	0	0	24	0
Oconto Marsh, OM1, D	919	985	80	53	544	4	2	2	277	0	0	0	6	0
Peshtigo Marsh, PR2, D	99	176	93	104	520	0	63	0	3	36	0	20	41	0
Upper Bay														
Whitefish River Mouth Wetland, WR1, U	99	0	0	0	411	0	388	0	5	327	0	0	0	182
Portage Marsh, PM1, U	20	0	37	0	5	1	8	0	0	205	0	0	0	71
Escanaba River Mouth Wetland, ER2, D	198	236	14	0	18	0	13	2	0	4	0	6	0	12
Gladstone Wetland, GW1, D	517	33	0	0	5	0	0	0	0	1	0	57	0	0
Beaches														
Lower Bay														
Long Tail Point Outer Beach, LTP3, U	312	386	86	1708	76	208	5	136	19	1	15	0	5	1
Point Sable Beach, PS1, U	695	399	74	7	27	34	13	259	8	0	56	0	193	0
Bay Beach, BB1, D	587	294	49	119	47	195	1	139	1	0	118	0	113	0
Long Tail Point Inner Beach, LTP2, D	709	191	75	250	87	514	12	151	54	0	74	0	23	6
Middle Bay														
Seagull Bar Outer Beach, SB3, U	5	106	65	4	3	0	2	2	0	2	0	0	0	0
Peshtigo River Outer Beach, PR4, U	57	242	685	330	83	0	109	1	5	0	0	75	4	0
Peshtigo River Inner Beach, PR3, D	342	2933	1136	465	39	19	30	17	7	0	1	6	0	0
Seagull Bar Inner Beach, SB2, D	29	1	49	0	0	0	4	0	0	0	0	0	4	0
Upper Bay														
Whitefish River Mouth Beach, WR2, U	141	79	1	0	534	0	83	0	1	4	0	58	0	2
Portage Point Beach, PM2, U	8	232	868	0	6	0	83	71	19	0	0	385	0	0
Escanaba River Mouth Beach, ER1, D	11	5	14	0	2	0	115	1	0	36	0	2	0	0
Escanaba River Delta Beach, ER3, D	13	2	28	1	8	0	43	0	0	1	0	18	0	0
Totals	11 106	8590	4321	4245	3720	1934	1452	1428	806	690	666	627	450	279

Site, code, and development*	RB	PS	JD	BL	BR	SB	CP	BK	FM	LB	BC	TP	FD	LP	RS	NP	CC	QB	YB	WY	BF	TS
Wetlands																						
Lower Bay																						
Long Tail Point Wetland, LTP1, U	0	3	5	6	1	0	19	1	0	1	1	0	4	0	0	0	0	2	2	1	0	1
Little Tail Point Wetland, LT1, U	0	1	0	3	1	0	10	2	4	0	2	0	4	0	1	2	0	0	0	0	0	0
Atkinson Marsh, AM1, D	0	0	0	0	0	0	3	0	1	0	1	0	7	0	0	1	3	6	0	0	0	0
Sensiba Wildlife Refuge, SWR1, D	0	1	1	2	0	2	1	1	26	1	1	0	1	1	0	0	0	4	0	0	0	0
Middle Bay																						
Pecor Point Marsh, PP1, U	0	0	5	1	4	0	2	15	0	0	0	0	0	0	0	5	0	0	0	0	0	0
Seagull Bar Wetland, SB1, U	8	0	3	3	0	7	0	15	1	5	0	0	0	0	0	1	1	0	1	0	1	0
Oconto Marsh, OM1, D	0	0	4	0	0	1	1	7	3	1	0	21	0	1	0	1	0	0	1	0	0	4
Peshtigo Marsh, PR2, D	0	8	7	93	79	0	7	10	1	0	0	0	0	0	0	0	0	3	7	0	1	0
Upper Bay																						
Whitefish River Mouth Wetland, WR1, U	88	88	52	1	3	3	2	0	1	40	12	0	0	10	0	4	0	0	0	3	2	0
Portage Marsh, PM1, U	1	72	1	5	5	0	4	3	3	0	6	0	0	0	0	13	0	0	0	0	2	1
Escanaba River Mouth Wetland, ER2, D	35	1	6	0	0	1	0	1	0	0	6	0	0	0	0	0	0	0	0	0	0	0
Gladstone Wetland, GW1, D	18	0	2	0	3	47	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0
Beaches																						
Lower Bay																						
Long Tail Point Outer Beach, LTP3, U	0	1	1	0	0	1	3	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0
Point Sable Beach, PS1, U	0	0	0	3	2	1	12	0	1	0	4	0	4	0	1	0	5	2	0	1	0	0
Bay Beach, BB1, D	1	0	1	6	0	0	11	0	5	0	1	1	1	0	0	0	15	5	0	1	0	0
Long Tail Point Inner Beach, LTP2, D	0	0	2	4	1	0	5	0	5	0	4	0	9	0	0	0	0	1	2	0	0	0
Middle Bay																						
Seagull Bar Outer Beach, SB3, U	9	0	1	0	0	1	1	0	2	0	0	8	0	0	4	0	0	0	0	0	0	1
Peshtigo River Outer Beach, PR4, U	0	0	4	1	0	1	0	18	1	0	0	1	0	0	1	0	0	0	0	0	0	1
Peshtigo River Inner Beach, PR3, D	1	1	2	0	0	0	1	1	14	0	0	1	0	0	18	0	0	0	1	0	0	0
Seagull Bar Inner Beach, SB2, D	8	0	1	0	0	2	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Upper Bay																						
Whitefish River Mouth Beach, WR2, U	43	15	80	2	8	6	0	0	0	10	2	0	0	15	0	1	0	0	0	3	1	0
Portage Point Beach, PM2, U	0	0	3	0	0	2	0	0	0	0	0	3	0	2	1	0	0	0	0	0	1	0
Escanaba River Mouth Beach, ER1, D	7	0	0	0	0	11	0	0	0	0	2	0	0	0	3	0	0	0	0	0	0	0
Escanaba River Delta Beach, ER3, D	5	0	0	0	0	6	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Totals	224	191	181	130	107	92	82	74	70	58	43	37	31	31	30	28	24	23	15	9	8	8

Note: The two-letter species codes are as follows: YP, yellow perch; ST, spottail shiner; AW, alewife; SF, spotfin shiner; BM, bluntnose minnow; GZ, gizzard shad; WS, white sucker; ES, emerald shiner; CS, common shiner; BG, bluegill; WB, white bass; SS, sand shiner; GR, green sunfish; GS, golden shiner; RB, rock bass; PS, pumpkin seed; JD, Johnny darter; BL, black bullhead; BR, brown bullhead; SB, smallmouth bass; CP, common carp; BK, banded killifish; FM, fathead minnow; LB, largemouth bass; BC, black crappie; TP, troutperch; FD, freshwater drum; LP, logperch; RS, rainbow smelt; NP, northern pike; CC, channel catfish; QB, quillback; YB, yellow bullhead; WY, walleye; BF, bowfin; TS, threespine stickleback.

*D, sites modified by human development; U, relatively undeveloped site.

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GIS

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CONTIGUITY AND EDGE CHARACTERISTICS OF WETLANDS IN FIVE COASTAL COUNTIES OF NORTH CAROLINA, USA

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Abstract: Wetland contiguity and edge were determined with a geographic information system (GIS) for five coastal counties in North Carolina, USA. The digital database was created from wetlands digitized from U.S. Fish and Wildlife Service National Wetlands Inventory maps. The GIS analysis was based on three classes of information: 1) all wetlands as one class; 2) wetlands separated by dominant vegetation community type (e.g., forest, shrub, or marsh); and 3) forest and shrub wetlands further separated by dominant vegetation (e.g., evergreen, deciduous, or mixed). The contiguity analysis supports the perception that the lower coastal plain counties are dominated by large contiguous wetlands When wetlands were clumped into one class, the number of wetlands > 1,000 ha ranged from 2 to 7 and the area accounted for 77 to 96% of the total wetland area. Several of those sites were > 100,000 ha in size. When wetlands were separated into more specific classes, the number of sites < 10 ha ranged from 416 to 3,370, but the wetland area in this size class was < 5% of the total wetland area. The average size of evergreen forest and shrub wetlands was typically much greater than deciduous forest and shrub wetlands, a reflection of the configuration of large, block pocosin wetlands. Percent edge was also typically lower for the evergreen forest and shrub wetlands than for deciduous forest and shrub wetlands. The counties with the highest number of wetland sites in transition to other uses have the most land owned by private timber companies. Contiguity analysis of wetlands with GIS provides landscape-scale information for natural resource management issues such as preserve design, habitat fragmentation, rare species management, and species migration opportunities.

Key Words: GIS, contiguity, edge, pocosins, landscape patterns, NWI, North Carolina

INTRODUCTION

Landscape pattern characteristics of ecosystems, such as contiguity and edge, are important aspects for understanding issues in landscape ecology such as migration of wildlife (Fahrig and Merriam 1985, Freemark and Merriam 1986), species diversity (Noss 1983), and persistence (Turner 1989) and for issues in natural resource management (Liu et al. 1995). Geographic information systems (GIS) offer tools to analyze landscape properties associated with ecosystem management. A GIS can readily determine shape and size of landscape patches and calculate distance to other similar patches. This information is useful for understanding fragmentation and edge characteristics of natural habitats. Fragmentation of the landscape produces a series of remnant vegetation patches embedded in a matrix of different vegetation and/or land uses and increases the amount of edge, which influences landscape functions such as wildlife habitat suitability, species movement, and energy or nutrient flow (Saunders et al. 1991).

Large, intact wetlands such as the pocosins (evergreen forest-shrub peatlands) in eastern North Carolina, USA are now the refuge habitat of species once more widely distributed (Wilbur 1981). Although size and shape of habitat patches clearly influence overall diversity of species, connections among patches may be as important to maintenance of diversity (Noss 1983). Wetlands associated with riverine floodplains are thought to represent natural corridors for animal migration (Cross et al. 1991) and may connect habitat patches. The size and shape of habitat patches also influence the amount of edge; the wetland corridors of narrow, riverine floodplains may not have distinct interior habitats and correspondingly lower species richness. Contiguity is a measure of the degree to which patches (represented as polygons in GIS) are in contact with one another or the amount of area occupied by connected polygons (DeMers 1997).

It is a common perception in North Carolina that large contiguous wetlands dominate the landscape of the eastern portion of the state in the Atlantic Coastal Plain physiographic province. Fueling that perception

is a dominance of hydric soils and wetlands as a percentage of the land area in many counties located in the Coastal Plain (Wilson 1962, Richardson et al. 1981, Moorhead 1992). Given the long history of wetland conversions in eastern North Carolina and the rapid population growth in several coastal counties (North Carolina 1989), the contiguity of remaining wetlands is probably less than anticipated.

The overall objective of this study was to use GIS to analyze landscapes dominated by wetlands in five coastal counties in North Carolina to determine habitat contiguity and quantify edge. Specific objectives were to 1) determine if wetland type (e.g., forest or shrub, deciduous, or evergreen) influenced landscape characteristics, and 2) examine land-ownership patterns in relation to landscape patterns of wetlands. I hypothesized that linear deciduous forested wetlands associated with river and stream corridors should have greater edge than the large evergreen-dominated pocosin wetlands of the lower Coastal Plain. Counties with extensive federal or state land ownership also should have more contiguous wetlands with less edge.

METHODS

The GIS analysis of wetlands was based on digital datasets created separately for five North Carolina counties: Brunswick, Carteret, Currituck, Dare, and Pender. Wetland community types were digitized from U.S. Fish and Wildlife Service National Wetland Inventory (NWI) maps (scale 1:24,000) on a GTCO Digipad (Model 36-48A, GTCO Corporation, Columbia, MD) with ERDAS (Version 7.0, ERDAS, Atlanta, GA) GIS software. The wetlands were identified on NWI maps as estuarine marsh, estuarine shrub, palustrine marsh, palustrine shrub, palustrine forest, partly drained, and other (Cowardin et al. 1979). The palustrine shrub and forest wetlands were digitized by dominant community type (deciduous, evergreen, mixed). Mixed NWI classes were digitized by the predominant class (i.e., forest for a forest/shrub mixed class). Other wetlands included waterfowl impoundments and unconsolidated shore. Partly drained wetlands have evidence of an artificially lowered water table but appear to support hydrophytes (Cowardin et al. 1979). Areas not delineated as wetlands on the NWI maps were digitized as one unit and referred to as nonwetland. County digital maps were thoroughly checked for digitizing errors and for edge matching of NWI maps. The NWI maps were originally developed from photointerpretation of color infrared high-altitude photography flown in the spring of 1981 and 1982 (scale 1:58,000).

Landscape characteristics were determined by county using the raster GIS modeling module of ERDAS. The digital data layers had a cell size of approximately 30 × 30 m. Contiguity was determined in the following sequence: 1) viewing all wetlands as one landscape unit, 2) separating palustrine and estuarine wetlands based on dominant vegetative structure (marsh, shrub, forest), and 3) separating palustrine forest and shrub wetlands based on dominant plant community type (deciduous, evergreen, and mixed). Edge characteristics were determined for wetlands separated into dominant plant community type.

Contiguity of wetlands was based on an analysis that identified contiguous groups of pixels in a specific landcover class. A connectivity radius of 3 was selected that specified that similar pixels must be within a radius of 3 or fewer pixels from each other to be considered contiguous. The connectivity radius is measured in pixels, from the center of one pixel to another. With the NWI data, this translated into contiguity based on wetlands about 90 m from each other. The connectivity radius of 90 m was selected for two reasons. The primary reason was to decrease the computer time required for analysis; the minimum radius is 1 (30 m for NWI maps), the maximum radius is 8 (240 m). The shorter the radius, the longer the time required for analysis. The second reason was based on average distances (90 m) that salamanders move from wetland breeding or nesting areas to more terrestrial habitats (Semlitsch 1981, Hairston 1987, Madison 1997). The rationale then assumes that if a wetland habitat is removed from the landscape, the salamander populations will move to a similar habitat if it is within 90 m. Salamanders were chosen as a target organism since they depend on wetland habitat for at least a portion of their life cycles, and habitat fragmentation or loss may influence migration patterns and/or persistence of salamander species.

Edge characteristics were determined using a GIS neighborhood process in which the value of a central pixel is compared to those of its neighbors within a moving window. In this study, each pixel was compared to pixels that surround it within a 3 × 3 pixel scanning window. Edges (i.e., neighbors with different pixel values or classes) were detected for each GIS class during the scanning process as the scanning window moved through the file, pixel by pixel.

RESULTS AND DISCUSSION

The total area of wetlands in the five counties is 337,299 ha, which is about 48% of the total land area (Table 1). The 337,299 ha represent 35% of the total wetland area (957,470 ha) in the 20 coastal counties of North Carolina (Moorhead 1992). The wetlands account for 36% of the land area in Brunswick County to 85% in Dare County. The majority of the wetlands

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Table 1. Area (ha) of wetlands of the five coastal counties of North Carolina.

Community Type	Currituck	Dare	Carteret	Pender	Brunswick
Deciduous forest	16,186	2,170	3,902	28,230	22,862
Evergreen forest	257	32,314	18,570	31,063	18,767
Mixed forest	2,042	15,394	8,179	13,552	6,850
Deciduous shrub	360	559	311	709	995
Evergreen shrub	474	8,837	6,686	7,562	7,771
Mixed shrub	44	744	2,612	7,272	1,298
Palustrine marsh	315	7,053	378	592	2,950
Estuarine marsh	10,833	12,358	23,817	3,239	6,611
Estuarine shrub	437	5,143	3,048	91	369
Partly drained	2,096	79	4,801	8,769	8,499
Other	410	1,716	3,486	1,416	2,219
Total Wetland	33,454	86,367	75,791	102,494	79,193
Nonwetland	34,994	14,983	65,393	122,443	142,865
Total land area	68,448	101,350	141,184	244,937	222,058

are palustrine forest or shrub (78%), and 17% of the wetlands are estuarine marsh.

The results of the contiguity analysis were expressed by listing the number and area of wetlands by a specified size classification for each county (Table 2). Contiguity of existing wetlands depends on how wetlands are viewed as units. Clumping all wetlands into one class for GIS analysis indicates the overall landscape patterns of wetlands to non-wetland areas. The number of wetland areas > 1,000 ha in size ranged from 2 to 7 when wetlands were clumped into one class, and the corresponding area accounted for an average of 87% (77 to 96%) of the total wetland area in the five counties. The contiguity analysis supports the perception that large contiguous wetlands are common in the lower Coastal Plain of North Carolina.

Table 2. Number of sites and area of wetlands. Analysis was based on all wetlands clumped together, wetlands separated by dominant structure (forest, shrub, marsh), and forest and shrub wetlands further separated by plant community types (deciduous, evergreen, mixed).

Wetland Size (ha)	All Wetlands		Dominant Structure		Community Type	
	Sites #	Area (ha)	Sites #	Area (ha)	Sites #	Area (ha)
CURRITUCK COUNTY						
<10	201	571	356	1,082	416	1,300
10–1,000	60	7,272	145	13,716	200	15,429
>1,000	5	25,611	6	18,656	7	16,724
DARE COUNTY						
<10	155	447	374	1,307	610	2,201
10–1,000	40	2,901	225	22,878	421	33,786
>1,000	7	83,019	9	62,182	12	50,380
CARTERET COUNTY						
<10	420	1,108	987	2,921	1,589	4,745
10–1,000	131	9,648	398	37,109	666	44,463
>1,000	6	65,035	7	35,761	8	26,583
PENDER COUNTY						
<10	543	1,399	1,480	4,246	2,195	5,555
10–1,000	147	7,051	320	17,086	700	41,552
>1,000	2	94,044	8	81,162	12	55,387
BRUNSWICK COUNTY						
<10	1,084	2,237	2,456	5,752	3,370	8,681
10–1,000	214	11,185	535	32,727	847	44,918
>1,000	6	65,681	8	40,714	10	25,594

Table 3. Number of sites by community type and average size.

Community Type	Currituck		Dare		Carteret		Pender		Brunswick	
	Sites #	Size ha	Sites #	Size ha	Sites #	Size ha	Sites #	Size ha	Sites #	Size ha
Deciduous forest	245	66	78	28	403	10	709	40	1,122	20
Evergreen forest	18	14	144	224	307	73	499	62	800	23
Mixed forest	60	34	107	143	254	32	512	26	523	13
Deciduous shrub	44	8	18	31	93	3	106	7	150	7
Evergreen shrub	28	17	136	65	102	66	133	57	228	34
Mixed shrub	3	15	30	25	34	77	78	93	63	21
Palustrine marsh	55	6	132	53	103	4	202	3	444	7
Estuarine marsh	131	83	220	56	394	60	38	85	144	46
Estuarine shrub	23	19	188	27	351	9	26	4	67	6
Partly drained	10	210	5	16	75	64	124	71	223	38
Other	6	68	5	343	147	24	490	3	493	5
Nonwetland	42	833	154	97	266	245	538	227	318	449

As wetlands were separated into more specific classes, the number of sites and total area increased for the smaller size classes (< 10, 10–1,000 ha), and the total area decreased in the largest size classification (> 1,000 ha; Table 2). Brunswick County had the largest number of wetland sites regardless of how wetlands were analyzed. When wetlands were clumped as one class, Brunswick had 1,304 wetland sites compared to 202 for Dare County. Separation of wetlands into specific communities increased the number of sites to 4,227 in Brunswick County and 1,043 in Dare County. The majority of the sites in all counties were < 10 ha, but the wetland area in this size class was < 5% of the total wetland area in most counties.

The number of wetland sites based on dominant plant community type and the average size of those sites varies considerably in the five counties (Table 3). The number of deciduous, forested wetland sites ranges from 1,122 in Brunswick County to 78 in Dare County and in average size from 10 ha in Carteret County to 66 ha in Currituck County. The average size of evergreen forested wetlands was greater than deciduous forested wetlands in all counties except Currituck. This is a reflection of the configuration of pocosin wetlands in the lower coastal plain. Pocosins tend to occur as large blocks, in basins, depressions, and on interfluves, compared to the deciduous forest strips located along river corridors (Brinson 1991). The greater average size of evergreen shrub communities compared to deciduous shrub communities is also a reflection of pocosin configuration. Pocosins characteristically have evergreen-dominated forest and shrub communities (Richardson et al. 1981, Sharitz and Gibbons 1982).

Palustrine marsh communities tend to be of small size (< 7 ha) in four of the five counties. The number of palustrine marsh sites ranged from 55 in Currituck County to 444 in Brunswick County. The number of estuarine marsh sites ranged from 38 in Pender County to 394 in Carteret County. The average size of estuarine marsh was greater than anticipated (46–85 ha), given the linear nature of estuarine marsh communities as fringing strips along the sound side of the five counties. The greater average size of estuarine marsh relative to the average size of linear bottomland deciduous forests suggests that there is less fragmentation of the marshes than the bottomland forests. The estuarine marshes are offered more protection (relative to the inland palustrine wetlands) as areas of environmental concern under the North Carolina Coastal Management Act (CAMA), in addition to Section 404 permitting under the Clean Water Act (CWA). In all, only about 2% of the coastal county estuarine marshes were altered due to authorized development under CAMA and Section 404 between 1970 and 1984 (Stockton and Richardson 1987).

The majority of the partly drained wetlands are the less protected inland palustrine wetlands in transition to other land uses. Only 10 partly drained sites are located in Currituck County, but the average size is 210 ha. In comparison, 223 partly drained wetland sites were found in Brunswick County, with an average size of 38 ha. The reason for conversion of wetlands to other land uses was not determined; the large average size of partly drained wetlands suggests conversion to agriculture or silviculture activities. Cashin et al. (1992) concluded that conversion of wetlands for forestry and agriculture caused 95% of total wetland loss in the Coastal Plain of North Carolina between the early 1950s and the early 1980s. The number of partly drained sites also indicates the relative development pressures in each county. Only 5 partly drained sites were located in Dare County, while Brunswick,

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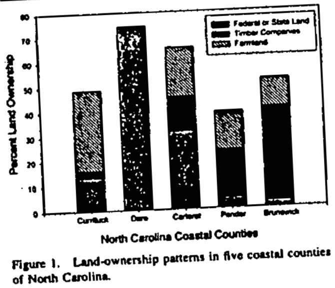

Figure 1. Land-ownership patterns in five coastal counties of North Carolina.

Pender, and Carteret Counties have 75 or more sites in transition to other land uses.

Land ownership may partially explain the increased probability of drainage, as well as the contiguity of wetlands in the five counties. Federal and state (public) land ownership ranges from 2.3% of Brunswick County to 74.4% in Dare County (Figure 1, based on data from Hall 1986). The major timber companies own 2.8% of the land area in Currituck County and 38.2% in Brunswick County. The counties with the highest number of partly drained sites have the most land owned by private timber companies. Farmland ranges from 11.4% of the land area in Brunswick County to 32.7% in Currituck County. Farmland has increased by 20% in Carteret County between 1940 and 1982 (Hall 1986). Farmland has decreased in the other counties (as much as 63% in Brunswick County) in the same time period. It seems that recent conversions of larger wetland sites are related to silvicultural activities; historical conversions are probably more associated with agricultural activities.

Edge characteristics of wetland communities were quite variable in the five counties (Table 4). Values of percent edge ranged from 11% edge for estuarine marshes in Currituck County to 71% edge for deciduous shrub wetlands in Carteret County. The most consistent pattern was the lower edge associated with estuarine marsh communities and nonwetland areas. The low edge values of nonwetland areas is not surprising given the typically larger blocks of land in artificially designated areas of agriculture or silviculture or areas of urban development. Such areas tend to have simple square or rectangular shapes with straight lines. The low percent edge of estuarine marshes supports the observation from the contiguity analysis that fragmentation of marshes is less than other types of wetlands.

Palustrine deciduous forest (commonly found in riverine floodplain areas) and deciduous shrub (frequently representing recent areas of timber harvest) wetlands typically have greater percent edge compared to estuarine marshes or palustrine evergreen forest and shrub wetlands. These edge percentages support the contiguity analysis that the large block configuration of pocosins (i.e., palustrine evergreen forest-shrub wetlands) results in larger patches with lower percent edge relative to the deciduous wetlands located primarily in linear floodplain areas.

Due to the common large block configuration of pocosins, contiguity becomes an issue only when these areas become increasingly fragmented (Brinson 1991). Fragmentation of wetlands results in a landscape mosaic of patches and increasing edge. Different patches can support isolated populations, which may grow or decline independently of populations in other patches (Wilbur 1981). Species that can move or disperse over patches of unsuitable habitat are more tolerant of fragmentation (Pearson 1994). Other biological consequences of ecosystem fragmentation have been reviewed by Saunders et al. (1991). At a minimum, fragmentation significantly alters the fluxes of water and nutrients across the landscape, which in turn influences the biota within remnant areas (Saunders et al. 1991).

Table 4. Edge characteristics of wetlands in five coastal counties of North Carolina.

Community Type	Currituck	Dare	Carteret	Pender	Brunswick	Average + STD
	Percent Edge					
Deciduous forest	21	43	61	39	46	42 ± 14
Evergreen forest	36	14	31	27	44	30 ± 11
Mixed forest	27	17	40	43	54	36 ± 14
Deciduous shrub	50	33	71	50	53	51 ± 14
Evergreen shrub	61	27	23	18	24	31 ± 17
Mixed shrub	55	34	23	16	36	33 ± 15
Palustrine marsh	63	18	63	60	32	47 ± 21
Estuarine marsh	11	18	15	20	22	17 ± 4
Estuarine shrub	34	38	58	10	68	42 ± 23
Partly drained	12	41	23	19	28	25 ± 11
Other	36	35	30	92	62	51 ± 26
Nonwetland	10	22	18	21	19	18 ± 5

CONCLUSIONS

The advantages of contiguity analysis of wetlands are obvious for natural resource management issues such as species migration or diversity, habitat location and contiguity for rare species, preserve design, and habitat fragmentation. The opportunity to select a connectivity radius in GIS allows for contiguity analysis based on the habitat/migration requirements of individual species. For example, salamanders typically move shorter distances from their breeding areas compared to frogs, turtles, and snakes (Petranka, personal communication). Actual distances vary dramatically for reptiles and amphibians (Semlitsch 1981, Congdon and Gatten 1989, Dodd 1996), and contiguity analysis could be designed for a specific species. Additional analysis may provide information on the type and quality of the upland or wetland areas available for animal movement, since movement may be hindered if the adjacent areas are highly degraded.

Appropriate expansion of protected land areas can also be addressed using GIS. A digital database of public land ownership could be combined with the wetlands database to show public wetland areas and relative distances to similar wetlands. Evaluating corridors for connecting two or more protected wetland areas would be a logical extension of combining the two digital databases.

Many land-management activities involve decisions that alter landscape patterns (Turner 1989). Wetlands in North Carolina have been drained and fragmented for a variety of reasons (Richardson et al. 1981, Hefner and Brown 1985, Cashin et al. 1992, Moorhead 1992), which should decrease contiguity and increase edge. The five counties evaluated have greater wetland contiguity than anticipated, given the rapid population growth of these coastal counties (North Carolina 1989). However, much of this growth is probably still a result of expanding urban areas adjacent to or near the open water areas of the sounds and the Atlantic Ocean. If rapid population growth continues, additional development pressure will result in further encroachment and fragmentation of wetlands and other natural habitats. The changes in landscape patterns of wetlands over time could be analyzed with a GIS if similar wetland inventories were conducted on a routine basis. The results would show the influence of an expanding human population on wetland contiguity and edge characteristics.

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NOTE

DISTRIBUTION OF THE INVASIVE REED *PHRAGMITES AUSTRALIS* RELATIVE TO SEDIMENT DEPTH IN A CREATED WETLAND

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Abstract: This study collected new data on sediment thickness and distribution and integrated it with existing data on the distribution of plant species within a small (0.5 ha) created, tidal salt marsh in Langley, Virginia, USA. The presence of the reed *Phragmites australis* was found to be inversely correlated with sediment accumulation on the marsh surface. Sediment-deficient areas seem at a higher risk for invasion by *P. australis* and subsequent loss of designed marsh habitat. The results indicate that areas of low sediment accumulation may be used as a proxy measure for areas vulnerable to invasion. These areas can be easily delimited both in the field and on aerial photography.

Key Words: created tidal marsh, sediment, *Phragmites australis*

INTRODUCTION

Created wetlands face a broad range of threats that have been documented in detail for Virginia's tidal wetlands by Barnard and Mason (1990). One specific threat is the loss of habitat and the displacement of existing species by invaders, such as the Common Reed, *Phragmites australis* (Cav.) Trin. ex Steudel. *Phragmites australis* is a cosmopolitan species occurring primarily in temperate lowland regions (Cross and Fleming 1989). *Phragmites australis* can occur as a stable and desirable component of ecosystems, as illustrated by European reed belts in coastal estuaries. However, some populations of *P. australis* are invasive and spread vigorously, displacing other wetland plants. These invasions typically follow disturbances or stress in the environment, such as an altered hydrologic regime, dredging, or increased nutrient availability (Marks et al. 1994). While evidence suggests that *P. australis* is native to North American wetlands, suspicion exists that a more invasive genotype has recently been introduced from European stock (Marks et al. 1994). On the Coastal Plain of Virginia, USA, *Phragmites australis* is considered a management problem, and it appears to be rapidly expanding in some tidal wetlands.

Havens et al. (1997) indicated that created wetlands in Tidewater Virginia are often heavily infested with this fast growing reed. Their work indicated that *P. australis* often expands rapidly within 6 years after construction. *Phragmites australis* invasion replaces the structure and function of relatively diverse *Spartina* spp. marshes that usually occupy coastal wetlands (Marks et al. 1994), and its presence adversely impacts avian and mammalian species (Jones and Lehman 1987). It is documented as a problem in many national fish and wildlife refuges along the East Coast, including Brigantine NWR in New Jersey, Bombay Hook

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Comparative Use of Riparian Corridors and Oases by Migrating Birds in Southeast Arizona

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Abstract: *The relative importance of cottonwood-willow riparian corridors and isolated oases to land birds migrating across southeastern Arizona was evaluated during four spring migrations, 1989 to 1994, based on patterns of species richness, relative abundance, density, and body condition of birds. We surveyed birds in 13 study sites ranging in size and connectivity from small isolated patches to extensive riparian forest, sampled vegetation and insects, and captured birds in mistnets. The continuous band of riparian vegetation along the San Pedro River does not appear to be functioning as a corridor for many migrating species, although it may for a few, namely Yellow-breasted Chats (*Icteria virens*), Summer Tanagers (*Piranga rubra*), and Northern Rough-winged Swallows (*Steldgopteryx serripennis*), which account for fewer than 10% of the individuals migrating through the area. Small, isolated oases hosted more avian species than the corridor sites, and the relative abundances of most migrating birds did not differ between sites relative to size-connectivity. There were few differences in between-year variability in the relative abundances of migrating birds between corridor and oasis sites. Between-year variability decreased with overall abundance of species and was greater for species with breeding ranges that centered north of 50°N latitude. Body condition of birds did not differ relative to the size-connectivity of the capture site, but individuals of species with more northerly breeding ranges had more body fat than species that breed nearby. Peak migration densities of several bird species far exceeded breeding densities reported for the San Pedro River, suggesting that large components of these species were en route migrants. Peak densities of Yellow Warblers (*Dendroica petechia*) reached 48.0 birds/ha, of Wilson's Warblers (*Wilsonia pusilla*) 33.7 birds/ha, and of Yellow-rumped Warblers (*D. coronata*) 30.1 birds/ha. Riparian vegetation is limited in extent in the vicinity of our study sites, covering less than 1% of the landscape. We conclude that all riparian patches in southeastern Arizona are important as stopover sites to en route migrants regardless of their size and degree of isolation or connectivity. In light of potential habitat limitations, the protection of both small, disjunct riparian patches and extensive riverine tracts in western landscapes is important.*

Uso Comparativo de Corredores Riparios y Oasis por Aves Migratorias en el Sureste de Arizona

Resumen: *Se evaluó la importancia relativa de los corredores riparios de sauces y los oasis aislados para las aves que migran a través del sureste de Arizona durante cuatro migraciones de primavera, de 1989 a 1994, en base a patrones de riqueza de especies, abundancia relativa, densidades y condición corporal de las aves. Estudiamos aves en 13 sitios variando en tamaño y conectividad desde parches pequeños aislados hasta bosques riparios extensos. Muestreamos la vegetación e insectos y capturamos aves con redes. Las bandas continuas de vegetación riparia a lo largo del río San Pedro no aparenta funcionar como un corredor para muchas de las aves migratorias, aunque podría serlo para algunas tales como: Icteria virens, Piranga rubra y Steldgopteryx serripennis, las cuales corresponen a menos de un 10% de los individuos migrando a través del área. Los oasis pequeños aislados hospedaron mas especies de aves que los sitios de corredor y las abundancias relativas de la mayoría de las especies migrando no fue diferente entre sitios en relación con el tamaño de la conectividad. Existieron pocas diferencias en variabilidad de la abundancia relativa entre años entre los corredores y los sitios con oasis. La variabilidad entre años disminuyó en general con la abundancia de especies y fue mayor para especies con rangos reproductivos centrados al norte de los 50° latitud norte. La condición corporal de las aves no difirió en relación con el tamaño de la conectividad del sitio de captura, pero los individuos de especies con rangos de reproducción mas hacia el norte tuvieron mas grasa corporal que las especies que se reproducen en las cercanías. Las densidades pico de migración de varias de las especies de aves excedía por mucho las densidades reproductivas reportadas para el río San Pedro, sugiriendo que los componentes grandes de estas especies fueron migrantes en ruta. Las densidades pico de Dendroica petechia alcanzó los 48.0 aves/ha, Wilsonia pusilla 33.7 aves/ha y D. coronata 30.1 aves/ha. La vegetación riparia esta limitada en extensión en las áreas cecinas al sitio de estudio, cubriendo menos de 1% del paisaje. Concluimos que todos los parches riparios en el sureste de Arizona son importantes como sitios de reposo para migrantes en ruta independientemente del tamaño y el grado de aislamiento o conectividad. En vista de la potencial limitante del habitat, es imperante la protección tanto de parches pequeños disjuntos como de áreas riverinas extensas en los paisajes del oeste.*

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Introduction

Research underlying conservation strategies for Neotropical migrants has concentrated largely on events on breeding and wintering grounds (Gradwohl & Greenberg 1989) and has generally ignored events during the migratory period (Moore et al. 1992). Tremendous energy demands are associated with long-distance migration, however, and many birds cannot successfully complete their journeys without replenishing fat reserves en route (Moore & Kerlinger 1987; Moore et al. 1992). Migrating birds therefore depend on suitable stopover sites, often riparian and other wetland habitats, and must find resources within spatially heterogeneous and temporally dynamic landscapes (Skagen & Knopf 1993, 1994).

Most evaluations of the influences of landscape pattern on habitat selection in birds apply to both breeding and wintering areas (Morse 1985; Brown & Dinsmore 1986; Askins et al. 1992; Freemark & Collins 1992; Robinson 1992). The theoretical basis for landscape-level decisions by migrating birds is now emerging (Hutto 1985a; Moore et al. 1992), yet little empirical evidence exists. Hutto (1985a) suggests that long-distance en route migrants may base their selection of stopover sites on factors extrinsic to rather than intrinsic to the sites, including meteorological conditions, physiological condition, and landscape-level attributes of the available stopover sites such as patch size and shape, degree of isolation or contagion and connectivity, patch orientation, and interception probabilities (Hutto 1985a; Gutzwiller & Anderson 1992). The relative importance of these attributes may differ between species, depending on migration distance and proximity to destinations.

In western North America insectivorous landbirds migrating in spring prefer riparian habitats for refueling (Johnson et al. 1977; Stevens et al. 1977; Emmerich & Vohs 1982; D. Krueper, personal communication), probably because food and cover are more abundant and predictable there than in other vegetation types in spring. Continuous extensive bands of riparian vegetation may attract more en route migrants than smaller, isolated patches simply because the larger patches are easier to find (Simberloff & Cox 1987). If extensive corridors are easier to find, abundances of en route migrants in continuous riparian forests may be greater and more consistent between years than abundances in smaller riparian patches. On the other hand, small, isolated oases may facilitate migration by providing a "stepping stone" (MacArthur & Wilson 1967:123) arrangement of stopover areas. Small oases in the Sahara desert regularly attract transient passerines for resting and refueling (Bairlein 1988, 1992; Biebach 1990).

We monitored the use of several riparian areas in southeastern Arizona by Neotropical migrant landbirds, short-distance migrants, and residents, and we examined the relative importance of corridors and isolated oases to migrating birds. We evaluated the following attributes of the bird communities: species richness, relative abundances, variability of abundances, and body condition of migrants. Specifically, we predicted that, if extensive corridors attracted more migrating birds than oases, we would detect one or more of the following patterns. Corridor sites would (1) host a greater number of avian species, (2) have greater abundances of migrating birds, (3) exhibit less year-to-year variability in bird abundances, or (4) provide more resources, reflected in greater biomass of insects or better body condition of birds. For a delineated region, we also determined the total area of cottonwood-willow riparian vegetation available to migrating birds in oases and in continuous riverine corridors.

Study Area and Methods

Site Descriptions

During spring migration (early April–mid-May) in 1989, 1991, 1993, and 1994, we conducted weekly bird s

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veys in 13 riparian sites in southeastern Arizona (Fig. 1). The riparian areas were dominated by Fremont cottonwood (*Populus fremontii*) and Gooding willow (*Salix goodingii*), each surrounded by dry grasslands, shrub lands, or oak woodlands. The 13 sites, under federal and private ownership (including Bureau of Land Management, The Nature Conservancy, and private individuals), ranged from samples of the continuously vegetated corridor of the San Pedro River to small, isolated oases (Fig. 1). The sites ranged in elevation from 900 to 1600 m and in latitude from 31° 30′ N to 32°20′ N. Sites at Muleshoe Ranch (MULR, MULB) and near Cascabel (CASN, CASS) were surveyed only in the springs of 1989 and 1991.

The study sites were selected because they represented the largest remaining riparian areas in the region, as determined from aerial photos and an overview flight

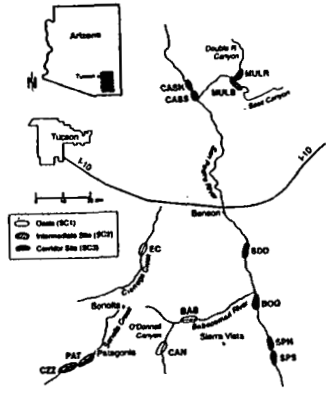

Figure 1. Location of 13 bird survey sites in southeastern Arizona. EC, Empire Cienega Ranch; BAB, Babocomari Ranch; CAN, Canelo Hills Cienega; CZZ, Circle-Z Ranch; PAT, Patagonia-Sonoita Creek Preserve; MULR, Double-R Canyon/Muleshoe Ranch; MULB, Bass Canyon/Muleshoe Ranch; CASN, Cascabel North; CASS, Cascabel South; SDD, St. David's Ditch; BOQ, Boquillas Ranch; SPN, San Pedro House North; SPS, San Pedro House South. Size-connectivity groups are described as oasis sites (small, <4 × 100 km, and relatively isolated), intermediate sites (larger habitat patches, 4–12 km), and corridor sites (part of extensive, linear forest).

in 1989. The San Pedro River sites were selected based on latitude (to match the latitude of oases) and accessibility (influenced by land ownership and occurrence of roads). Even though some sites were on the same water course, we considered sites to be independent if they were separated by 500 m.

Precipitation patterns varied among the years of our study. Monthly precipitation from January through April was below average during 2 years of our study, 1989 (40% of an 85-year average) and 1994 (24% of average). In contrast, monthly precipitation was above average during January and February in 1991 (127%) and 1993 (217%) and below average during March and April of the same years (70% and 45% of average, respectively). Flooding of the San Pedro River resulted from heavy rainfall in January of 1993, when precipitation totaled 270% of the monthly average. Data for weather stations at Sierra Vista and Canelo, Arizona, were provided by the Western Regional Climate Center, the National Weather Service, and the National Oceanic and Atmospheric Administration.

We grouped the 13 survey sites into three categories based on both relative size and connectivity (SC) with similar habitat types. Because riparian woodlands in this study area were linear and narrow (generally 50–200 m wide), it was difficult to separate the effects of the size of riparian forest patches and connectivity to other habitat patches. Oasis sites (SC1: EC, BAB, CAN) were small (limited to the area surveyed, <4 km linear extent) and relatively isolated (>8 km) from similar cottonwood-willow riparian habitats; they ranged in area from 40 to 100 ha. Intermediate sites (SC2: CZZ, PAT, MULR, MULB) were located within larger habitat patches (4–12 km linear extent), ranging in area from 120 to 180 ha. San Pedro River sites (SC3: CASN, CASS, SDD, BOQ, SPN, SPS) were part of an extensive linear forest exceeding 2000 ha and were contiguous with similar riparian vegetation.

Some habitat attributes—elevation, latitude, vegetation structure, size-connectivity—were correlated among sites. But replicates in the sense of classical experimentation are rarely, if ever, possible in landscape or regional studies (Hargrove & Pickering 1992). An ideal experimental design for this study would have allowed the separation of the effects of patch size, connectivity, elevation, latitude, and vegetation structure on bird abundances. In southeastern Arizona, however, most of the isolated sites were higher in elevation, smaller in extent, and lower in shrub volume than the more connected riverine sites. Alternative sites did not exist in this region at the scale of this project.

Bird Surveys

Birds were surveyed weekly at each site for 6 weeks (3 April–14 May) in 1989, 1993, and 1994 and for 4 weeks (20 April–9 May) in 1991. Two or three observers rotated

between sites to reduce observer bias. Using a standard point-count method (Reynolds et al. 1980; Bibby et al. 1992), we recorded all birds heard and seen during 7 minutes at each of 20 points within each study site and specified the distance (0–10, 10–25, 25–50, 50–75, 75–100 m) to each bird. To maximize the area sampled at each site, we placed points approximately 100 m apart. All surveys were begun within 20 minutes of sunrise and were concluded in 4 hours.

To facilitate data analyses, all bird species were grouped into three functional guilds (Table 1). Using information from several references, we categorized bird species by migration pattern, latitudinal ranges, macrohabitat, and foraging microhabitat (National Geographic Society 1981,1987; American Ornithologists' Union 1983; Davis & Russell 1984; Hayman et al. 1986; Banks et al. 1987; Ehrlich et al. 1988; DeGraaf et al. 1991). Migration categories based on distance traveled range from nonmigratory residents (category 1) to species that occur in southeast Arizona only during migration (category 5). We also distinguished species that breed and winter in southeastern Arizona but also migrate to more northern or southern latitudes (category 2) from species that are present only during migration and the breeding season (category 3) and species that occur only during winter and migration (category 4). Macrohabitat guilds separate species that are usually or often associated with riparian areas from those that occur primarily in more upland habitats. Foraging microhabitat guilds primarily distinguish species that forage in different vegetation layers. When searching for patterns relative to size-connectivity, we grouped species according to these functional guilds and also evaluated the data on the basis of individual species.

Vegetation Sampling

We recorded broad habitat features for general classification of sites and more detailed vegetation characteristics at survey points. Broad habitat features included width of the riparian forest, canopy height, and shrub and tree species comprising more than 10% cover. We estimated relative foliage density for each site in 1993 using a modified version of the MacArthur board technique (MacArthur & MacArthur 1961). In four quadrants (northeast, southeast, southwest, northwest; determined

Table 1. Functional guilds of birds recorded during spring migration in southeastern Arizona, 1989–1994.[a]

	Present in southeastern Arizona[b]	Description	Number of species
Migration category			
1	W, M, B	Resident, primarily non-migratory although altitudinal movements may occur	38
2	W, M, B	Winters in SE Arizona, migrates through SE Arizona, breeds in SE Arizona	50
3	M, B	Winters south of SE Arizona, migrates through SE Arizona, breeds in and north of SE Arizona	48
4	W, M	Winters in and south of SE Arizona, migrates through SE Arizona, breeds north of SE Arizona	29
5	M	Winters south of SE Arizona, migrates through SE Arizona, breeds north of SE Arizona	15
6	—	Vagrant in SE Arizona	6
Macrohabitat guild			
1		Especially or generally near water	35
2		Riparian or water mentioned in habitat accounts	67
3		Woodlands, chaparral-scrub, grasslands, savannah, desert; no mention of water in habitat accounts	84
Foraging microhabitat guild			
0		Terrestrial generalist	25
1		Aerial insectivore, sweeper	7
2		Aerial insectivore, sallying and hawking	23
3		Middle and upper canopy; foliage gleaner	27
4		Lower canopy and shrub layer; foliage gleaner	21
5		Forb layer, ground and litter; gleaner	17
6		Trunk insectivore, trunk and branches; gleaner	8
7		Forest generalist	9
8		Shoreline gleaner, prober	5
9		Aquatic bird	14

[a] Functional guilds are based on information from the National Geographic Society (1981, 1987), the American Ornithologists' Union (1983), Davis and Russell (1984), Hayman et al. (1986); Banks et al. (1987); Ehrlich et al. (1988); and DeGraaf et al. (1991).
[b] Birds are present during winter (W), spring or fall migration (M), and breeding season (B).

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with a compass) around each stake, the distance to the nearest vegetation (including stems, trunks, and dead vegetation) that would obscure one-half of an 8.5 × 11-inch (22 × 28 cm) board was estimated at each of the following heights: 0.25, 0.5, 1, 2, 5, 10, 15, 20, 25, 30, 35, and 40 m. A maximum of 960 estimates was made at each site. We truncated horizontal measurements at 100 m. Clinometers were used to determine height categories. Because the foliage in the lowest layers at some sites was scoured by floods in 1993, measurements were taken again in 1994 at 0.25, 0.5, 1, and 2 m.

We calculated an index of foliage density—the amount of leaf surface area per cubic unit of space—using the following formula: foliage density = ln2/distance. We grouped height intervals into three vegetation layers: ground layer, 0.25 and 0.5 m; shrub layer, 1 and 2 m; and canopy, 5, 10, 15, 20, 25, 30, 35, and 40 m; we computed the foliage density for these three layers as the average of the foliage densities for each height in the layer. Foliage density profiles were used in conjunction with estimates of riparian coverage in subsequent analyses.

Because vegetation within sites was patchy and uneven in coverage and extent, we developed a general index of riparian vegetation coverage. At each stake observers sketched the location and extent of riparian vegetation, upland vegetation, and river channel on a circular template with radius intervals of 25, 50, and 100 m. A dot-grid overlay was used to determine the areal extent of channel and riparian vegetation within 50 m. Values were converted to percentages and averaged to yield the percentage of riparian cover for each site.

Foliage volume indices were calculated as the sum of the products of foliage density, the percentage of riparian cover, and the vertical distance between height intervals within each vegetation layer. Indices for ground and shrub layers were based on average foliage densities for 1993 and 1994, which represented years of both above and below average precipitation from January through April.

Insect Sampling

We developed an index of insect biomass in 1989 and 1991 by sampling aerial insects at four sites, EC, PAT, SDD, and SPS. We collected aerial insects using sticky board traps (12 × 20-cm squares coated with Tanglefoot™). Traps consisted of four sticky boards attached to a wooden lathe and surrounded by plastic mesh (3 cm), which allowed the passage of insects but not birds. At four randomly chosen stakes at each of the four sites, traps were suspended from branches within the vegetation at two heights, low (2–4 m) and high (6–8 m). Traps were placed immediately after the weekly bird surveys were finished and were removed and replaced 1 week later following the subsequent survey. Traps were disassembled, and sticky boards were frozen in plastic wrap. We identified all insects to order, measured lengths, and applied the following standard formula to estimate an index of biomass of aerial invertebrates for each site: $M = 0.0305\ L^{1.62}$, where M equals biomass (mg) and L equals length in millimeters (Rogers et al. 1976).

Assessment of Body Condition and Data Analyses

In the spring of 1989, we captured birds with mist nets at SPS, SDD, CAN, and PAT, following the animal care guidelines of the American Ornithologists' Union (1988). Measurements and attributes recorded immediately for each bird included body mass (0.1 g, Pesola scales), length of unflattened wing chord, retrix length, age, and sex. We also scored the amount of visible fat in the furcular and abdominal regions on a scale of 0 (no fat) to 6 (very obese), after Helms and Drury (1960).

Analyses of variance and multivariate analysis of variance (MANOVA) were used in detecting patterns of species richness by functional guilds and size-connectivity. We used several measures of relative abundance, defined as the number of birds within 50 m, to examine distribution patterns of functional guilds and individual species by size-connectivity. We minimized double counting of individuals by restricting our data to sightings within 50 m. Our relative abundance measures included the maximum number of each species per guild per site each year and during 1993 and 1994 combined, and the total relative abundance (i.e., the sum of individuals sighted during all surveys) of each guild per site each year and during 1993 and 1994 combined. We used Kruskal-Wallis nonparametric analyses of variance and nonparametric multiple contrast tests (Zar 1984) to determine patterns of distribution relative to size-connectivity. We conducted separate analyses for the 29 most abundant species that together comprised 80% of all sightings and for an additional 15 species, so 80% of all guilds were represented. Because we conducted four surveys in 1991 and six in the other 3 years, we multiplied total relative abundance by 1.5 for 1991 data to allow for between-year comparisons. Total relative abundances were also adjusted if necessary to account for missing data (6% of scheduled surveys were missed because of logistical difficulties). Statistical analyses (parametric and nonparametric analysis of variance, analyses of covariance [ANCOVAs], multiple regressions, Tukey pairwise comparisons, t tests, chi-square analyses, log-likelihood ratio tests) were conducted using SYSTAT 5.0. Findings with p values of 0.10 and greater are reported as nonsignificant.

Two indices of between-year variability were calculated as the coefficient of variation (SD/mean) of total relative abundance, hereafter referred to as CV(abundance), and the coefficient of variation of maximum counts, hereafter CV(maximum), at each of nine sites surveyed across the 4 years of the study. We used Kruskal-Wallis nonparametric analyses of variance and nonparametric multiple contrast tests (Zar 1984) to determine patterns of variability relative to size-connectivity. Median CV(abundance) and median CV(maximum) across all sites for each species were used in additional analyses.

Density estimates were obtained with Program DISTANCE (Buckland et al. 1993; Laake et al. 1993). Because of potential differences in detection in different habitats, detection curves were calculated for individual sites; data were truncated at 75 m. In distance sampling, double counting does not bias estimates as long as the observations are independent. Maximum densities were calculated for specific days at some sites by means of site-specific detection curves calculated across all days. Model selection followed appropriate guidelines (Buckland et al. 1993; Laake et al. 1993).

Determination of the Extent of Riparian Vegetation

We determined the total amount of cottonwood-willow and mixed broadleaf habitats available to migrants within a delineated land area (≈10,000 km²) extending from the Mexican border to the northern boundary of Cochise County, Arizona (31°18′ to 32°26′N) along a band extending 40 km on either side of the western boundary of Cochise County (110°00′ to 110°50′ W). We used the Arizona Statewide Riparian Mapping and Inventory database, created by the Arizona Game and Fish Department and based on Landsat images, which defines the location and extent of several vegetation types within permanent riparian areas throughout Arizona. We also used two related databases, one with coverages of the intermittent stretches of the San Pedro River and another including polygon-specific vegetation data collected during ground-truthing.

Using ARC/INFO (Environmental Systems Research Institute 1995), we determined the areal extent of the cover types "cottonwood-willow" and "mixed broadleaf," the vegetation types in which bird surveys were conducted, from both the permanent and intermittent riparian coverages. From the polygon-specific vegetation data, we estimated that 12.2% of the area of salt cedar (*Tamarisk* spp.) stands was composed of cottonwoods and willows. We therefore included 12.2% of the areal extent of salt cedar in our calculations of available habitat because cottonwoods and willows were often subdominant within stands of salt cedar.

Results

Vegetation Profiles

The canopy vegetation of all sites was dominated by Fremont cottonwood and Gooding willow, except for the Muleshoe Ranch sites where Arizona sycamore (*Platanus wrightii*) was abundant. Velvet ash (*Fraxinus pennsylvanica*), Arizona black walnut (*Juglans major*), netleaf hackberry (*Celtis reticulata*), alligatorbark juniper (*Juniperus deppeana*), and oaks (*Quercus* spp.) also occurred at several sites. Lower canopy and understory plants included honey mesquite (*Prosopis glandulosa*), salt cedar, graythorn (*Ziziphus obtusifolia*), elderberry (*Sambucus mexicana*), and seepwillow (*Baccharis* spp.).

In general, small, isolated sites had smaller indices of foliage volume than other sites for all vegetation layers (Fig. 2). This was due to differences in foliage densities and smaller percentages of riparian cover in the small,

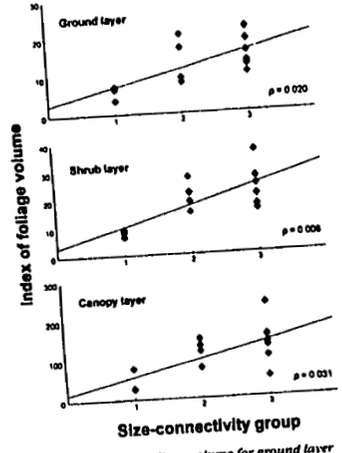

Figure 2. Indices of foliage volume for ground layer (heights 0.25 and 0.5 m), shrub layer (heights 1 and 2 m), and canopy (heights 5–40 m) at 13 sites grouped by size-connectivity (1, small isolated; 2, intermediate; and 3, large connected). Index is the sum of the products of foliage density at each height interval within the vegetation layer, the average percentage of riparian cover of 50-m radius circles, and the vertical distance from the height interval immediately below. Indices for canopy are based on data from 1993 and for ground and shrub layers on average foliage densities for 1993 and 1994.

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isolated sites relative to other sites. Foliage volumes of all layers were negatively correlated with elevation ($r = -0.630$, df = 12, $p < 0.02$ for ground layer; $r = -0.829$, df = 12, $p < 0.001$ for shrub layer; $r = -0.486$, df = 12, $p < 0.10$ for canopy). Latitude and elevation were negatively correlated ($r = -0.585$, df = 12, $p < 0.05$); the northern sites on the San Pedro River, CASN and CASS, were at the lowest elevations.

Species Richness

Migrant and resident birds of 186 species were recorded during 230 surveys in four spring field seasons; total sightings approximated 85,500 birds, *primarily* passerines. The numbers of species recorded at the 13 sites during 1993 and 1994 were significantly correlated with size-connectivity of the sites ($F = 7.787$, df = 1, 11, $p = 0.018$; Fig. 3). The isolated oases sites hosted more species (101–109) than corridor sites (84–102), with more species in migration categories 2, 4, and 5 ($F = 9.064$, df = 1, 11, $p = 0.012$, $F = 4.680$, df = 1, 11, $p = 0.053$; and $F = 4.423$, df = 1, 11, $p = 0.059$, respectively; Fig. 3). The 10 species that occurred only in oases during 1993 and 1994 were rarely sighted, however, averaging only 1.1 (±1.34 SD) sightings per year. More species occurred at higher elevations ($F = 11.269$, df = 1, 11, $p = 0.006$) and at lower latitudes ($F = 5.544$, df = 1, 11, $p = 0.038$).

Oases had more species of ground-foraging birds than intermediate sites and corridor sites (Table 2), but there were no differences between oases and corridor sites in numbers of shrub- and canopy-foraging birds. Intermediate sites hosted more shrub-foraging birds than did oases and corridor sites (Table 2). There were no significant relationships between numbers of species and foliage volume for three foraging microhabitat guilds (ground-, shrub-, and canopy-foraging birds; Table 2).

Patterns of Relative Abundance

During 1993 and 1994, the 15 most abundant species composed 60.2% of all bird sightings (42,206 total sightings within 50 m) and 54.7% of the maximum numbers

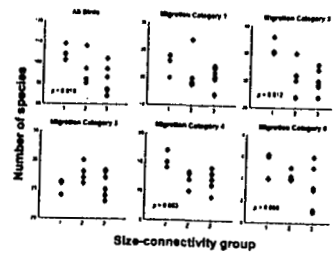

Figure 3. The numbers of bird species relative to the size-connectivity groups (defined in Fig. 2 legend) and migration categories (defined in Table 1) at 13 survey sites during the springs of 1993 and 1994 ($p = 0.284$ and $p = 0.350$ for migration categories 1 and 3, respectively).

for all species (9706 individuals). Species in migration categories 3 and 2 were the most numerous (Table 3), whereas species in migration categories 4 and 5 accounted for fewer than 10% of all sightings and for 15% of the maximum numbers. Total abundances of all birds within 50 m at all sites during the study and percentage of representation by species are available from S. K. S.

Some patterns of distribution relative to size-connectivity were evident for migration category and macrohabitat guild. For the five migration categories, the sums of the maximum counts of all birds during the springs of 1993 and 1994 were greater in corridor sites than in oases, but only for migration category 3 ($H = 7.775$, df = 2, $p = 0.02$; Fig. 4). The largest numbers of birds in migration categories 4 and 5 occurred at two of the isolated oases (EC and BAB).

We examined distribution patterns of 29 species that collectively comprised 80% of all sightings (hereafter abundant species) in 1993 and 1994 and of an additional

Table 2. Relationship between numbers of bird species, size-connectivity, and foliage volume of 13 survey sites in southeastern Arizona during spring migration of 1993 and 1994.

Foraging microhabitat	Size-connectivity[a] F (p)[b]	Size-connectivity[a] Relationship[c]	Foliage volume F (p)[b]
Ground and forb layer	4.772 (0.039)	1 > 2 = 3	1.195 (0.303)
Shrub and lower canopy layer	7.669 (0.011)	2 > 1 = 3	0.475 (0.508)
Middle and upper canopy	2.763 (0.116)	1 = 2 = 3	1.063 (0.330)

[a] *Size-connectivity groups are defined as 1: oasis sites, small (<3 km by 100 m) and relatively isolated, 2: intermediate sites located in larger habitat patches (4–12 km); 3: part of extensive linear forest.*
[b] *From multiple regression analyses, df = 2, 10.*
[c] *Relationship of the number of species in three size-connectivity groups, from Tukey patriotic comparison tests.*

Table 3. Patterns of bird species abundance relative to size-connectivity based on maximum counts of individual species during four spring migrations, 1989–1994.

Migration category and species[a]	Percentage of migration category	p[b] 1989	1991	1993	1994
1					
Abert's Towhee[c,d]	21.5	<0.001	<0.001	<0.005	<0.005
Gila Woodpecker[c,d]	20.0	ns	ns	ns	ns
House Finch[c,d,e]	13.1	ns	ns	ns	ns
Bushtit[c,d,e]	6.9	ns	ns	ns	ns
Ladder-backed Woodpecker[d]	5.5	ns	ns	ns	ns
Bridled Titmouse[d]	4.8	(<0.005)	(<0.005)	ns	ns
Northern Cardinal[d,e]	4.7	ns	<0.10	<0.01	ns
European Starling[d,e]	4.7	ns	ns	ns	ns
White-breasted Nuthatch	4.5	ns	(<0.001)	ns	ns[f]
Gambel's Quail	2.8	<0.001	<0.001	ns[f]	ns[f]
2					
Bewick's Wren[c,d]	18.3	<0.001	ns	ns	ns
Yellow-rumped Warbler[c,d,e]	9.9	ns	ns	ns	ns
Song Sparrow[c,d,e]	8.5	ns	<0.001	ns	ns
Common Yellowthroat[c,d,e]	8.4	ns	ns	ns	ns
Vermillion Flycatcher[c,d]	7.3	ns	ns	<0.001	<0.05
Mourning Dove[c,d,e]	7.2	ns	ns	ns	ns
Lesser Goldfinch[c,d]	7.0	ns	ns	ns	ns
White-winged Dove[c,d]	6.0	ns	ns	ns	ns
Brown-headed Cowbird[c,d,e]	4.0	ns	ns	ns	ns
Ruby-crowned Kinglet[c,d,e]	3.6	ns	ns	ns	ns
Black Phoebe[c]	2.9	ns	ns	ns	ns
Lincoln's Sparrow[c,e]	2.8	ns	ns	ns	(<0.005)
Northern Flicker	2.4	ns	(0.001)	ns	(0.001)
3					
Yellow Warbler[c,d,e]	35.5	ns	<0.10	ns	ns
Lucy's Warbler[c,d]	13.3	ns	ns	<0.001	<0.005
Summer Tanager[c,d]	8.2	<0.001	<0.001	<0.001	<0.001
Yellow-breasted Chat[c,d,e]	5.1	<0.001	<0.001	<0.001	<0.001
Cassin's Kingbird[c,d]	4.4	(<0.05)	ns	ns	ns
Bell's Vireo[c,d]	4.2	<0.001	ns	<0.001	<0.001
Bullock's Oriole[c,d,e]	4.1	ns	ns	<0.005	<0.005
Hooded Oriole[c,d]	3.9	ns	ns	ns	ns
Black-chinned Hummingbird[c,d,e]	3.2	ns	ns	ns	ns
Ash-throated Flycatcher[c]	2.8	<0.001	ns	ns	<0.001
Brown-crested Flycatcher	2.4	<0.001	<0.001	<0.05	<0.05
Northern Rough-winged Swallow[c,e]	2.0	<0.001	ns	<0.001	<0.05
Black-headed Grosbeak	1.7	ns	ns	ns	ns
Western Kingbird	1.4	ns	(<0.001)	ns	(<0.001)
4					
Chipping Sparrow[c,d,e]	41.2	ns	ns	ns	ns
White-crowned Sparrow[d,e]	10.4	ns	ns	ns	ns
Cedar Waxwing[d,e]	9.8	ns	ns	ns	ns
Green-tailed Towhee[d]	9.4	ns	ns	ns	ns
Pine Siskin[d,e]	9.1	ns	ns	(<0.005)	ns
5					
Wilson's Warbler[c,d,e]	83.2	ns	ns	(<0.001)	ns
Lazuli Bunting	3.9	ns	ns	(<0.001)	ns

[a] *Category 1 had 16.0% of all sightings and 14.9% of maximum numbers; category 2, 33.9% and 32.8%, respectively; category 3, 41.1% and 36.8%, respectively; category 4, 4.6% and 7.9%, respectively; category 5, 4.3% and 7.6%, respectively.*
[b] *The p values are from multiple comparison tests following Kruskal-Wallis nonparametric analyses of variance (ns, $p > 0.10$). The p values without parentheses indicate that more birds occurred in corridor sites; p values in parentheses indicate that more birds occurred at oases than at corridor sites.*
[c] *One of the most abundant species, comprising 80% of all sightings.*
[d] *One of the most abundant species, comprising 80% of the migration category.*
[e] *Breeding ranges extend north of 31°N latitude.*
[f] *No differences in bird abundances between corridors and oases, but abundances at intermediate sites differ from corridor and oasis sites.*

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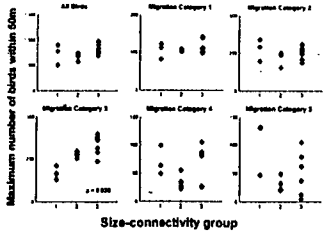

Figure 4. The maximum number of birds recorded within 50 m during all surveys, springs of 1993 and 1994, by migration category and size-connectivity group. See Table 1 for definitions of migration categories. The p values are for all species combined in the respective migration categories (p = 0.575, 0.389, 0.202, and 0.149 for migration categories 1, 2, 4, and 5, respectively).

15 species, so that 80% of each functional guild was represented. Maximum counts of 12 (41%) of the 29 abundant species were higher in corridor than oasis sites in at least 1 year and were consistently so for 3–4 years for five (17%) of these species (Table 3). Abundant species in migration category 3 were more likely associated with corridor sites than abundant species in migration categories 1 and 2 ($G = 3.771$, df = 1, $p = 0.052$). Eight (73%) of 11 abundant species in migration category 3 were associated with corridor rather than oasis sites in at least one year (Table 3); whereas only 4 (25%) of 16 abundant species in migration categories 1 and 2 and none of the 6 abundant species in migration categories 4 and 5 were associated with corridor rather than oasis sites (Table 3). Of the five abundant species associated with corridor sites for 3–4 years, four were in migration category 3 (Summer Tanager [*Piranga rubra*], Yellow-breasted Chat [*Icteria virens*], Bell's Vireo [*Vireo bellii*], and Brown-crested Flycatcher [*Myiarchus tyrannulus*]), and one (Abert's Towhee [*Pipilo aberti*]) was in migration category 1 (Table 3). Another species in migration category 3, the Northern Rough-winged Swallow (*Stelgidopteryx serripennis*), also preferred riverine sites during 3 years.

Species in macrohabitat guilds 1 and 2 (generally or sometimes associated with riparian areas) were more likely to prefer the river sites than species in macrohabitat guild 3 ($G = 6.863$, df = 1, $p = 0.009$). Four (24%) of 17 species in macrohabitat guilds 1 and 2—Abert's Towhee, Summer Tanager, Yellow-breasted Chat, and Bell's Vireo—were associated with corridor sites for 3–4 years (Table 3). Macrohabitat guild 1 was comprised of nearly 75% Wilson's Warblers (*Wilsonia pusilla*), Abert's Towhees, Song Sparrows (*Melospiza melodia*), and Common Yellowthroats (*Geothlypis trichas*), based on relative abundance within 50 m in 1993 and 1994, and more than half of macrohabitat guild 2 was Yellow Warblers (*Dendroica petechia*), Bewick's Wrens (*Thryomanes bewickii*), Lucy's Warblers (*Vermivora luciae*), and Summer Tanagers. None of the 14 species in macrohabitat guild 3, including Yellow-rumped Warblers (*D. coronata*), Mourning Doves (*Zenaida macroura*), Lesser Goldfinches (*Carduelis psaltria*), House Finches (*Carpodacus mexicanus*), and Chipping Sparrows (*Spizella passerina*), were associated with corridor sites in even 1 year.

The breeding ranges of several species in migration categories 2 and 3 extend north of 50°N latitude (Table 3), suggesting that some individuals are migrating through rather than breeding in the area. We estimated the proportion of seven abundant species in these two migration categories that are en route migrants by comparing peak migration densities (using the highest counts at a given site on a given day) with peak breeding densities along the San Pedro River (Krueper 1992). We also calculated the peak density of the most abundant through-migrant, Wilson's Warbler. Peak migration densities of Yellow Warblers reached as high as 48.0 birds/ha, of Wilson's Warblers as high as 33.7 birds/ha, and of Yellow-rumped Warblers as high as 30.1 birds/ha (Table 4). Based on these comparisons, it seems likely that nearly 90% of the peak populations of Yellow Warblers and Bullock's Orioles (*Icterus bullockii*), 79% of Song Sparrows, and 65% of Yellow-breasted Chats are en route migrants (Table 4). Fewer Common Yellowthroats and Summer Tanagers were likely en route migrants because their peak migration densities were more similar to breeding densities. Presumably, all Yellow-rumped Warblers were migrating through because they do not breed in the riparian areas even though they breed in southeast Arizona (D. Krueper, personal communication). All Wilson's Warblers are en route migrants here. Peak migration densities of Yellow Warblers were lower at the more southern San Pedro River sites (12.4 birds/ha at SDD and 14.2 birds/ha at SPN) than at the more northern river sites (Table 4).

Variability in Abundances and Body Condition

Patterns of variability in abundance were evaluated at the original nine sites for 33 species representing the 7 most abundant species in five migration categories for which there were adequate data (Table 3; additional species in migration categories 4 and 5 included Hammond's Flycatcher [*Empidonax hammondii*], Orange-crowned Warbler [*V. celata*], Townsend's Warbler [*D. townsendii*], Nashville Warbler [*V. ruficapilla*], and Hermit Warbler [*D. occidentalis*]). For each species, using nonparametric analyses of variance, we determined if total relative abundances and yearly maximum abundances for each site were more variable between years at the oases sites than in corridor or intermediate sites. Patterns of variability reflected by CV(abundance) and CV(maximum) were similar. Twenty-eight (85%) of the 33 species did not differ in variability between sites (p values ranged from 0.105 to 0.868). Our data suggest that five species (15%) were more variable in oases. The CV(abundance) and CV(maximum) were greater in oases than along the river for Yellow-breasted Chats ($p = 0.082$ and $p = 0.064$, respectively), Song Sparrows ($p = 0.066$ and $p = 0.067$), Cedar Waxwings (*Bombycilla cedrorum*; $p = 0.061$ and $p = 0.046$), and Bridled Titmice (*Parus wollweberi*; $p = 0.066$ and $p = 0.067$).

The CV(abundance) but not CV(maximum) was greater in oases than corridor sites for Abert's Towhees ($p = 0.047$ and $p = 0.112$, respectively). Between-year variability of both total abundance and maximum counts was greater in species that breed farther north and that were less abundant. Median CV(abundance) and median CV(maximum) were both significantly negatively correlated with the latitude of the estimated center of the breeding range (partial $t = 2.607$, df = 2,30, $p = 0.014$; partial $t = 2.832$, df = 2,30, $p = 0.008$; Fig. 5) and ln(median abundance) (partial $t = 7.910$, df = 2,30, $p < 0.0001$; partial $t = 6.037$, df = 2,30, $p < 0.0001$; Fig. 5).

We captured 263 individuals of 36 species between 1 April and 2 May 1989. Nearly half (49%) of these captures were of five species, Wilson's Warblers, Bewick's Wrens, Abert's Towhees, Yellow-rumped Warblers, and Lincoln's Sparrows (*M. lincolnii*). Fat scores of all individuals averaged 1.04 (±1.30 SD) and ranged from 0 to 5. There were no differences in body condition (reflected by fat scores) attributable to size-connectivity of the capture site ($p = 0.244$) or to date of capture ($p = 0.141$). The distance that birds had yet to travel (expressed relatively as the latitude of the center of the species' breeding range) significantly influenced body condition of birds (partial $t = 7.453$, df = 2,260, $p < 0.001$); individuals of species that breed the farthest north (center of breeding range >45°N; Wilson's Warblers, Yellow-rumped Warblers, Lincoln's Sparrows, White-crowned Sparrows [*Zonotrichia leucophrys*], Orange-crowned Warblers; $n = 103$) carried more fat than more southerly breeding individuals (Bewick's Wrens, Abert's Towhees,

Table 4. Peak densities (birds/ha) of eight bird species in which all or some individuals are en route migrants.

Species	Site and date[b]	Peak density (birds/ha)[a] Density[c]	95% CI	CV (%)[d]	N(detect)[e]	San Pedro River breeding density[f]	Estimated percentage en route
Wilson's Warbler	BAB, 6 May 94	33.5	25.0–44.8	14.4	176	0	100
	SPN, 3 May 94	33.7	24.5–46.3	15.5	128		
Yellow Warbler	CASS, 21 April 94	48.0	37.2–62.0	12.8	428	5.7	88
	CASN, 7 April 94	42.4	33.6–53.5	11.7	609		
Yellow-rumped Warbler	SPS, 3 May 94	30.1	18.1–50.0	25.5	282	0	100
Song Sparrow	PAT, 2 May 94	7.1	5.1–9.9	16.9	429	1.5	79
Common Yellowthroat	SPN, 26 April 94	4.2	3.3–5.4	12.5	440	3.7	12
Yellow-breasted Chat	CASS, 7 May 94	8.0	6.2–10.2	12.2	262	2.8	65
Bullock's Oriole	SPS, 3 May 94	7.9	5.1–12.2	21.4	220	0.9	89
Summer Tanager	SDD, 8 May 93	5.3	3.6–7.7	18.9	456	4.2	21

[a] Based on the highest count during one survey during the entire study; two values are given for the most abundant species.
[b] See Fig. 1 for site codes.
[c] Calculated using program distance (Buckland et al. 1993).
[d] Coefficient of variation expressed as a percentage.
[e] N (detect): the sample over which detection curves were developed equals all sightings of a given species at a given site in the 4-year period. Minimum sample sizes of 60–80 are recommended for calculation of detection curves (Buckland et al. 1993).
[f] Estimates of maximum breeding densities from the San Pedro River (Krueper 1992).

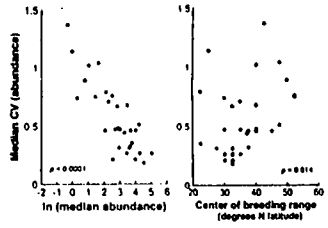

Figure 5. Relationships among between-year variability (median CV(abundance)), median abundance (log-transformed) for 4 years at nine original sites, and the latitude of the center of the breeding range for 33 species. The patterns are similar for CV(abundance) based on maximum counts rather than total relative abundances.

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Yellow-breasted Chats, Lucy's Warblers, Song Sparrows, Chipping Sparrows, Common Yellowthroats, Green-tailed Towhees [*P. chlorurus*], Yellow Warblers: n = 167). *Time of day also significantly influenced fat levels* (partial t = 3.987, df = 2.260, p < 0.001); birds captured in the afternoon and evening had higher fat scores than birds captured in the morning.

Insect Biomass and Extent of Riparian Vegetation

The biomass of aerial insects at the four sites was significantly greater in 1989 than in 1991 (*average biomass* 654.5 g/site ± 144.25 SE and 206.7 g/site ± 40.09 SE for 1989 and 1991, *respectively*; p = 0.001; Kruskal-Wallis test), primarily because of greater average insect lengths rather than greater numbers of insects. Although EC and PAT occasionally had greater biomass of insects, differences in biomass between sites were not statistically significant in either 1989 or 1991. *There were no relationships between aerial insect biomass and indices of foliage volume in seven of eight samples*, and in one sample in 1989 insect biomass was negatively correlated with foliage volume, primarily because of large Diptera occurring in the grazed oasis (EC).

The four prominent vegetation types in these riparian areas—cottonwood-willow, mixed *broadleaf*, tamarisk, and mesquite—together totaled about 8100 ha, or approximately 0.8% of the area of the 10,000-km^2 region that corresponds with our study sites. Riparian cottonwood-willow and mixed broadleaf habitats alone totaled 3272 ha or about 0.3% of the land area. Approximately 68% of the cottonwood-willow habitat was located along the San Pedro River and 32% *in isolated oases and* sites of intermediate size and connectivity. Along the San *Pedro River*, the southern *half* had 88.8% of the 2053 ha of cottonwood-willow stands within our delineated region, whereas the northern half contained 83.7% of 1359 ha of tamarisk stands. North of the Cascabel *sites and* beyond our delineated region, cottonwood-willow was relatively sparse along the San Pedro *River, covering only* 82 ha in the 60 km of river between the Cascabel sites and *Dudleyville. Between* Dudleyville and the confluence of the San Pedro River with the Gila River there were only 111 ha of cottonwood-willow in about 15 km of river.

Discussion

Importance of Continuous Tracts of Riparian Vegetation and Oases

We tested four predictions related to the hypothesis that extensive river corridors are more important than smaller, isolated patches to en route *migrants. We found* little support for this hypothesis for most birds migrating across southeastern Arizona. First, the corridor sites did not host more species than oases; rather, the species richness of migrants tended to be greater in oases than in corridor sites. Second, abundant *species in migration* categories 4 and 5, such as Chipping Sparrows, White-crowned Sparrows, and Wilson's Warblers, showed no preference for corridor sites; instead, three species in these migration categories were associated with oases in 1 of 4 years. Other abundant *migrants*, such as Yellow Warblers (89% estimated migrants) and Yellow-rumped Warblers, used *riparian sites regardless of size-connectivity*. But three migration category 3 species with large components of migrants—Yellow-breasted Chats (65% estimated migrants), Summer Tanagers (21% estimated migrants), and Northern Rough-winged Swallows (breeding range extends *north of 50°N*) were consistently associated with corridor sites. Migrants of these three species *probably account for fewer* than 10% of the individuals migrating through the area.

Third, few differences in between-year variability of abundances of migrating birds were apparent among corridor and oasis sites. Both measures of between-year variability were greater *in oases than corridor sites* for four of the 33 species evaluated; three of these species had migrating as well as breeding components—Yellow-breasted Chats, Song Sparrows (79% estimated migrants) and Cedar Waxwings (breeding range extends north of 50°N). Variability is more closely tied to rarity of a species than to isolation of a site. Species that primarily breed far north of the study area were *less* abundant and more variable than species that breed closer to the study area.

There were no suggestions of differences in general resource abundance, as reflected in aerial insect biomass, between corridor *and oasis sites. We* acknowledge, however, that the abundances of foliage and bark insects, which are *primary food sources* of insectivorous songbirds, were not measured in this study. Finally, there were no differences in the body condition of birds captured along the San Pedro River, an oasis, and an intermediate site. We believed that the body condition methodology was powerful *enough to detect* differences if they existed because we were able to find patterns in body *condition relative to migration distance* and time of day.

Our study does not indicate that riparian sites along the San Pedro River are preferred over isolated oases by most migrating birds. Most long-distance migrants travel at night and follow paths that *are strongly* influenced by variable wind patterns. The use of the oases and intermediate sites as well as *the river corridor* by many migrating birds is consistent with the passage of migrants in broad fronts rather than along north-south corridors. The spatial arrangement of habitat patches and other landscape-level features may not be of major importance to birds that travel long distances (*Fahrig & Paloheimo* 1988). Similarly, transient passerines use oases in the Sahara as "stepping stones" as they cross the desert (Bairlein 1988, 1992; Biebach 1990).

Oasis sites were higher in elevation and had less vegetation than riparian sites. In spite of these confounding factors, the patterns of species presence and abundance relative to size-connectivity were clear. More species occurred in oases even though shrub and canopy foliage volumes were smaller there, and the abundance of most migrating species did not differ between sites regardless of differences in foliage volume.

Exceptions to the Pattern

Although the continuous band of riparian vegetation along the San Pedro did not appear to function as a migration conduit for most species, it may for a few—namely Yellow-breasted Chats, Summer Tanagers, and Northern Rough-winged Swallows. *Evidence is inconsistent* for Song Sparrows—more variable in oases but more abundant *in corridor sites in only 1 year*—and weakly suggestive for Bullock's Orioles (89% estimated migrants)—more abundant in corridor sites for 2 years. It is possible that breeding birds prefer the river sites with greater foliage volumes, whereas migrating birds disperse among the different sites irrespective *of size-connectivity* and vegetation structure. Our study did not permit us to detect patterns *for en route migrants in these species* separately from the breeding components of the populations. Studies that incorporate radio telemetry to determine the residency periods of individual birds, thereby separating migrant from breeding components, would be useful in answering this question.

High Densities of Migrating Birds

The estimated densities of some species far exceed the breeding and *migration densities reported* elsewhere. The peak densities of Yellow Warblers (48.0 birds/ha) were *much greater than reported breeding densities* in southwestern riparian areas (San Pedro River, Arizona, peak of 5.7 birds/ha [Krueper 1992]; Rio Grande River, New Mexico, 3.3 birds/ha [Stahlecker et al. 1989] and 0.6 birds/ha [V. C. Hink & R. D. Ohmart, unpublished manuscript]; and at 2500 *m in Colorado, 2.5 birds/ha* [Knopf et al. 1988]), verifying that these stopover sites provide habitat *for a great number of northbound* migrants. Peak densities of Yellow Warblers, Wilson's Warblers (33.7 birds/ha), and Yellow-rumped Warblers (30.1 birds/ha) in this study also surpass estimates of densities during spring and fall migration along the Rio Grande (Yellow Warblers, <0.5 *birds/ha in spring*; Wilson's Warblers, 1.3 birds/ha in spring and 2.5 birds/ha in fall; Yellow-*rumped Warblers, 5.1 birds/ha* in spring and 22.1 birds/ha in fall; V. C. Hink and R. D. Ohmart, unpublished manuscript) and in a variety of habitats in the Chiricahua Mountains of southeastern Arizona (Yellow Warblers, 0.36 birds/ha in fall; Wilson's Warblers, 0.5 birds/ha in spring and 2.0 birds/ha in fall; Yellow-rumped Warblers, 3.0 birds/ha in spring and 1.1 birds/ha in fall; Hutto 1985*b*).

The stopover sites that host these great densities of spring migrants in southeastern Arizona may be limited. Less than 1% of the land area within the designated 10,000 km^2 is primarily cottonwood-willow vegetation, of which one-third is in oases and intermediate sites. All of the sites we surveyed may have been important to *migrating birds*, because suitable stopover habitat here is limited. We acknowledge that the patterns detected here may not hold in regions with more extensive cottonwood-willow riparian vegetation or *fewer en route* migrants.

Implications for Conservation and Management

We propose that all riparian areas in southeast Arizona, regardless of size-connectivity and vegetation structure, are important to en route migrants. In southeastern Arizona, riparian habitats make up a small fraction of the desert landscape. Here, all suitable *stopover sites* are important, regardless of the degree of isolation or connectivity. [redacted] Our study presents *an example of a system in* which these traditional insights may not apply. [redacted] 1982). The *riverine vegetation* represents a small proportion of the landscape and is connected only along narrow ribbon-like bands; desert oases are often isolated from similar vegetation patches. Migrating birds in need of refueling resources are opportunistic, finding and using small, disjunct patches as well as larger more continuous patches.

Evidence of such high densities and limited habitat availability during migration accentuates the interdependence of geographic and political regions in providing resource requirements for birds throughout their life cycles. Many western North American migrants pass through or over Arizona. Arizona provides a critical link between breeding and wintering habitats of species that are highly dependent on the presence and *condition of* stopover sites along their migration routes. Riparian habitats in the southwestern United States have undergone extensive deterioration (Minckley & Brown 1982), invasions by exotic plants (Davis 1977; Ohmart & Anderson 1982), and alterations in hydrology and salinity that further threaten cottonwood-willow associations (Busch & Smith 1995). Further elimination or *degradation of ripar-*

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ian stopover sites could adversely affect the breeding success of northern bird populations. In light of potential habitat limitation during migration and the specific results of this study, the protection of both small, disjunct riparian patches and extensive riverine tracts in western landscapes is imperative.

Acknowledgments

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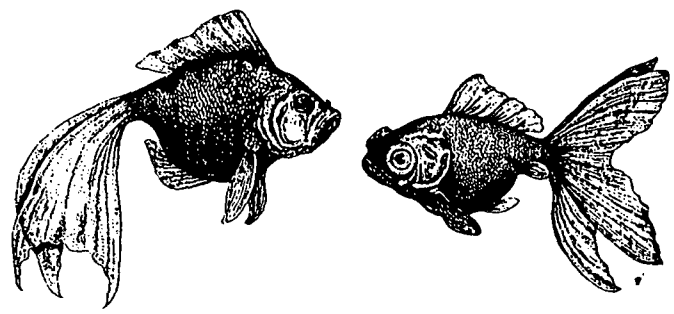

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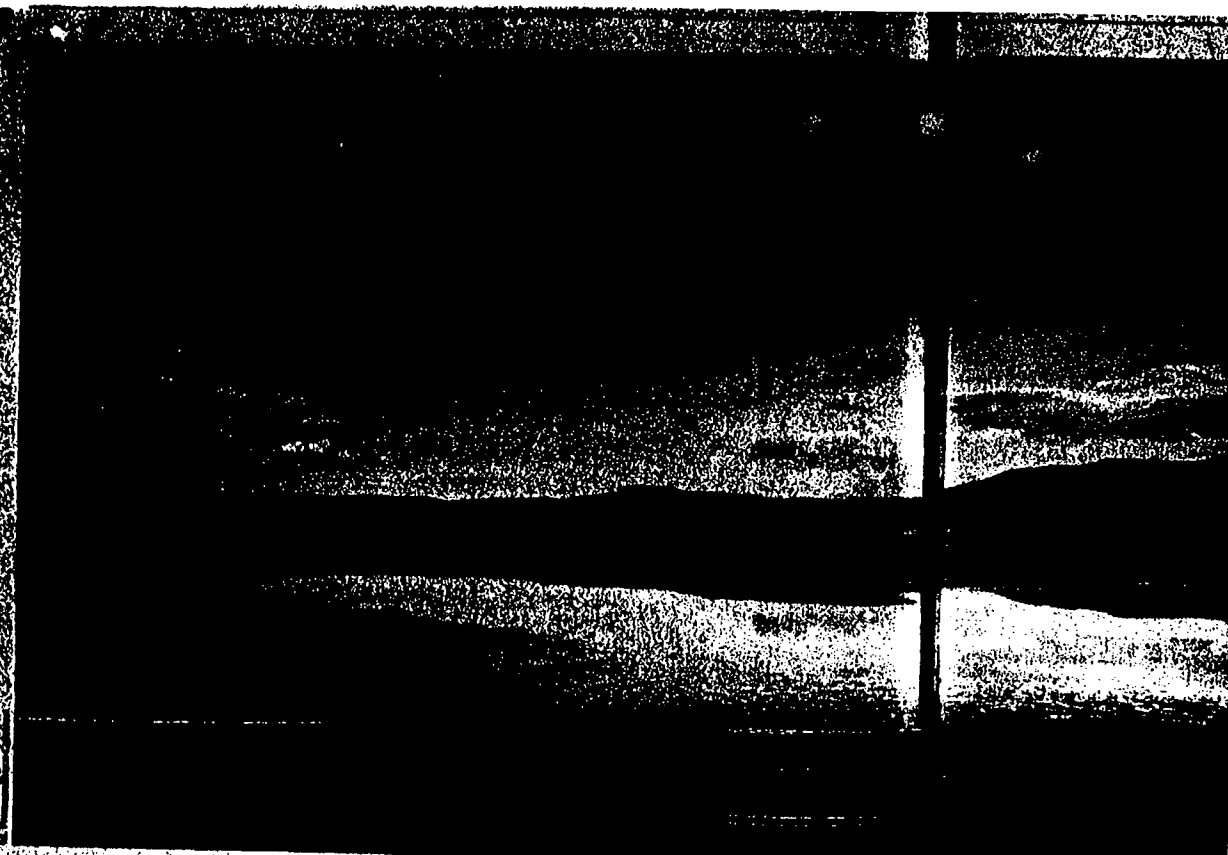
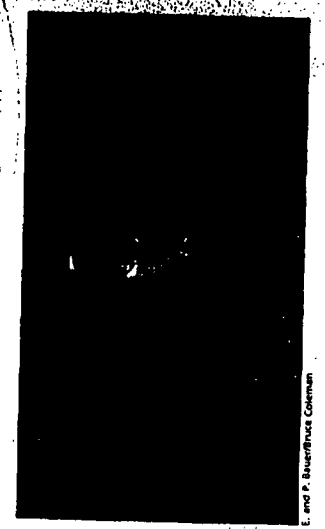


A. Dawson/Bruce Coleman

Open road: from urban wildlife sanctuaries to the great plains of the Serengeti, environmentalists have promoted the idea of corridors that allow isolated animal communities to migrate from one reserve to the next



E. and P. Bauer/Bruce Coleman

Corridors connecting fragmented islands of natural habitat are all the rage. John Bonner asks whether they are routes to survival for threatened species or expensive dead ends

Wildlife's roads to nowhere?

AS MORE and more of the Earth's surface is swallowed up by towns, roads and agriculture, pressure grows on the remaining areas of truly wild habitat. In the most developed parts of the world, only small pockets remain as sanctuaries where wildlife can hang on. Growing concern over the dwindling number of plant and animal species has led to a hunt for ways to save them, and in the past decade, the idea of maintaining wildlife corridors—strips of land to connect these sanctuaries—has become popular among conservationists.

It is an idea that is easy to grasp and has obvious, intuitive appeal. Some of the most ambitious schemes cross national boundaries: for example, there is a corridor linking the massive game reserves of Masai Mara in Kenya and the Serengeti across the border in Tanzania. At the other end of the scale are the modest efforts that make use of disused railway lines to join patches of wasteland in inner cities, bringing a taste of the countryside to town dwellers.

But it is as channels for the movement of rare or endangered species that the idea has captured the imagination of environmentalists. The hope is that wildlife corridors will allow plants and animals to colonise new areas, or bring much-needed new blood into small populations that are in danger through inbreeding. As a result, corridors are being hailed by some conservation groups, especially in the US, as potential saviours of the Florida panther, North American black bear (*Ursus americanus*) and many other high-profile animals.

Hard sell

But not all scientists share this enthusiasm. There is a dearth of observational evidence to show that corridors actually work, says Daniel Simberloff, professor of biology at Florida State University, Tallahassee, who believes the concept has been oversold. The huge costs of creating wildlife corridors may sometimes outweigh the benefits, he says, and the money may be better spent setting up and monitoring conventional reserves.

Most schemes that are in operation today are designed with individual species such as tigers, elephants and other large mammals in mind. But advocates of wildlife corridors say they could be used to preserve ecological communities. Fears that rapid global warming might outpace species' abilities to adapt to changing conditions have led to proposals for corridors that would allow animals and plants to migrate when conditions change. There is a plan on the table for a 300-metre-wide "global change" corridor stretching thousands of kilometres through North America.

A corridor this wide linking Florida to Canada would cover some 720 square kilometres. Even if it were possible to buy this amount of land, critics are sceptical about the likely results. Such a thin strip would be useless for species which can

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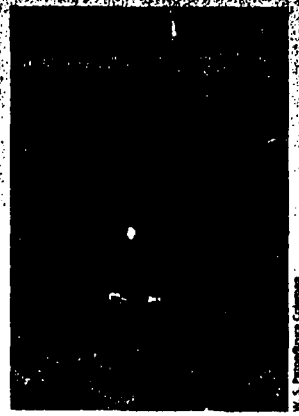
only disperse slowly, says Simberloff. "If a corridor is intended to preserve an entire community, it is particularly important that it is wide enough to permit breeding as well as movement."

Simberloff believes that some corridors are being promoted for less than creditable reasons, particularly in the forests of the northwestern US. "I have dealt in various ways with enough logging companies and developers to have seen a pattern," he says. "They offer skinny corridors of dubious value, stating that conservation biology shows that these will preserve biodiversity, then they seek to destroy much larger tracts."

Thin end of the hedge

In 1985, for example, a construction company proposed a complex of condominiums and golf courses for Fort George, a small island off the coast of north Florida. The construction company hired an environmental consultant to produce a report that looked at the best way to preserve the Antillian hard wood habitat that naturally covered the island. The agency proposed leaving about 150 acres of the original habitat including corridors as thin as 10 metres. Simberloff says this example is typical of many corridor proposals.

Biologists began investigating the theory of wildlife corridors in the mid-1970s. The Harvard University zoologist Edward O. Wilson argued in his book *Ecology and Evolution of Communities*, published in 1975, that corridors were a protection against extinction. If a habitat has to be divided, "extinctions will be lower when the fragments can be connected by corridors of natural habitat, no matter how thin the corridors", he wrote.



W. S. Paton/Bruce Coleman

Empire building: do animals such as the cheetah and the European bison need corridors for migration? Or is the land just extra foraging ground for the animals and for predators such as hawks?

The theory was later developed using mathematical models of how communities of different species interact (see "The case for corridors"). The idea of wildlife corridors was adopted in the early 1980s and promoted by such influential international conservation organisations as the World Wide Fund for Nature and the International Union for the Conservation of Nature and Natural Resources (now renamed the World Conservation Union). In December 1991, a report by the Institute for European Environmental Policy, an EC-funded research organisation, argued that "ecological corridors" were an essential feature of a network linking European nature reserves

Simberloff singles out the IEEP document as "a masterpiece of uncritical thinking and glib generalisations". Critics also point out that mathematical models have yet to be tested in practice, and say that the evidence apparently showing that mammals and birds will use corridors is flawed. Researchers in the US and Australia did record plenty of sightings and trappings of birds and small mammals in corridors during the 1980s. But Simberloff says this evidence does not show whether the animals were using the strips of land for migration or as a foraging area to supplement their home territory.

Simberloff is not the only scientist who is sceptical about the validity of the evidence for the effectiveness of corridors. David Dawson of the London Ecology Unit has just published a report on the subject for English Nature, one of the British government's main advisers on conservation. He concludes that what firm evidence there is only shows movement in a limited range of circumstances, between small, closely spaced patches in an agricultural landscape.

One frequently quoted investigation is a study by Gray Merriam and colleagues from Carleton University, Ottawa.

Working in eastern Canada in the 1980s, they deliberately removed fieldmice and chipmunks from patches of woodland, then studied the animals' movement along hedges that linked the patches. The researchers found that the hedges helped these species to recolonise the woods. Scientists do not, however, accept that this justifies most existing corridors, which have been set up mainly to protect much larger, more glamorous species such as bears and big cats. These animals may have home territories stretching over several square miles. Nobody has yet proved that corridors can work on such a scale, Dawson says.

Big ideas

Doing so would be a huge undertaking. Take the case of the Chila Motichur corridor in India, between the Corbett and Rajaji National Parks in the foothills of the Himalayas. Including adjacent areas of forest and small sanctuaries, it covers an area of 2500 square kilometres. Indian researchers have tried valiantly to assess movements of elephants, tigers and other species along this enormous corridor, but the difficult terrain forces them to rely on patchy evidence from dung samples.

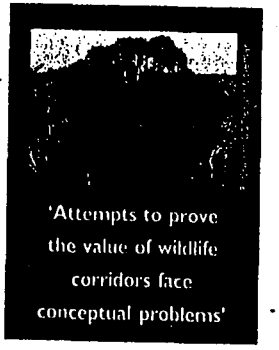
Attempts to prove the value of wildlife corridors face conceptual problems, too, their critics say. One is that the strips of land in question are anything from a few metres to several kilometres wide. The Grider Creek corridor that connects two forest wilderness areas in the extreme north of California and southern Oregon is 5·5 kilometres wide and 26 kilometres long.

Such corridors are likely to function much better than narrower ones, says Simberloff. For one thing, they provide real habitats, not just travel routes. And in a strip there may be nowhere that is far enough away from the edge to be insulated from the environment beyond the corridor. Weeds that thrive in the surrounding farmland, for instance, may intrude into the corridor and upset the ecological balance, while species such as woodland birds may be vulnerable to attacks by predators such as hawks and crows. At corridor edges, forest plants may also suffer from being exposed to too much wind, light or humidity.

One of the justifications cited for wildlife corridors is the idea that the genetic vitality of isolated populations is improved by the migration of animals from outside. The standard argument is that matings between close relatives result in unfavourable genetic characteristics being maintained, when in a larger population they would be lost through genetic mixing. But this picture is not always borne out by reality, says Simberloff. Species such as the European bison (*Bison bonasus*) and the Pere David's deer (*Elaphurus davidianus*) have no such problems, even though they have been rescued from the point of extinction and are now highly inbred. And African cheetahs are extremely uniform genetically—possibly due to having come close to extinction in the distant past—but do not appear to suffer for it. Small populations do not necessarily become extinct, says Simberloff. Researchers keeping tabs on the red-tailed hawk (*Buteo jamaicensis socorroensis*) on the Pacific island of Socorro, off the coast of Mexico, have found that the bird has survived for several decades as a stable population of about twenty pairs. There is no reason to suppose the population was ever any larger, they say.

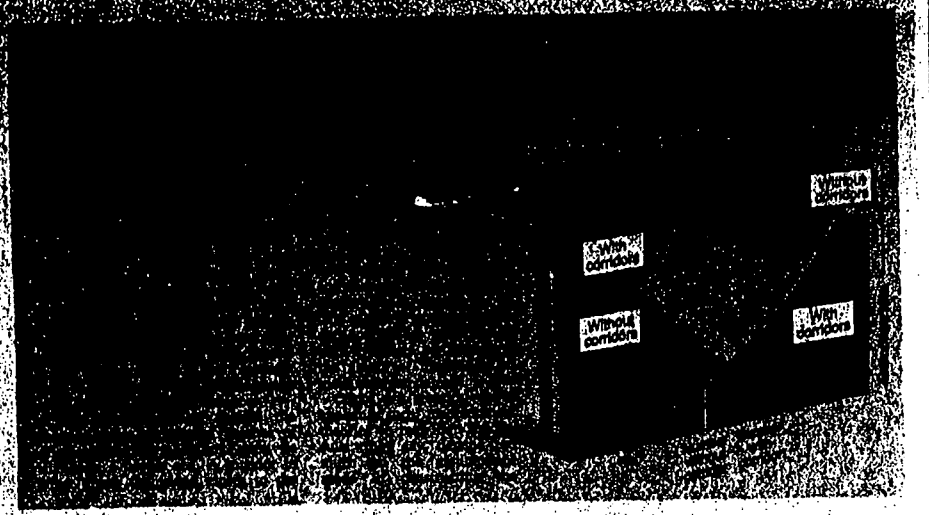
J. Bates/CEPA

If inbreeding did become a problem, one solution might be to trap a few individuals from outside and release them into the isolated area, says Simberloff. "The number of individuals that must be transferred among populations can be surprisingly small—so small that it might be genetically advantageous and far less expensive to move animals manually rather than to provide corridors." Transferring birds' eggs between populations has been tried successfully in many species, he says. And in the northern US, timber wolves (*Canis lupus*) have been transported from one state to another.



'Attempts to prove the value of wildlife corridors face conceptual problems'

Others are less impressed by this option. Reed Noss, a research associate at Stanford University's Center for Conservation Biology, questions the ethics of "shipping animals about in crates". He also warns that trapping and transporting individuals would be impractical, except for a few species. Critics of transportation also point out that it can never conserve entire communities of plants and ani-



mals, only individual species.

Another pitfall, which could in principle apply to wildlife corridors as well, is the problem of genetic dilution—the fear that mixing populations could lead to the loss of useful local characteristics, a phenomenon known as outbreeding depression. But Noss does not think that this is a real drawback with wildlife corridors. "Maintaining or restoring natural landscape connectivity has never been shown to cause outbreeding depression in wild populations," he says.

Transmission route

Another worry is that corridors might become pathways for the transmission of disease. The risk may be all the greater if the corridor connects small, crowded populations of animals and plants, warns George Hess of North Carolina State University. This effect can be seen where animals are crowded together in a game reserve. Max Appel, a virologist at Cornell University veterinary school in New York, has recently identified an outbreak of canine distemper as having killed more than 60 lions in the Serengeti.

Wildlife corridors could also act as conduits for fire, predator species or weeds that could disrupt the natural plant communities. That isolation can benefit some species is evident from observations from New Zealand. Wild pigs have wiped out *Paryphanta* snails from many of the larger forest refuges, but they survive in small isolated patches that the pigs have not been able to invade.

Simberloff cites conservation projects from his home state of Florida as examples of "uncritical advocacy of extremely expensive corridors". In 1990, the state's Department of Natural Resources devised the Pal-Mar project to create a 8860-hectare conservation area in Palm Beach and Martin counties. The project was intended to preserve some of the best woodland and marsh remaining in south Florida east of the Everglades. So far so good. But later the department decided to extend the project to create a corridor 1·6 kilometres wide and 10 kilometres long that would connect Pal-Mar to the Jonathan Dickinson State Park. Simberloff says that the proposal was submitted without any accompanying biological data on which species would use it, and why it was necessary. But more importantly, the proposed corridor would cross two highways—the six lanes of Interstate 95 and the four-lane Florida turnpike—both potentially lethal obstacles to animals trying to use the route.

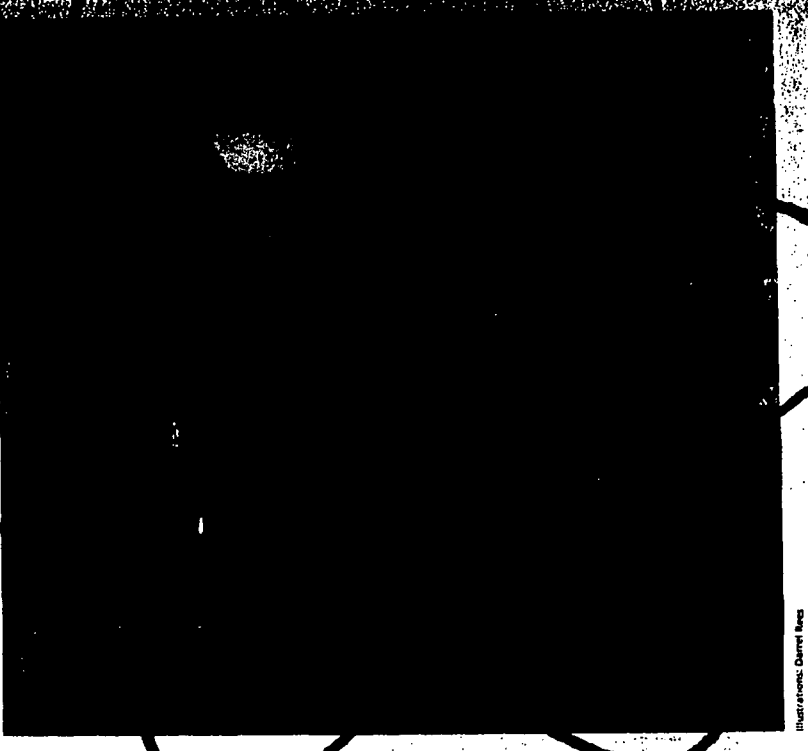
> 'Wildlife corridors could also act as conduits for fire, predator species or weeds'

The department claimed that the corridor—which would have cost at least $21 million—was the key to the whole Pal-Mar scheme and that the necessary land should be bought before the reserve itself was acquired. But this plan has now been put on the back burner, partly as a result of fierce criticisms from Simberloff and like-minded critics. Work is going ahead on the first stage of a three-phase plan to preserve the main wetland system. The corridor phase may still go ahead, but only after the first two stages have been completed.

Part of the problem stems from a shortage of money: earmark funds for corridors, and there isn't much left for anything else. Florida's Conservation and Recreation Lands programme had a budget of $185 million for acquiring land in 1991. But 93 separate projects were given initial approval, and the top 60 alone would have cost nearly $1 billion. Simberloff believes that with resources so scare, every project ought to undergo a cost benefit analysis—except that the information to show whether a corridor scheme would be worthwhile is rarely if ever available.

Conservation biologists should be working towards making such an analysis possible, says Dawson. Until it is, he says scientists should adopt the precautionary principle and assume that existing corridors could be important. Richard Hobbs, an ecologist based in Western Australia, sees corridors as neither a cure-all nor a complete disaster. They "will benefit some species but not others", he says. "With careful planning they can form part of a regional conservation network."

John Bonner *is a freelance science writer.*



Illustrations: Darrel Rees

Quantum states of mind

Most biologists believe the answer to what makes us conscious lies buried in brain cells and their chemistry. John McCrone talks to the mavericks who prefer to look for clues in quantum physics

DAVID CHALMERS, a philospher from Washington University, jokingly calls it the law for the minimisation of mysteries. "Consciousness is a mystery, quantum mechanics is a mystery. When you have two mysteries, well maybe there is really only one. Perhaps they are the same thing."

That the answer to consciousness might be found in the strange world of the quantum is a suggestion that dates back at least as far as the musings of physicist, David Bohm, in his 1951 book, *Quantum Theory*. In the past few years, however, such speculation has taken on a new urgency. What else, ask a host of thinkers, including Roger Penrose, the Oxford mathematician famed for his work on the geometry of tiling patterns and black holes, could explain aspects of the mind such as free will, in tion, creativity and the subjective unity of experience?

In the odd world of the quantum, things appear to exist i multitude of states—describable only as the set of probabili known as a wave function—until tipped into a definite outc by an act of "measurement". An electron or atom (and s would even argue the whole Universe) remains an open f of possibilities until forced into an interaction. It is as if physical world wants to explore many alternative pathways fore collapsing into a settled state. For the champions of qu tum consciousness, this seems to be just what the crea human mind does: sample many paths and outcomes befor

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poral conditions greatly affect response. Operations in a sequence may alter the effects of subsequent or earlier operations. Because the C factor for semimonthly intervals is multiplied by the percentage of EI in the interval, the specific operation may be effective for only a small part of the year. For example, we modified the roughness, percentage of area disturbed, percentage residue left, and depth of disturbance parameters within the row planter operation. Percentage of area disturbed changes caused minimal change in predicted soil loss. Roughness and depth change results were on the order of 1%. Percentage cover changes caused changes in calculated soil loss from 4 to −5%, varying inversely with parameter changes.

The same exercise was then performed perturbing the parameters of the spike harrow operation. Similar results were obtained.

These results should not lead one to infer model insensitivity to operations parameters. This is an obvious example of other conditions masking the effects of these parameters. In this case, the planting and cover of a corn crop mitigated effects of previous disk, cultivator, and harrow operations. To illustrate, we deleted operations from the schedule (Table 2), as though the farmer skipped an operation or stopped working midseason. Figure 13 shows the results, as compared to the base run results. Eliminating either the cultivator or disk operation reduced soil loss slightly. The impact of plants is apparent when either the harvest or both planting and harvest are deleted. Eliminating plants increased the predicted soil loss from the base value of 2.3 to 25.8 tons acre^{-1} (5.2–57.8 t ha^{-1}). Results on the same order of magnitude were also achieved by deleting all operations following the cultivator and by eliminating all after the disk.

SUMMARY AND CONCLUSIONS

The RUSLE model is a useful tool to assist in making field-management decisions that affect soil loss. In this study, a sensitivity analysis on parameters and variables in the CITY, CROP and OPERATIONS DATABASES discovered a range from minimal sensitivity to extreme sensitivity. For the case of corn grown under conventional tillage in the Chicago, IL, area, moderate sensitivity (10–40% change in prediction resulting from 20% change in a variable) was found for city code, precipitation, temperatures, *R* factor, harvest residue, fall height, and percentage canopy cover. Only slight sensitivity (< 10%) was found for reasonably nearby EI distribution codes, freeze-free days, root mass, and residue at 30, 60, and 90% cover. An EI distribution code from a dramatically different climate caused large changes in soil loss (magnitude of change more than 50% from the base). While many parameters and variables exhibited nearly linear response, freeze-free days and percentage canopy cover responses were nonlinear. Results of changing such field operation parameters as percentage of area disturbed, roughness, depth, and residue left were shown to be masked by later operations and plant growth. Insensitivity under the base conditions cannot be extrapolated to other conditions, as was shown by eliminating several field operations.

It is stressed that such a sensitivity analysis produces valuable information to help users determine which parameters and variables to put effort and resources into. Model users are encouraged to perform a simple sensitivity analysis such as these for their unique situation.

Surface water quality has historically meant soil erosion and sedimentation in rivers and reservoirs. Adsorbed agricultural chemical transported from upland areas has become a concern in recent decades. Incorporating RUSLE in more comprehensive models, such as EPIC and AGNPS, should permit more complete problem resolutions.

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Nutrient Interception by a Riparian Forest Receiving Inputs from Adjacent Cropland

Thomas E. Jordan,* David L. Correll, and Donald E. Weller

ABSTRACT

To investigate the ability of riparian forest to intercept nutrients leaving adjacent cropland, we examined changes in the chemistry of groundwater flowing from a corn (*Zea mays* L.) field through a riparian forest. This study provided a comparison to previous studies of a different forest. We sampled groundwater from a transect of wells, and used a Br^- tracer to confirm that groundwater moved laterally along the transect through the forest. As groundwater flowed through the forest, NO_3^- concentrations decreased from about 8 mg/L at the edge of the corn field to <0.4 mg/L halfway through the forest. Dissolved organic N and NH_4^+ increased by less than 0.1 mg/L, and dissolved organic C did not change with distance. Sulfate remained constant with distance until midway through the forest, where it began to increase. Chloride concentration rose until midway through the forest, then fell. Values of pH increased from under 5 at the edge of the corn field to over 7 at the stream bank, perhaps as a result of the NO_3^- consumption. Most of the change in NO_3^- occurred abruptly at the edge of a floodplain within the forest. There the water table was closest to the surface and soil Eh below the water table was less than −90 mV. Such strongly reducing conditions may have promoted denitrification in the floodplain. In contrast, soil Eh on the adjacent hill slope was above 500 mV, too high to support denitrification. There were only slight seasonal changes in groundwater chemistry. We also studied the net annual accretion of sediment in the riparian forest by measuring changes in the elevation of the soil surface. There was little or no accretion in the forest, but along a path of overland storm flow there was net erosion. Thus, nutrient retention by this forest, in contrast with the forest we previously studied, was entirely a below ground process. Functional differences within sections of this forest and among different riparian forests suggest a need for research on the factors that control nutrient retention.

SEVERAL STUDIES have shown that riparian forests can take up N, P, and sediment from discharges leaving adjacent croplands (e.g., Lowrance et al., 1984a,b; Peterjohn and Correll, 1984, 1986; Jacobs and Gilliam, 1985; Pinay and Decamps, 1988; Correll and Weller, 1989; Haycock and Pinay, 1993). This finding has important implications for land use management. Removal of NO_3^- reduces the hazards of high NO_3^- concentrations in drinking water. Nitrate removal also raises the pH of the groundwater, thus reducing acidification of downstream aquatic ecosystems. Removal of N and P also reduces eutrophication of aquatic ecosystems. Removal of sediment from surface runoff reduces turbidity and sediment deposition downstream.

Strong effects of riparian forests on agricultural runoff have consistently been reported for coastal plain forests with shallow underlying aquicludes. The aquicludes force cropland groundwater flowing toward the stream to move laterally through the near-surface layers of the riparian forest. Such forests can remove large percentages of materials they receive from the croplands. Moreover, the removals can take place over narrow widths of forest. For example, riparian forests can retain 70 to 90% of the total N inputs from adjacent croplands (Lowrance et al., 1984b; Peterjohn and Correll, 1984), and most of the NO_3^- removal occurs within 20 m of the forest–field boundary (Peterjohn and Correll, 1984; Jacobs and Gilliam, 1985).

Many questions remain about the function of riparian forests. For example, how similar are the functions of different forests? How much forest is necessary to remove nutrients effectively? Does nutrient removal occur evenly throughout the forest or are there particular areas within the forest where nutrient removal is greatest? Is nutrient removal constant throughout the year?

In this study we examined the changes in the chemistry of groundwater flowing out of a corn field and through a riparian forest, and we measured the net sediment accretion in the forest. Our goals were to test the generality of our previous findings at a similar forest (Peterjohn and Correll, 1984, 1986; Correll and Weller, 1989) and to examine the spatial and seasonal variability of groundwater chemistry and sediment accretion in the forest.

METHODS

We studied a riparian forest located on a hill slope and a floodplain adjacent to cropland on the Delmarva peninsula near Centreville, MD (39° 8′ N, 75° 56′ W). The forest is deciduous, dominated by beech (*Fagus grandifolia* Ehrh.) and tulip poplar (*Liriodendron tulipifera* L.) on the hill slope and by sycamore (*Platanus occidentalis* L.) and box elder (*Acer negundo* L.) on the floodplain near the stream. The stream is the northern branch of Southeast Creek, a third-order tributary of the Chester River. The cropland was planted to corn during the study but has been rotated to soybean (*Glycine max* (L.) Merr.). The corn was grown by no-till methods. Surface sediments in this coastal plain region are part of the Pensauken formation, which forms the Columbia aquifer, which is perched on the less permeable sediments of the Chesapeake Group throughout the region (Bachman and Wilson, 1984). The Pensauken sediments are feldspathic sands, which become gravelly at the bottom of the formation just above the clayey sediments of the Chesapeake Group at about 10 m above sea level in our study area (Bachman and Wilson, 1984). The thickness of the underlying clayey sediments is variable. At our study site we verified that the clay extended at least 0.5 m below the Pensauken sediments. Deeper drillings near our site penetrated 2 to 4 m into the clay (Bachman and Wilson, 1984).

In July 1990, we dug a transect of groundwater sampling wells using a 5.5-cm diam. bucket auger. The wells were lined with a 5-cm diam. PVC pipe perforated from the surface down to the Chesapeake clay at a depth of 4.2 to 5.3 m (Fig. 1). Initially, we installed three replicate wells at each of four distances from the stream (Fig. 2). Later, six additional wells were added in the middle of the transect (Fig. 2) to examine in detail the region where NO_3^- concentration changed rapidly with distance from the corn field. The wells were pumped out several times after installation to remove loose particulate matter.

We sampled the wells about once a month from July 1990

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Abbreviations: DOP, dissolved organic phosphorus; DON, dissolved organic nitrogen; DOC, dissolved organic carbon.

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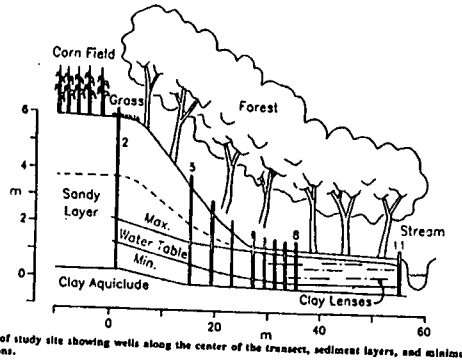

Fig. 1. Cross-section of study site showing wells along the center of the transect, sediment layers, and minimum and maximum water table elevations.

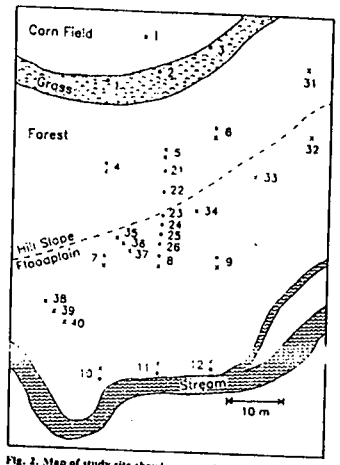

Fig. 2. Map of study site showing groundwater sampling wells (•) and deposition posts (×). Posts 31–40 are distributed along the path of overland storm-water flow. Point J in the cornfield marks an auger hole where NaBr tracer was added.

to August 1991 by first pumping the wells dry, then sampling the water that immediately refilled them. Usually we mixed together equal volumes of sample from the three replicate wells to produce one composite sample for each distance from the stream. Just prior to pumping, the water level in the wells was measured by lowering a float on a measuring tape.

The samples were filtered through 0.45-μm membrane filters and analyzed for dissolved N, P, and organic C species. Total P was digested to phosphate with perchloric acid (King, 1932). Phosphate in the digestate as well as in the undigested samples was analyzed by reaction with stannous chloride and ammonium molybdate (APHA, 1976). Dissolved organic P (DOP) was calculated by difference. Total Kjeldhal N was digested with sulfuric acid, Hengar granules, and hydrogen peroxide (Martin, 1972). The resultant NH_4^+ was distilled and analyzed by Nesslerization (APHA, 1976). In the undigested samples, NH_4^+ was oxidized to NO_3^- with alkaline hypochlorite (Strickland and Parsons, 1972). NO_3^- was reduced to NO_2^- with Cd amalgam, and NO_2^- was analyzed by reaction with sulfanilamide (APHA, 1976). When NO_3^- concentrations exceeded 1 mg/L, NO_3^- was analyzed with a Dionex Series 4000i ion chromatograph (Dionex Corporation, Smyrna, GA). We present data on the sum of NO_3^- and NO_2^- concentrations. Dissolved organic N (DON) was calculated by difference. Dissolved organic C (DOC) was analyzed by drying samples at 60 °C, followed by reaction with potassium dichromate in 67% sulfuric acid at 100 °C for 3 h (Maciolek, 1962) with $HgSO_4$ added to complex halides (Dobbs and Williams, 1963). Organic C was calculated from the amount of unreacted dichromate measured colorimetrically (Maciolek, 1962; Gaudy and Ramanathan, 1964). The pH was measured with a Ross electrode after the sample equilibrated with air. Conductivity was measured with a Yellow Springs Instruments Model 32 conductivity meter (Yellow Springs Instruments, Yellow Springs, OH), and SO_4^{2-} and Cl^- were analyzed with the Dionex ion chromatograph.

The path of groundwater flow was traced by adding NaBr to groundwater and observing the appearance of elevated Br^- concentrations in wells downslope. Bromide was analyzed by ion chromatography. We introduced 1.5 L of 8 *M* NaBr into a hole augured in the corn field and observed its subsequent appearance in Well 2 at the edge of the field (Fig. 2). Then we added 1.5 L of Br^- solution to Well 2, and observed its

appearance in Wells 4 and 6 farther down the transect. Finally we added 1.5 L of Br^- solution to Wells 4 to 6 and observed its appearance in Wells 7 and 8. In this way, we verified that groundwater moves through the forest toward the stream.

We used slug tests (Bouwer and Rice, 1976; Bouwer 1989) to measure hydraulic conductivity in the saturated zone of the Columbia aquifer and in the underlying clay. For these tests, four piezometers extending down into the Columbia aquifer and two into the underlying clay (Fig. 2) were installed in holes dug with a 5.5-cm bucket auger. The holes were lined with 5-cm diam. PVC pipes perforated along the bottom 20 cm. Sand was packed around the end of each piezometer and a bentonite seal was packed on top of the sand.

We used platinum electrodes (Faulkner et al., 1991) to measure Eh in the soil below the water table at four distances along transect (Fig. 2). The electrodes consisted of 1-mm diam. platinum wire soldered to insulated 2-mm diam. single-stranded copper wire. The solder joint was covered by epoxy leaving 8 cm of the platinum wire exposed. The Eh was measured with an Orion model 407 ion meter (Orion Research, Cambridge, MA) as mV potential relative to a calomel reference electrode and converted to mV relative to hydrogen by adding 250 mV (assuming groundwater temperature averaged about 13 °C). The electrodes were calibrated with saturated quinhydrone solution buffered at pH 7 (40.8 mV at 25 °C) and pH 4 (218 mV). Each electrode was buried below the water table in a hole dug with a screw auger 1 m from a groundwater well. For Eh readings in the field, the calomel reference electrode was lowered into the water in the nearby well.

We measured the net accretion (or erosion) of soil in the transect using a grid of vertical posts projecting about 30 cm above the soil surface. Posts were placed 2 m from each well and additional posts were placed in a path of overland flow through the study site (Fig. 1). Initially, a metal washer loosely fitted over each post was placed on the soil surface, and the distance from the top of the post to the washer was measured. After a year, we measured the distances from the top of the post to the litter layer, the soil surface, and the washer. If deposition occurred, the washer would be buried by the deposited material. If erosion occurred, the washer would be further below the top of the post after a year. If both erosion and deposition occurred, the washer would be farther below the top of the post and buried.

RESULTS

The chemistry of groundwater differed dramatically among wells at different distances from the corn field, but did not change very much seasonally. Nitrate concentration showed the greatest spatial variation, dropping from about 8 mg/L at the edge of the corn field to less than 0.4 mg/L halfway through the forest (Fig. 3). Most of the change in NO_3^- concentration occurred 25 to 35 m from the edge of the corn field. In contrast, DON and NH_4^+ concentrations increased by less than 0.1 mg/L with increasing distance from the corn field, and DOC did not change with distance from the corn field. Sulfate remained constant with distance from the corn field until midway through the forest, where it increased in conjunction with the decrease in NO_3^-. Values of pH increased from under 5 at the edge of the corn field to over 7 at the stream bank. Groundwater near the stream was unique. It had high DOP and phosphate concentrations, high conductivity, and low Cl^- concentration compared with groundwater from other locations along the transect. Soil Eh below the water table also changed markedly along the transect, averaging about 210 mV at the edge of the corn field, about 570 mV on the hill slope, and −95 to −260 mV on the floodplain (Table 1).

Groundwater chemistry varied little through time. However, NO_3^- concentration at the edge of the corn field rose slightly in the winter and spring, whereas NO_3^- concentrations 15 m into the forest declined (Fig. 4). Groundwater DOC and DON concentrations declined from late July to late October. Dissolved organic C concentrations rose again the following May through July, suggesting a summer maximum and winter minimum in concentration, but DON concentrations did not rise in the late spring. Ammonium and phosphate concentrations 35 m into the forest rose during June through August. Of course, with only 1 yr of data we cannot conclude that any of these temporal changes are part of a repeating seasonal cycle.

Interpreting the spatial variation in groundwater chemistry requires knowledge of the groundwater hydrology. Observations of Br^- movement verified that groundwater moved laterally from the cropland through the forest to the stream. Lateral movement is induced by the relatively impermeable clay underlying the much more permeable surface sediments. Hydraulic conductivity within the clay ranged from 1.7×10^{-6} to 2.3×10^{-4} cm/h, but in the surface sediments it was more than a thousand-fold greater (0.7–18 cm/h). The hydraulic characteristics of our site are typical for the Columbia aquifer, although the hydraulic conductivity of the surface sediments at our site is at the low end of the range for region (Bachman and Wilson, 1984).

Water table elevation declined toward the stream, suggesting groundwater flow nearly parallel to the transect and perpendicular to the stream. Water table elevation varied seasonally with the cycle of evapotranspiration (Fig. 5). The seasonal variation in water table elevation resulted in variation in groundwater flow. We used water table elevation and hydraulic conductivity data and methods of Todd (1964) to estimate groundwater flow between Wells 5 and 8, where most of the NO_3^- decline took place. Flow through a 1 m wide by 20 m long path ranged from 1.2 L/h in fall to 2.6 L/h in spring. These rates of groundwater flow and the difference in NO_3^- concentrations between Wells 5 and imply removal of NO_3^--N at a rate of 0.4 mg·m^{-2} per h in fall and 0.9 mg/m^2 per h in spring.

Annual soil deposition or erosion, measured by elevation changes at posts (Fig. 2), was highly variable (Table 2). Erosion predominated along the overland flow channel with net erosion of 1 to 4 mm in most locations and net erosion of 10 to 30 mm in one area (posts 35–37, Fig. 2). Burial of the washers along the overland flow path indicated that, although there was net erosion, both erosion and deposition occurred at the same locations. Outside of the overland flow path, there was neither erosion nor deposition in the forest near the cropland, and 1 to 5 mm of erosion nearer the stream at Posts 7 to 12. However, one location near Well 10, at the edge of the overland flow path, showed 18 mm of deposition. Litter layouts of up to 60 mm built-up throughout the site over the year. At one location (Post 21), the post snagged litter carried in overland flow and built up an artifically thick layer 190 mm deep.

DISCUSSION

Others have found, as we have, that NO_3^- concentrations in groundwater are much lower in riparian forests than in adjacent croplands (Lowrance et al., 1984a,b;

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Peterjohn and Correll, 1984, 1986; Jacobs and Gilliam, 1985; Correll and Weller, 1989; Weil et al., 1990; Pinay and Decamps, 1988; Haycock and Pinay, 1993). Such concentration differences could arise if groundwater in the forest originates from infiltration of rainwater or emergence of NO_3^--poor groundwater from an underlying aquifer. However, in our study, and those cited above, an aquiclude forces the lateral flow of groundwater and blocks emergence of deep groundwater. Moreover, infiltration of rainwater in our forest evidently cannot account for the change in NO_3^- concentration, because corresponding change in Cl^- concentration did not occur (Fig. 3). Thus, we conclude that the decline in NO_3^- concentration with distance from the cropland must be

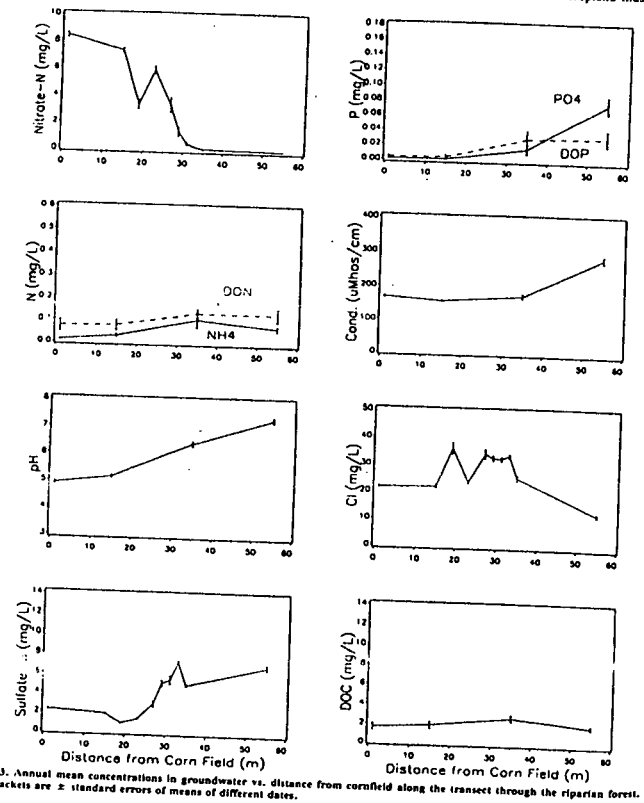

Fig. 3. Annual mean concentrations in groundwater vs. distance from cornfield along the transect through the riparian forest. Brackets are ± standard errors of means of different dates.

Table 1. The Eh in saturated soil at different depths below the soil surface. Eh is the average (± SD) of monthly measurements from December 1991 to March 1992. Eh electrodes were 1 m from nearest well. Well positions are shown in Fig. 2.

Location	Nearest well	Depth	Eh
		m	mV
Edge of field	2	4.5	222 ± 15
	3	4.1	197 ± 10
Hill slope	5	2.8	560 ± 66
	6	2.9	580 ± 12
Floodplain	8	1.0	−132 ± 33
	9	1.2	−130 ± 36
	11	1.0	−95 ± 21
	12	1.0	−510 ± 12

due to removal of NO_3^- from groundwater flowing laterally from the cropland through the forest.

The amount of removal implied by the drop in NO_3^- concentration depends on the rate of lateral groundwater flow. Various methods have been used to estimate this rate. For example, hydrologic models (Lowrance et al., 1984a; Jacobs and Gilliam, 1985), stream hydrograph analysis (Peterjohn and Correll, 1984), and watershed budgets of Cl^- (Peterjohn and Correll, 1986). Our estimates of groundwater flow, based on methods similar to Lowrance et al. (1984a), imply removal of NO_3^--N from groundwater at rates of 0.4 to 0.9 mg·m^{-2} per h (=60 kg NO_3^--N ha per yr) in the section of forest where removal rates were highest. In comparison, estimates for total annual N removal in two other riparian forests are 40 kg/ha (Peterjohn and Correll, 1984; 1986) and 70 kg/ha (Lowrance et al., 1984b).

How is the NO_3^- removed? It is clear that the NO_3^- is not being transformed into DON or NH_4^+, dissolved in groundwater, because their concentrations do not increase very much in conjunction with the decrease in NO_3^- concentration (Fig. 3). Nitrate may be removed both by assimilation by trees and by denitrification. Most of the change in NO_3^- occurs abruptly 25 to 35 m from the forest field boundary (Fig. 3) where the hill slope ends and the floodplain begins (Fig. 1). In this zone, groundwater is forced closer to the soil surface by the underlying aquiclude. There, NO_3^- removal may be promoted as groundwater comes in increasing contact with tree roots, and as the organic-rich surface soils become increasingly waterlogged, producing low Eh conditions favoring denitrification. Lowrance (1992) concluded that denitrification could remove large amounts of NO_3^- from riparian forest groundwater if the water table was within 60 cm of the soil surface where denitrification rates were highest. In our forest, the water table is often near the surface in the floodplain (Fig. 5). Denitrification requires Eh levels below 300 mV (Kralova et al., 1992). Such levels were found in the floodplain but not on the hill slope (Table 1). Others have found higher denitrification potential in floodplains than in hill slope soils in both deciduous and coniferous riparian forests (Davidson and Swank, 1986; Gregory et al., 1991; Groffman et al., 1991, 1992). However, there are few estimates of actual denitrification rates in riparian forests, because of the general lack of accurate field methods (Tiedje et al., 1989; Payne, 1991). Deciduous forests are thought to have annual denitrification rates of up to 50 kg N/ha with

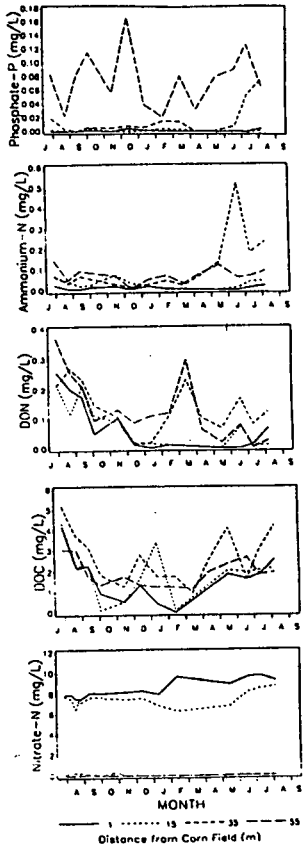

Fig. 4. Concentration versus date at different distances from the cornfield along the transect through the riparian forest.

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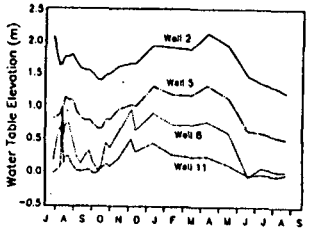

Fig. 5. Elevation of watertable (m) at center wells in the transect vs. date. The elevation scale is the same as the vertical scale in Fig. 1.

most between 0 and 10 kg N/ha (Davidson et al., 1990), but higher annual rates have been reported for riparian forests (32 kg/ha, Lowarance et al., 1984b; 6–194 kg/ha, Pinay and Decamps, 1988; 475 kg/ha, Fustec et al., 1991). Such rates could account for much of the NO_3^- removal we estimated (≈60 kg NO_3^--N/ha per yr). Assimilation could also account for much of the annual removal. Net long-term incorporation of N into aboveground biomass in other riparian forests has been estimated as 15 kg/ha per yr (Peterjohn and Correll, 1984) and 52 kg/ha per yr (Lowrance et al., 1984b).

Denitrification of a mole of NO_3^- requires 1 to 2.5 moles of organic C (Peterjohn and Correll, 1986). Although there was little change in DOC concentrations throughout the forest (Fig. 3), DOC may be consumed and continuously replenished by transformation of particulate organic C. Temperate forests produce more than enough organic matter to support denitrification at rates high enough to account for our estimated removal of NO_3^- (Peterjohn and Correll, 1986), but it is not clear how much of the organic matter produced is available to denitrifiers.

The removal of NO_3^- by either assimilation or denitrification probably helped raise the pH of groundwater traversing the forest (Fig. 3). The increase in pH would protect stream waters from acidification, which has been detrimental to aquatic ecosystems in this region (Correll et al., 1987). The pH trend may have been dampened by the concomitant increase in SO_4^{2-} in groundwater (Fig. 3), but the net change in concentrations of the anions we measured was more than enough to account for the pH change. Of course, cations and anions that we did not measure would also be involved in determining groundwater pH.

The increase in SO_4^{2-} indicates that reduction of SO_4^{2-} to sulfides was not a dominant process. This is consistent with our Eh measurements, which were usually above −220 mV, too high to favor SO_4^{2-} reduction (Correll and Weller, 1989). Oxidation of sulfides such as particulate iron sulfide may have occurred instead. Oxidation of sulfides can drive denitrification and result in concomitant increases in groundwater SO_4^{2-} with decreases in NO_3^- (Postma et al., 1991).

The increase in dissolved phosphate concentration near

Table 2. Accretion or erosion, and litter accumulation after 1 yr measured at posts. Accretion is the build up of soil at the post. Negative accretion is erosion. Burial of the washer is the depth of the washer below the soil. Posts numbered 4–12 are located near wells of the same number (Fig. 3). Posts numbered 31–40 are distributed along the path of overland storm-water flow.

Post no.	Accretion	Burial of washer	Litter
	(mm)		
4	0	0	14
5	0	2	6
6	0	0	54
7	−3	0	14
8	−5	0	33
9	−3	0	28
10	18	7	0
11	−1	0	30
12	−1	0	2
31	−3	27	190
32	2	5	60
33	0	10	5
34	4	9	20
35	−10	0	8
36	−21	4	0
37	−30	7	12
38	0	0	8
39	−3	0	3
40	−1	0	8

the stream bank (Fig. 3) may be due to reduction of iron oxyhydroxides that bind phosphate to soil particles (Richardson, 1985). Iron reduction can occur at Eh below −200 mV after the more energetically favored reduction of NO_3^- is complete (Correll and Weller, 1989). Low NO_3^- concentrations (Fig. 3) and Eh of −510 mV (Table 1) were found near the stream.

Other studies have stressed the importance of riparian forests in trapping sediment and particulate nutrients borne in overland flow. Peterjohn and Correll (1984) sampled surface runoff and found a large decrease in suspended load with distance into the forest. Cooper et al. (1986) measured sediment accumulation above the soil horizon labelled with Cs-137 from bomb testing of the 1950s to 1960s. Lowrance et al. (1984b) observed accumulation of sediment above a layer of buried woody vegetation deposited in the last century. In contrast, we found net erosion along a surface runoff pathway through our study site. However, deposition or erosion of sediment is extremely variable spatially, and erosion was confined to the relatively narrow flow path of surface runoff at our sites. At other sites in the forest, there may be little surface flow from the field into the forest, or surface flow may be spread out rather than concentrated along one path. The channeling of suface flow promotes erosion by producing high flow velocities.

Differences among riparian forests clearly affect their nutrient retention properties. The forest of our present study, near Centreville, differs in important ways from one we previously studied (e.g., Peterjohn and Correll, 1984), near the Rhode River. First, the area of corn field draining into the Centreville forest is about 800 m wide, whereas the area draining into the Rhode River forest is about 150 m wide. This suggests greater hydrologic and nutrient loading of the Centreville forest than of the Rhode River forest. Greater hydrologic loading at the Centreville forest may account for the channelization of overland storm flow there. Groundwater flow may be further enhanced at the Centreville forest by the presence of a

thick layer of sandy sediment (Fig. 2) not present at the Rhode River forest. Also, the Centreville forest has two distinct zones, the hill slope and the floodplain (Fig. 2), whereas the Rhode River site lacks a hill slope. These differences may account for the observation that NO_3^- uptake occurred at the field-forest boundary of the Rhode River forest, but did not occur until the edge of the floodplain in the Centreville forest. Despite the differences, both forests seem to remove large amounts of NO_3^- from groundwater, perhaps as a result of lateral flow of groundwater confined near the surface by underlying aquicludes. Functional differences among riparian forests and within zones of particular forests suggest the need for further research to determine the environmental conditions that promote nutrient removal and how commonly such conditions are met.

ACKNOWLEDGMENTS

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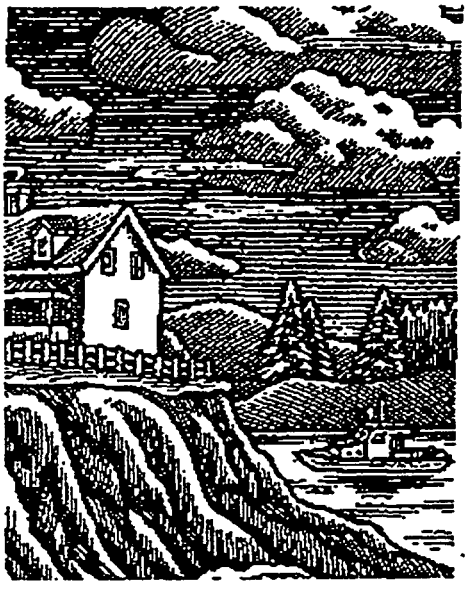
Lakeshore and Streambank Erosion Control



What causes lakeshore and streambank erosion?

Lakeshores and streambanks are areas of dynamic energy. The powerful forces of waves, currents, and ice move soil particles toward, away from, and along the shoreline.

Streams are continually downcutting into their valley, carrying sediments downstream particle by particle. The current moves from side to side, undercutting banks and causing the stream channel to meander.

The ice of frozen lakes can expand shoreward with a force of many tons per square foot, moving most obstacles in its path (including shoreline soil). Masses of ice put in motion by winds or currents can scour the banks of lakes and streams.

Even in quite small inland lakes, breaking waves and nearshore currents can dislodge sediments. Headlands (points) usually have relatively high erosion rates because the waves, currents, and ice attack from all sides and eventually transport the sediments to bays, where they are deposited. Bays are usually the most erosion-resistant areas.

Erosion and the transport and deposition of sediments is a natural process along shorelines. Typically, natural erosional processes proceed very slowly, and the plants and animals that live along the shoreline can adjust to these slow changes, maintaining a stable, healthy, productive ecosystem. When some catastrophic natural or human disturbance causes this equilibrium to be upset, accelerated erosion can result. Examples of natural disturbances include large trees uprooted by a windstorm, or a flood resulting from a torrential rainstorm. Human disturbances include vegetation removal, dredging, filling, or contruction on or near the shoreline.

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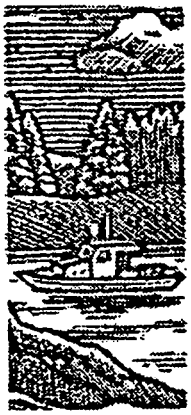
What are the impacts of shoreline erosion?

Eroded soils are, by volume, the greatest pollutant of lakes and streams in the United States. Although most sediment comes from overland erosion throughout a watershed, shoreline erosion contributes its share. In aquatic environments, sediment pollution:

- Degrades aquatic and nearshore land habitats, killing aquatic organisms and negatively impacting birds and animals which depend on aquatic habitats.
- Reduces water clarity, light penetration, and plant productivity.
- Causes warming (which is most serious in cold water trout streams).
- Releases nutrients stimulating undesirable plant and algae growth.
- Affects angling success and fish feeding. spawning, and gill function.
- Changes bottom substrate, reduces channel capacities, and increases flooding.

Shoreline erosion can also cause the loss of valuable waterfront property, including nearshore buildings and other structures.

How do you know if there is a serious erosion problem on your shoreline?



Signs of serious problem situations include:

- A large area of bare soil on a steep, high shoreline bank.
- A noticeable recession of the shoreline over a period of time.
- Leaning or downed trees with exposed roots on the shoreline.
- Large patches of muddy water near a lakeshore, or unusually muddy streams during periods of high water or following a rainstorm.
- Excessive deposits of sand or other sediments on the stream bed, or very wide, shallow areas in a stream.

How can shoreline erosion be controlled?

One of the best ways to control shoreline erosion is through preventive measures. Some basic preventive guidelines include:

- Preserve the rocks and vegetation which naturally occur along the shoreline.
- Prevent impervious surface (i.e. roofs, driveways) runoff from flowing to the shoreline, especially bluff areas.
- Avoid construction within 100 feet of the shoreline or the edge of nearshore bluffs.
- Protect nearshore berms pushed up by ice action along lakeshores. They prevent excessive surface runoff and trap sand which "nourishes" the beach.
- Limit the amount of foot traffic and other recreational activities in erosion prone areas. Regardless of preventive measures, the right combination of conditions (such as high water level, violent windstorms, drastic ice movement, and certain shoreline configurations) may result in serious shoreline erosion.

There are three basic types of reactive shoreline erosion control methods:

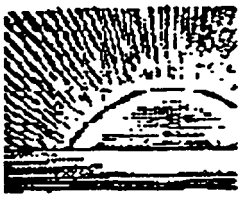
Vegatative: This method involves planting trees or woody shrubs for the soil binding properties of their large root systems, grass and other herbaceous plants to protect against raindrop impact and scouring from surface runoff, or emergent acquatic plants to stabilize bottom sediments and dampen wave action.

Structural: This includes protective structures. The placement of rock of various sizes (referred to as rip-rap) has traditionally been the preferred and most common method. Other structural methods include bulkheads, gabions (rock filled baskets), sandbags filled with concrete, and railroad ties. However, these other methods are often most visually unappealing, require more heavy equipment and technical expertise, and may be more prone to failure in comparision ro simple rip-rap.

Manipulative: Mostly used on streams, this includes removing streamflow obstructions, grading shoreline banks, or, in special circumstances, rerouting the stream channel.

A new technology called soill bioengineering is now being used with good success. Soil bioengineering combines mechanical, biological, and ecological concepts to arrest and prevent shoreline erosion. An example is the planting of willows interspersed with rock rip-rap. The rock provides immediate resistance to erosion. As the willows become established, roots invade and permeate the rock and underlying soil, binding them together into an erosion resistant mass. The willows also impart a more "natural" looks to the shoreline.

Planning an erosional control project



Before beginning any actions to correct erosion, determine why the erosion is occuring. Without understanding the problem, any actions may be a waste of time and money. Decide if the problem is serious enough to warrant correcting. How is the habitat or water qualiuty of the lake or stream being degraded? What are the threats to private property?

Even though there have been numerous studies and publications on this topic, each problem is unique and there are no manuals with generic plans for bank protection projects which are guarunteed to work. Although it may be possible to install a simple erosion control structure by yourself, most techiques have techinacal standards for size, height, shape, underlayment, and placement of structures. It is best to consult with a resource professional familiar with geotechnical engineering when planning the installation of erosion control structures.

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STREAM STABILIZATION PROJECT UNDERWAY AT SITE M

ASHLAND, ILL. -- The Illinois Department of Natural Resources, in cooperation with the Cass County Soil and Water Conservation District and the Natural Resource Conservation Service, is undertaking a unique, long-term stream stabilization and erosion control project at the Site M State Fish and Wildlife Area in Cass County, Natural Resources Director Brent Manning said today.

"Management of the Panther-Cox Creek Watershed, along with construction of a medium-size lake and several smaller lakes, are among our top priorities in protecting and developing Site M," Manning said. "The watershed stabilization work now underway will not only enhance this ecosystem, but will serve as a model for stream and river basin stabilization projects statewide."

Work crews have stabilized several severely degraded segments of Panther and Cox creeks near their confluence in an area located in the northwest corner of Site M.

"When we first surveyed the creeks in 1994, we found that decades of bank slumping and collapse had caused 15 to 20 feet of bank to be lost into the stream," said Jim Mick, Department of Natural Resources Streams Program Administrator. "With the help of our Illinois State Water Survey staff, we chose a restoration technique often used in Canada that virtually rebuilds the creek bed and stream bank, protecting them against future degradation."

The stream stabilization consists of three main components:

-- Installation of in-stream "lunker" structures, large wooden boxes partially buried near the base of the stream bank that stabilize the bank "toes," the lowest portion of the bank where it meets the stream bed. The lunker structures also provide fish habitat and concentrate fish for anglers.

-more-

DNR/2222

-- Grading of the stream bank to reduce slope, and the planting of dormant willow posts to stabilize the upper portion of the bank and, eventually, to provide shade.

-- construction of rock "riffles" in the stream bed, which provide a lasting foundation for the stream bed, help control water flow and prevent further deterioration.

The initial phase of work on the stream stabilization project involved several locations along an 1,800-foot section of Cox and Panther creeks. Project planners hope to do more riffle construction, lunker installation and stream bank stabilization downstream on the creeks in future years as funding

allows.

Stabilization of the Cox and Panther creeks should allow for flooding of traditional floodplain areas in the northern part of

Site M, improving natural species plant growth prospects and wildlife habitat.

The project also includes relocation of the nearby Creek Road and planned construction of a bridge near the low-water ford on Cox Creek. A surfaced trail is to be built to connect a scenic overlook for the project site and the surrounding Cox Creek Hill Prairie Natural Area to the Creek Road equestrian trailhead in the northernmost section of Site M.

Other Site M watershed improvements include riparian floodplain plantings, terracing, riprapping and installation of dry dam berms and other water control structures to reduce cropland erosion.

The Department of Natural Resources and the Illinois Department of Agriculture are cooperating in a multi-year study of soil erosion abatement techniques and sustainable agriculture farm management practices on Site M property. Approximately 5,000 acres out of the 15,574 acres which comprise Site M are being used for agricultural crop production.

The DNR is working with the Department of Agriculture, the Natural Resource Conservation Service, the Cass County Soil and Water Conservation District and neighboring landowners on all elements of the ecosystem-based watershed management and development plan for Site M.

Other projects at Site M underway or due to begin this year include an equestrian campground, scenic driving loop and bicycle trail in the northern portion of the site, improvements to primary access roads and initial work on a 210-acre lake.

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Stabilization of Earth Slopes with Fiber Reinforcement

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Stabilization of Earth Slopes with Fiber Reinforcement

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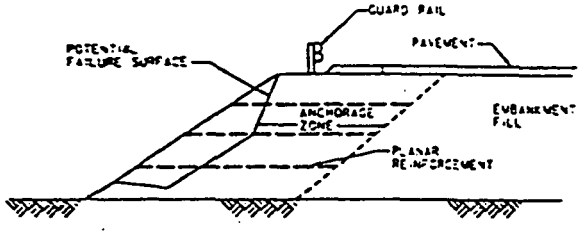
ABSTRACT: The use of fiber reinforcement (geofibers) for stabilization of earth slopes was investigated by laboratory testing of non-reinforced and fiber-reinforced clay soils in the direct shear and triaxial shear apparatus. Fiber contents included 0.2 and 0.25 percent by dry weight for this study. The test results show increases in maximum shear stress (τ') at failure in the range of 20 to 50 percent for the fiber-reinforced specimens. Slope stability analyses were performed for a highway interchange embankment in Beaumont, Texas, USA, which had experienced repeated slope failures. The stability analyses produced an increase in calculated factor of safety from essentially one (imminent failure) for the non-reinforced case, to above 1.5 for the fiber-reinforced case. The slope was repaired with fiber-reinforced soil at a dosage rate of 0.25 percent, and has performed well to date.

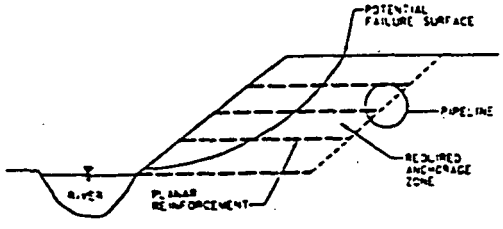
KEYWORDS: Geofibers, Micro-reinforcement, Slope Stabilization, Earth slopes, Factor of Safety

1 INTRODUCTION

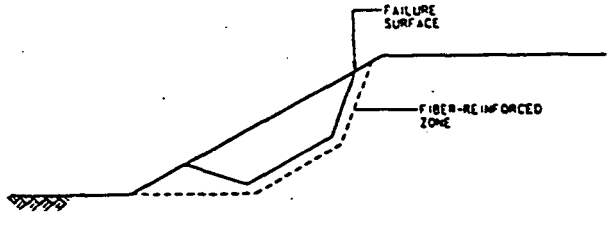
The use of geofibers for earth slope reinforcement has attracted significant interest in the past five years. Geofibers consist of relatively small fiber inclusions, distributed as an additive throughout the soil mass in the reinforced zone. Accordingly, the geofibers may be categorized as micro-reinforcement. Planar or continuous-sheet reinforcement elements, such as geotextiles and geogrids, are placed at discrete locations (usually horizontally) within the soil mass, with non-reinforced soil intervals between. Planar materials may be categorized as macro-reinforcement. Geosynthetic macro-reinforcement materials provide an effective solution to a wide variety of slope reinforcement problems, but have limitations in applications where the required anchorage zone is not available due to obstructions, as illustrated in Figures 1(a) and 1(b). Micro-reinforcement materials do not have these limitations since they reinforce the entire soil mass as a soil additive. The large anchorage zone is not required, and it is only necessary to extend the fiber-reinforced zone approximately 0.3 to 0.6 meters beyond the critical failure surface as illustrated in Figure 1(c). Therefore, micro-reinforcement geofibers can provide ideal solutions to slope stability conditions which previously were not practical with geosynthetics. The geofibers used in this study consisted of fibrillated polypropylene (FIBERGRIDS®, Synthetic Industries, Chattanooga, Tennessee, USA) in nominal 25 mm and 50 mm lengths.



(a) anchorage-zone limitations from highway obstructions



(b) anchorage-zone limitations from pipeline obstructions



(c) large anchorage zone not required for geofibers

Figure 1. Anchorage-zone limitations of planar reinforcement compared to reinforced zone for geofibers.

2 BEAUMONT SLOPE

2.1 Project Description

The highway interchange embankment (Beaumont slope) is located at the intersection of U.S. Highway 69 and F.M. 347 in Beaumont, Texas, USA. The embankment is approximately 6 m in height at the tallest section, and has a slope ratio of 2.5 horizontal to 1 vertical (2.5H:1V) at the steepest section.

The fill soil in the slopes consists of a brown clay with some sand, gravel, and shells. The embankment soil has a liquid limit of 50, and a plastic limit of 17, with 68 percent passing the US No. 200 sieve. The material classifies as fat clay (CH), in accordance with ASTM D 2487. The embankment slopes on the northeast and northwest quadrants of this intersection had experienced repeated slope failures over the years. The failure-surface geometry typically consisted of a near-vertical scarp near the slope crest, a central failure surface about 1.5 to 2 m deep parallel to the slope, with an exit point about 1 to 1.5 m above the toe. These failures were typically repaired by excavating the failed areas and recompacting the same soil back into the

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slope without the use of soil additives or reinforcement. In the fall of 1995 both the northeast and northwest slopes had failed again. The northeast slope was repaired as previously described, without reinforcement or additives. The northwest slope was repaired with geofibers reinforcement. The laboratory testing program, slope stability analyses, and slope repair details are presented in subsequent sections.

2.2 Conceptual Model

A conceptual model was developed of the slope failure mechanism for use in planning the laboratory testing program and slope stability analyses. Embankment slopes of clay soils, with height ranges of 6 to 10 m and slope ratios in the range of 2.5H:1V to 3H:1V, often experience shallow failures within a few years after construction. The compacted soils initially have relatively high shear strength values throughout, and may have a significant level of preconsolidation stress induced by the compaction process.

Slope stability analyses using the "as compacted" shear strength properties do not predict the shallow failures. From these analyses, it is apparent that the initial as-compacted shear strengths deteriorate with time in the shallow zone. The strength loss is caused by a number of factors such as desiccation, shrink-swell, water infiltration, and down-hill creep. The principal author has investigated a large number of shallow slope failures in clay soils. The loss of shear strength is not uniform throughout the shallow zone. Three distinct soil zones are usually present, consisting of a weak zone along the failure surface, a weathered zone above the failure surface, and the relatively undisturbed zone below the failure surface. The actual failure surface may be less than 10 mm thick in many cases. The material in the thin failure zone is usually of a soft, paste-like consistency, with a high moisture content. This zone has obviously lost the preconsolidation stress induced during the compaction process, and has degraded to a normally-consolidated condition at the shallow overburden pressure. Consequently, under effective-stress conditions, the soil in the failure zone will have c' = 0. The principal author has found similar thin, paste-like weak zones paralleling the surface at depths of about 1.5 to 2 m in adjacent embankments which had not experienced slope failures, but which later failed. Accordingly, it is believed that the weak normally-consolidated zone is created prior to actual failure by the weathering processes previously discussed, and by stress concentrations at the base of the weathered zone due to down-hill creep. The weathered soil in the zone above the failure surface generally contains many desiccation cracks and secondary weathering features, and the soil mass in this zone has a substantially lower shear strength than when initially compacted. However, this zone may still retain some long-term cohesion, and will exhibit a higher mass shear strength than the failure zone. The embankment soil below the failure surface in the deeper zone may remain relatively undisturbed and retain most or all of its initial shear strength. The laboratory testing program and slope stability analyses were performed in a manner consistent with the three distinct soil zones.

3 LABORATORY TESTING PROGRAM

3.1 Sample Preparation and Testing

The laboratory testing program included non-reinforced (control) and fiber-reinforced soil specimens. The direct shear tests were performed as consolidated-drained (CD) tests, and included nominal 100-mm and 300-mm square specimens, and the ICU triaxial tests were performed on nominal 70 mm-diameter by 150 mm-length specimens. The direct shear tests included specimens prepared by standard compaction methods (95 percent ASTM D 698), and slurry-processed normally-consolidated (SPNC) specimens. All triaxial tests for this study were performed on specimens prepared by standard compaction methods. A consolidation test was also performed on a compacted specimen of the Beaumont clay, to determine the preconsolidation stress induced by the compaction process. The preconsolidation value was used in interpreting the direct shear test results.

The SPNC specimens were prepared by blending the soil in a mixer with sufficient water to form a thick slurry. The slurry was then partially consolidated in a 150-mm diameter CBR apparatus under approximately 70 percent of the normal stress to be used in the direct shear device. Following a consolidation period of about 24 hours, the sample reached a thick paste-like consistency, at which time it was removed from the CBR apparatus and trimmed into a 100-mm square shear box for testing. The remainder of the consolidation stage was completed in the direct shear machine, with the final consolidation stress equal to the normal stress to be used during the shear test. The normal stress range was selected to represent conditions along the actual failure surface in the slope. This procedure assured that the specimen would be normally consolidated during the test, to model the condition along the actual failure surface. Standard-compaction specimens were prepared using a controlled weight-volume relationship and static compaction techniques. The reinforced specimens were prepared by mixing the fibers and soil in a heavy-duty 19-liter mixer. Detailed descriptions of the sample preparation methods are available in a design guide for fiber-reinforced slopes (Gregory 1996).

3.2 Test Results

A total of 86 direct shear specimens and 32 triaxial shear specimens of clay soils were tested for this study. Twenty-one of the direct shear specimens were tested in the 300 mm square shear device, and the remainder were tested in the 100 mm square shear device. Twenty of the direct shear specimens and 12 of the triaxial shear specimens were performed for the Beaumont slope project. The remainder of the tests were performed for other slope projects or for research purposes.

Direct shear test results performed on 12 specimens of the Beaumont clay are presented on shear stress-normal stress plots in Figure 2. These tests were performed in a 100 mm square by 30 mm deep shear box. The geofibers were 25 mm in length for the reinforced specimens. The strain rate was 0.0076 mm/minute for all direct shear tests.

Figure 2 contains results for 8 specimens prepared with standard compaction methods. Figure 2 (a) was plotted using a bilinear fit. The first three points on each envelope have normal stress values below the preconsolidation stress induced by compaction (P_{cc}), and the fourth point is above the P_{cc} value. Clay soils during shearing, with normal stresses below the preconsolidation stress, may exhibit significant effective cohesion (c'), while those with normal stress values above the preconsolidation value exhibit c' = 0 (Gregory and Doane, 1996). Accordingly, the strength envelopes in Figure 2(a) were fit with a bilinear line to obtain shear strength parameters in both the preconsolidated and normally consolidated (NC) ranges of normal stress. The test results show an increase of approximately 35 percent in c' for the reinforced specimens compared to the non-reinforced.

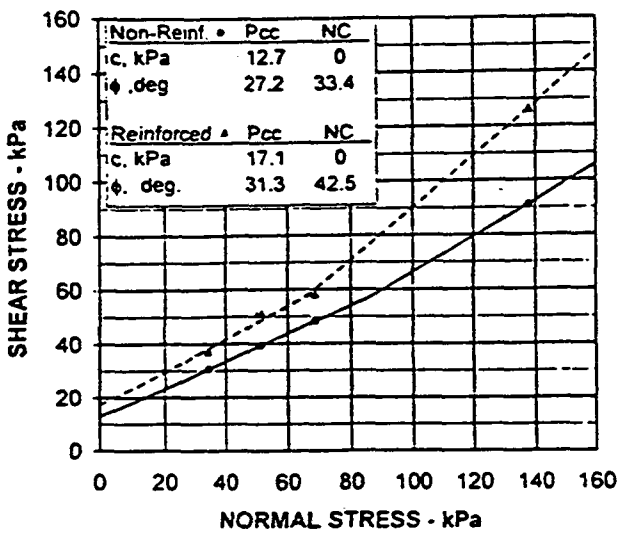
Increases in ϕ' were 15 and 27 percent, respectively, for the preconsolidated and NC ranges of normal stress.

Figure 2(b) contains results performed on 6 specimens prepared by SPNC methods. The results in this figure were plotted with a linear fit since all specimens were normally consolidated during the tests. These results show an increase in ϕ' of 33 percent for the reinforced specimens compared to the non-reinforced. Triaxial shear test results performed on 6 specimens of the Beaumont clay are presented in Figure 3. These specimens were prepared using standard compaction methods, and were performed as ICU tests, with pore-pressure measurements. A strain rate of 0.015 mm/minute was used for these tests.

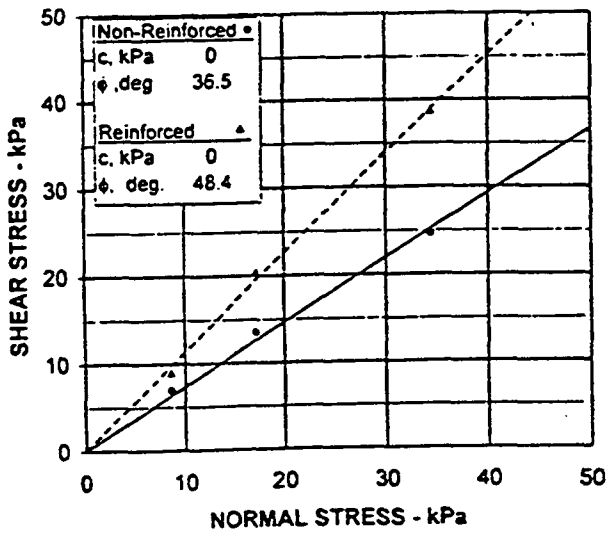
Figure 3(a) contains the results of three non-reinforced specimens plotted on a mohr-coulomb shear stress-normal stress diagram. Figure 3(b) contains the results of three specimens reinforced with 0.25 percent, 25 mm-long fibers. The test results on the specimens reinforced with 25 mm-long fibers in Figure 3(b) show an increase in ϕ' of 16.5 percent, and an increase in c' of 8.5 percent, when compared to the control test results.

Four mechanisms are believed to be involved in the increased shear strength of fiber-reinforced soil. These mechanisms are : (1) friction between individual fibers and the surrounding soil, (2) adhesion between individual fibers and the surrounding soil, in soils exhibiting significant cohesion properties, (3) micro-bearing capacity of the soil mobilized during pull-out resistance of looped fibers crossing the shear plane, and (4) increased localized normal stress in the soil across the shear surface resulting from the pull-out resistance of the fibers during shearing of the soil. The individual interaction and contribution of these mechanisms to the apparent increase in shear strength is complex and difficult to determine accurately. However, the combined effects, including any synergistic effects, is relatively easy to determine by conducting shear strength tests on both non-reinforced and reinforced specimens, as was performed for this study.

A summary of average direct shear and triaxial shear test results from all specimens tested during this study is presented in Table 1.

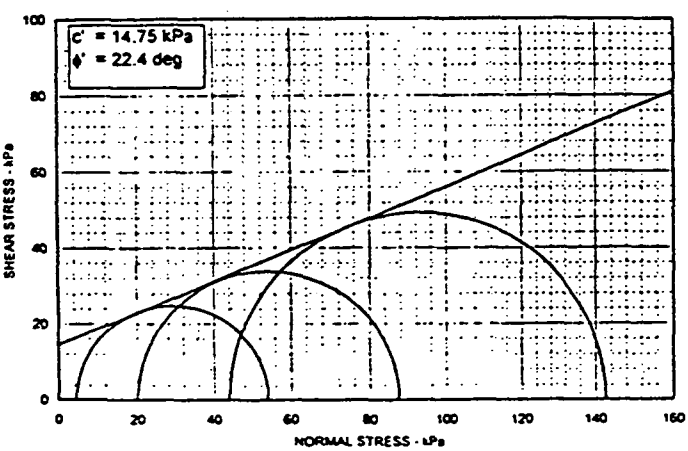


(a) Standard Compaction

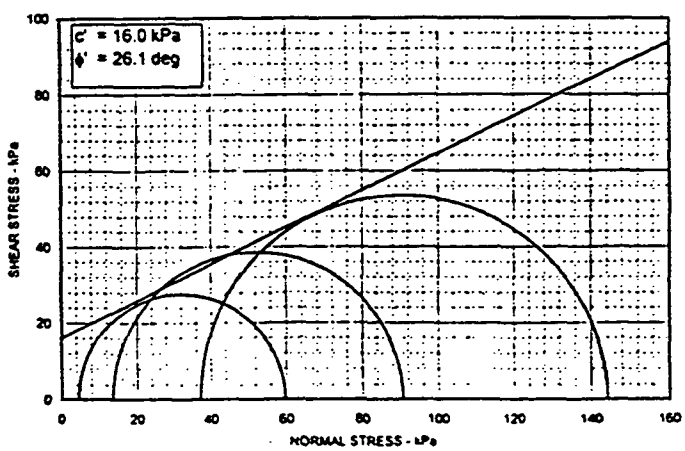


(b) SPNC Preparation

Figure 2. Direct shear test results on 100 mm Specimens.



(a) Non-reinforced Specimens



(b) Reinforced Specimens

Figure 3. Triaxial test results on 70mm diameter specimens.

Table 1. Summary of Direct Shear and Triaxial Shear Test Results (Average values, including 0.2 and 0.25 % fibers)

Test Description	Number of Specimens	ϕ' (Deg.)	c' (kPa)
Direct Shear – 100mm Non-Reinforced	25	32.6	6.6
Direct Shear – 100mm Reinforced – 25mm Fibers	40	38.0	10.0
Direct Shear – 300mm Non-Reinforced	6	27.7	3.1
Direct Shear – 300mm Reinforced – 25mm Fibers	9	27.3	6.7
Direct Shear – 300mm Reinforced – 50mm Fibers	6	22.8	9.5
Triaxial Shear Non-Reinforced	9	22.0	14.8
Triaxial Shear Reinforced – 25mm Fibers	16	24.4	15.9
Triaxial Shear Reinforced – 50mm Fibers	7	30.8	15.4

It should be understood that the results in Table 1 are average values, based upon a range of fat clay (CH) and lean clay (CL) soils tested for this study. The averages for the direct shear tests in the 100mm device show increases of approximately 17 percent and 52 percent in ϕ' and c', respectively, for the reinforced specimens. The averages for the direct shear tests in the 300mm device show essentially the same ϕ' values, and an increase in c' values of 116 percent for the specimens reinforced with 25mm fibers. The average results from the 300mm direct shear device also show a decrease of 21 percent in ϕ' values and an increase of 206 percent in c' values for the specimens reinforced with 50mm fibers. The triaxial shear test average results show an increase in ϕ' values of 11 percent and an increase in c' values of 7 percent for the specimens reinforced with 25mm fibers. The average triaxial results with the 50mm fibers show an increase of 40 percent in ϕ' values, and an increase of 4 percent in c' values. In all cases where one shear strength parameter increased only a small amount or decreased slightly, the other parameter increased by a relatively large amount. Averaging the results in Table 1 for all clay types tested resulted in considerably more scatter than was observed for each individual soil type tested.

4 SLOPE STABILITY ANALYSES

4.1 Slope Geometry

The geometry of the existing slope, slide geometry, and subsurface stratigraphy were obtained from observations and measurements in the field, and from existing data and a new soil boring provided by the Texas Department of Transportation (TxDOT).

4.2 Soil Parameters

The soil parameters were obtained from the laboratory test results, adjusted in accordance with local practice. The unit weight values for the in situ soils were obtained from thin-wall tube samples taken from the boring. The unit weight values of the compacted soils were taken as 95 percent of maximum density as determined by ASTM D 698. Soil shear-strength parameters selected for the analyses are presented in Table 2. The labels and soil type numbers match those on the graphical output sheets from the computer analyses, presented in subsequent sections. The unit weight values are not included in Table 2, in order to conserve space. Unit weight values of 18.9 and 20.9 KN/m^3 were used for moist and saturated unit weights, respectively.

4.3 Analysis Methodology

Slope stability analyses of the Beaumont slope were performed using the computer program GSTABL7, an enhanced version of PCSTABL6 (Humphrey and Holtz, 1986), modified by the principal author. The limit equilibrium method, using a sliding-block search routine and the Modified Janbu method (Janbu 1954, 1973), was used in the analyses.

Table 2. Soil Parameters Selected for the Stability Analyses

Label	Soil type No.	c' (kPa)	ϕ' (Degrees)
Analysis of Initial Failure (Non-Reinforced)			
Surface-CH clay	1	9.3	24
Shoulder-CH clay	2	9.3	24
Weak-CH clay (failure surface)	3	0.0	32
Fill-CH clay	4	11.1	24
Base-CH clay	5	11.1	24
Deep-CH clay	6	11.1	24
Analysis of Repaired Slope (Fiber-Reinforced)			
Surface-CH clay	1	10.2	24
Shoulder-CH clay	2	10.2	24
Weak-CH clay (failure surface)	3	0.0	42
Fill-CH clay	4	11.1	24
Base-CH clay	5	11.1	24
Deep-CH clay	6	11.1	24

The shear strength of the failure surface zone (Weak-CH clay) was obtained from the direct shear test results on the SPNC specimens. The shear strength of the undisturbed embankment fill (Fill-CH clay) below the failure surface and in the protected shoulder of the roadway was obtained from the direct shear test results on the specimens prepared with standard compaction methods. In accordance with local practice and experience with similar soils, the ϕ' and c' values obtained in the tests were reduced by approximately 12 percent for use in the analyses, to account for uncertainties in stratigraphic distribution and construction quality control.

The shear strength of the surficial soil in the weathered zone (Surface-CH clay) above the failure surface cannot be obtained readily with laboratory tests. Samples taken from this zone will not be representative of the desiccation cracks and secondary weathering features throughout the soil mass. However, the apparent shear strength of the weathered zone may be obtained by computer analyses, using the known data.

The shear strength values of the failure-surface and undisturbed-fill zones are known from laboratory test results. The geometry of the failure surface is known from observations and measurements in the field, following failure. It is also known that the stability factor of safety (resisting forces and moments divided by the driving forces and moments) for the slope at the time of failure was one or slightly below one. Therefore, stability analyses of the failed slope can be performed with the known shear strengths of the failure-surface and undisturbed fill zones, and an initial estimate of the mass shear strength parameters in the weathered zone. An iterative analysis can then be performed by changing the estimated shear strength

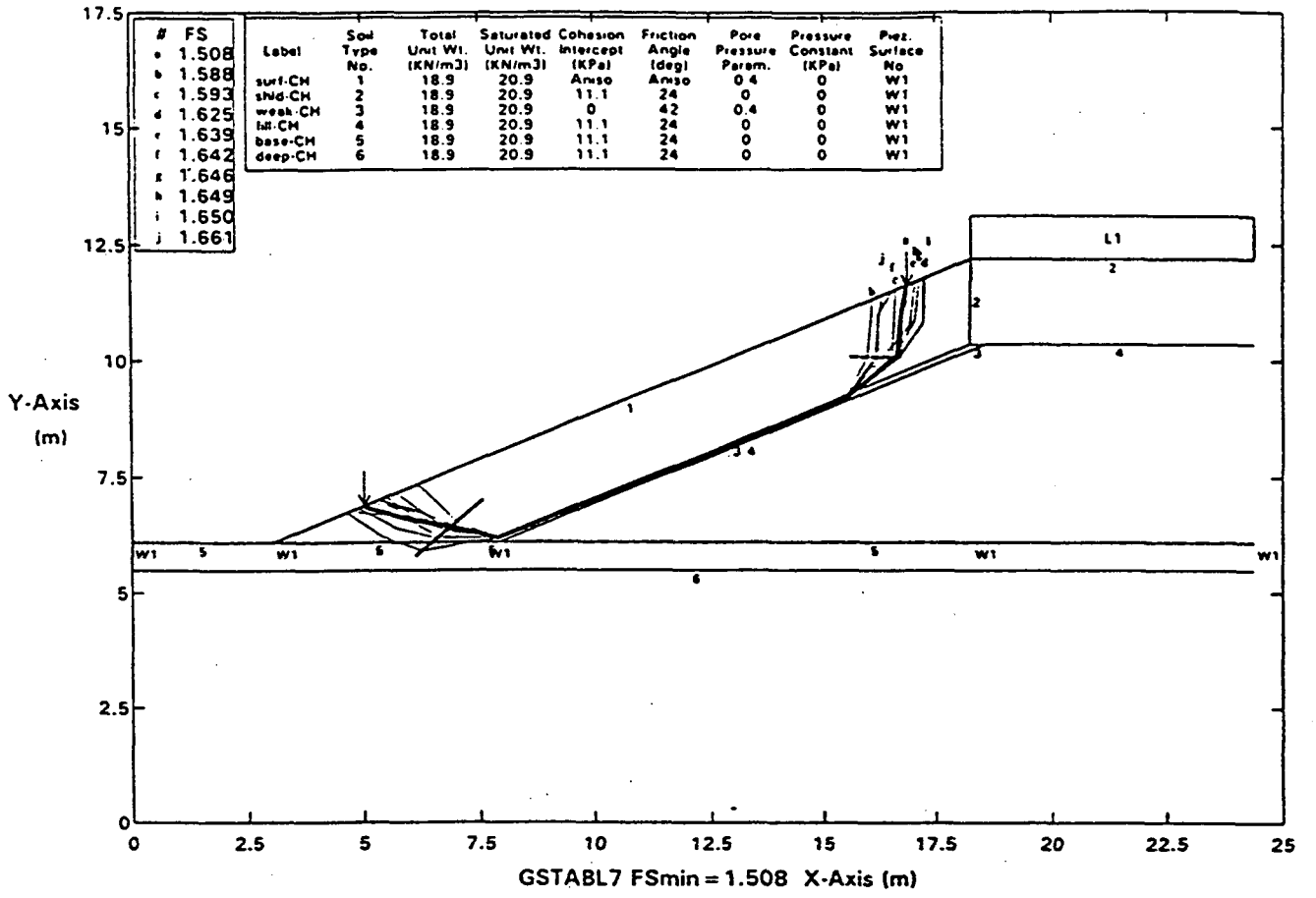


Figure 4. Graphical Computer output for the fiber-reinforced slope analysis.

parameters in each successive run until the calculated factor of safety converges to one or slightly below one. The changes in strength parameters can generally be applied uniformly to both ϕ' and c'. It has been found from experience that a good initial estimate of the shear strength parameters for the weathered zone is approximately 50 percent of those of the undisturbed fill zone.

The mass shear strength of the fiber-reinforced weathered zone may be determined as follows. Assume that the ratio of the shear strength of the reinforced weathered zone to the shear strength of the fiber-reinforced laboratory specimens, is the same as the ratio of the shear strength of the non-reinforced weathered zone to the shear strength of the non-reinforced laboratory specimens. The shear strength of the non-reinforced weathered zone to be used in the ratio comparisons is the value determined in the iterative analyses discussed previously. This approach provides rational values of shear strength parameters in all soil zones, for both the initial failure condition and fiber-reinforced slope condition.

The stability analyses were performed using the sliding-block search routine by forcing the trial failure surfaces to pass through the failure zone parallel to the slope, while allowing the trial surfaces to exit near the upper and lower ends of the slope in a more random manner. The weathered zone was assigned anisotropic properties in the analyses, with zero shear strength within zones plus or minus 10 degrees from vertical, to model tension cracks. The failure-surface zone was modeled as 150 mm thick for convenience in the analyses, although it is much thinner in the actual slope. For each analysis run, 110 trial failure surfaces were evaluated. The results of the slope stability analysis for the fiber-reinforced slope are presented in Figure 4 for illustration purposes. The initial failure analysis is not shown to conserve space. The 10 most critical (with respect to calculated factor of safety) trial failure surfaces are plotted in the figure. The most critical trial failure surface is shown with the heavy line. The failure surfaces are labeled with lower case letters, in ascending order of calculated factor of safety. The soil types are numbered below each boundary. The highway traffic loading at the top of the slope was included as a uniformly distributed load with an intensity of 9.6 kPa, and is shown on the figure by the designation L1. The ground-water surface detected in the boring is shown near the toe elevation with the designation w1. The ground-water surface and soil zones below the failure-surface zone were not used in the shallow failure analyses, but were used in a deep-seated global analysis performed for this slope, but not included in this study.

The slope stability analyses show an increase in calculated factor of safety from 1.007 (imminent failure) for the initial failure to 1.508 for the repaired, fiber-reinforced slope. This

is an increase in calculated factor of safety of approximately 50 percent due to the geofiber inclusion.

5 CONSTRUCTION AND PERFORMANCE

5.1 Construction

The slope was repaired in late November of 1995 in general accordance with the assumptions made in the analyses. The area was prepared by excavating the failed area approximately 0.6 m below the primary failure surface. The excavated soil was spread in approximately 200 mm-thick loose lifts prior to compaction. Geofibers were spread at the calculated dosage rate of 0.25 percent by dry weight of soil, and each lift was processed and the 25 mm-length fibers mixed into the soil with a minimum of three passes of a roto-till pulverizing mixer of the type commonly used in lime-subgrade stabilization. Each lift was compacted to approximately 95 percent of maximum dry density at a moisture in the general range of optimum to 5 percentage points wet of optimum in accordance with ASTM D 698. The fill was placed in essentially horizontal lifts.

5.2 Performance

The fiber-reinforced northwest slope has performed well to date. No additional signs of movement have been observed. The northeast slope at the same interchange was repaired without fiber reinforcement approximately six weeks prior to the northwest slope. The non-reinforced slope has again failed.

6 ADDITIONAL PROJECTS

The authors have been involved in more than 10 slope projects on which geofibers were utilized for slope repair and stabilization. These projects have included roadway embankments, pipeline embankments adjacent to rivers or creeks, and an earth-fill dam. One of the pipeline projects involved the use of geofibers for deep-seated stability, as well as shallow stability. The oldest installation of geofibers on these projects was completed approximately six years ago. Most of the other projects were completed within the past three years. These installations have performed well. A detailed discussion of these projects is not possible due to space limitations.

7 CONCLUSIONS

The use of geofibers for earth slope reinforcement was investigated by laboratory testing of non-reinforced and fiber-reinforced specimens of compacted clay soils. A highway embankment slope in Beaumont, Texas, USA, was used as the primary case study. Extensive slope stability analyses were performed for the initial failure and fiber-reinforced slope conditions. The factor of safety was increased from essentially one at the initial failure condition, to approximately 1.5 for the repaired slope using the same soil reinforced with geofibers.

Increases in effective shear strength (τ') in the range of 20 to 50 percent due to geofibers inclusion were observed for [illegible]dy, based upon ϕ' and c' increases from laboratory [illegible]d the slope geometries considered. Similar increases in shear-strength parameters using fiber reinforcement have been reported by other researchers (Maher and Ho 1994, Alwahab and Al-Ourna 1995, Nataraj and McManis 1997). Additional research and development of analysis methods for the reinforcement mechanisms and influence of fiber properties are needed. Ranjan, et al (1996) performed a study of these influences and proposed a model for analysis of fiber-reinforced cohesionless soils.

Based upon the results of this study, observation of actual installations of fiber-reinforced slopes, and research performed by others, the geofibers are a viable and cost effective method for slope repair using micro-reinforcement where macro-reinforcement elements may not be practical due to space limitations for the anchorage zone. The geofibers can provide solutions to an entire class of slope problems which were not previously practical with geosynthetics.

Additional research is desirable using a broader range of fiber lengths and soil types. Standardization of laboratory testing and analysis methods is needed. Additional case histories are needed, and are expected to occur at an accelerated rate due to the increased use of geofibers.

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"REINFORCED SLOPES USING GEOTEXTILE – FIBERS COMPOSITE"

BY

Garry H. Gregory, P.E. [1]

ABSTRACT: Planar geosynthetics such as high-strength geotextiles and geogrids have been in widespread use as earth slope reinforcement for more than a decade. The use of these materials in slope applications has been highly successful. Common practice has been to provide primary reinforcement in discrete layers throughout the reinforced zone, with shorter, intermittent layers of the planar reinforcement placed between the primary layers at the slope face to act as secondary reinforcement. The primary reinforcement provides overall stability, while the intended purpose of the secondary reinforcement is to reduce raveling and mini-failures of the slope face between the primary reinforcement layers. However, in many cases the secondary reinforcement does not effectively reduce the raveling and mini-failures long term. This has resulted in significantly increased maintenance costs on many projects. Until recently, no viable solution for this problem was available. Within the past seven years, short geosynthetic fibers (*Geofibers®*) have been successfully used on more than 25 slope projects in the United States. These projects have involved repairs of shallow slope failures, repair of deep-seated slope failures, and veneer reinforcement in new slope construction to reduce future maintenance costs. These fibers also have tremendous potential for use as veneer and secondary reinforcement in geotextile – fibers composite reinforcement of slopes. This combination of geosynthetics has the potential to virtually eliminate any significant future maintenance problems due to raveling and mini-failures at the slope face, for properly designed reinforced embankments. Brief case histories of slopes constructed using fiber-reinforced soil, and design examples using high-strength geotextile – fibers composite are discussed.

INTRODUCTION

Planar reinforcement materials, such as geogrids and high-strength geotextiles, provide an effective solution to a broad range of slope stability applications. The planar material provides "macro-reinforcement" by adding tensile strength to the soil-reinforcement composite at the discrete reinforcement locations. The vertical spacing of the primary geotextile layers has typically been in the range of 2 to 5 feet for many slope applications. It is more efficient to increase the vertical spacing of the primary geotextile for taller slopes. It is desirable to maintain a similar spacing ratio S/H (geotextile to slope height ratio), for each different height slope. However, as the slope height becomes taller, the driving forces become greater, so it is also desirable to gradually decrease the spacing ratio for taller slopes. This can be efficiently achieved by use of equation (1) below (Gregory, 1995).

$$S = \ln H + 0.05H \qquad (1)$$

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Where S equals the geotextile vertical spacing and H equals the total slope height. As a practical matter, the spacing calculated using equation (1) should be rounded to the nearest lift thickness in the embankment. Equation (1) results in a 5-foot vertical spacing for a 30-foot slope height, as used in the example slope discussed later.

Common practice has been to supplement the primary planar reinforcement layers with short, intermediate "secondary" reinforcement layers in a attempt to prevent raveling and mini-failures of the slope face between primary layers. In many cases, especially on steeper slopes, the secondary reinforcement layers have not prevented long-term raveling and mini-failures. This has resulted in large on-going maintenance costs on many projects. While the use of planar reinforcement has been a tremendous solution to steep slope stability problems, the long-term deterioration of the slope face between primary reinforcement layers has resulted in the lack of a complete solution. The dilemma has been how many secondary layers should be placed between primary layers. There is a practical limit on the number due to constructability as well as cost considerations. In any case, the secondary reinforcement is still macro-reinforcement and results in non-reinforced intervals at the slope face.

GEOTEXTILE-FIBERS COMPOSITE

About seven years ago, short (1 to 2 inch) geosynthetic fibers became commercially available for soil reinforcement purposes. Since that time, more than 25 slopes have been successfully reinforced with fibers in the United States. These projects have included highway embankments, riverbanks, general earth embankments, and a major earth dam. These fibers are mixed into the entire soil mass in the reinforced zone, as a soil additive. Accordingly, the fibers provide micro-reinforcement by reinforcing the soil throughout, not just in discrete layers. A 2-inch long fiber, for example, requires only 1-inch for full anchorage, whereas planar reinforcement materials may require 2 feet or more for the anchorage zone. The fiber reinforcement increases the shear strength of the soil by resistance to pullout across the shear plane. Large increases in shear strength can be achieved with economical amounts of fiber additive (Gregory and Chill, 1998). It is should be immediately apparent that a combination of the planar reinforcement and fibers (geotextile-fibers composite) has the potential of providing a very efficient, effective, long-term solution to slope reinforcement problems. The combination of the macro-reinforcement function of the geotextile in the primary zone, and the micro-reinforcement function of the fibers in the secondary veneer zone, can provide a synergistic, virtually complete solution, which was not previously available. The use of geotextile-fibers composite is illustrated in the following example slope.

EXAMPLE SLOPE ANALYSIS

An example slope was selected for analysis for illustration purposes. The slope has the following characteristics.

- 30 feet tall, 1.5H:1V slope ratio
- Gravelly, clayey sand (SC) fill, raw soil ϕ = 35.9 degrees (actual test results)
- Primary Geotextile: $T_{allowable}$ = 1,500 lb/ft
- Fiber Reinforcement = 2-inch long, 360 denier polypropylene fibrillated fibers
- Fiber-Reinforced soil with 0.2 percent fibers, ϕ = 45.1 degrees (actual test results)

- Fiber-Reinforced soil with 0.4 percent fibers, ϕ = 53.9 degrees (actual test results)

The actual laboratory triaxial shear test results on the non-reinforced (control) soil and fiber-reinforced soil, are presented on the attached test-result summary plate. All shear strength values should be understood to be effective stress values. The geometry of the example slope is presented on the attached Example Embankment Slope plate. The various slope stability analyses are shown in graphical form on the attached plates, and discussed below. The actual graphical computer output plates are attached at the end of the paper for reference purposes. All slope stability analyses were performed with the computer program GSTABL7, developed by the Author from the original STABL6 by Purdue University. The Modified Bishop Method (Bishop, 1955) was used in the analyses.

Non-Reinforced Slope

The non-reinforced slope analysis indicates a shallow failure with a calculated factor of safety (FS) of 1.109, considerably below the required 1.5. This condition requires reinforcement for stability.

Geotextile-Reinforced Slope

In this analysis, a vertical spacing of 5 feet was selected for the geotextile, using equation (1). The analysis was iterated with various lengths of geotextile until the critical failure surface was pushed back into the slope far enough to achieve a FS just above 1.5. The required effective length of geotextile was 18 feet to achieve a calculated FS of 1.512. It should be noted that the geotextile length shown on the analysis plates is the *effective* length. The total length must include the required anchorage length, which is not shown on the plates. This analysis does not consider the raveling and mini-failures on the slope face.

Geotextile-Fiber Reinforced Slope with 0.2 Percent Fibers

This analysis includes a 5-foot thick (perpendicular to slope face) fiber-reinforced zone for secondary and veneer reinforcement, along with the geotextile primary reinforcement. The analyses were again iterated based upon geotextile length until a calculated FS of 1.513 was achieved with a 16.5-foot length of geotextile. This is a reduction of 1.5 feet in required effective length of the geotextile.

Geotextile-Fiber Reinforced Slope with 0.4 Percent Fibers

The 5-foot thick fiber-reinforced zone was also included in this analysis, except the shear strength representative of the 0.4 percent fibers was used. A geotextile length of only 12.5 feet was required to achieve a calculated FS of 1.517. This represents a reduction of 5.5 feet in required effective length of the geotextile.

Truncated Slope Surface Zone Analysis with Primary Geotextile Only

This analysis is for a truncated section of the slope to evaluate the potential for raveling and mini-failures between the primary geotextile layers. This analysis assumes that there is no secondary planar reinforcement and no fiber-reinforced zone. The calculated FS for this condition is 1.092, significantly below the required 1.5. Accordingly, as expected, secondary reinforcement is required.

Truncated Slope Surface Zone Analysis with Primary and Secondary Geotextile- 5 ft Zone

This analysis considers the stability of the entire 5-foot zone between primary geotextile layers, with an intermediate secondary geotextile layer, but without fiber reinforcement. As would be expected, the calculated FS for the entire 5-foot zone is well above 1.5, at 1.886.

Truncated Slope Surface Zone Analysis with Primary and Secondary Geotextile – 2.5 ft Zone

The geometry for this analysis is the same as for the previous analysis, except the search zone was forced into the non-reinforced zone between the primary and secondary geotextile reinforcement. The calculated FS is 1.388, which is substantially below the required 1.5. Although the FS is comfortably above one, over the long term, with surface saturation, down-hill creep, and weathering, the raveling and mini-failures are likely to occur (Desi, et al, 1995; Gregory, 1998; Sowers, 1979).

Truncated Slope Surface Zone Analysis with Primary Geotextile and 0.2 Percent Fibers

In this analysis, the primary geotextile is included without the secondary geotextile, but with the fiber-reinforced veneer zone for secondary reinforcement. The calculated FS is 1.684, well above the required 1.5, and can be expected to have long-term stability with low maintenance costs. If the fiber zone was reinforced with the 0.4 percent fibers, the FS would obviously increase significantly, but the FS with the 0.2 percent is fully adequate for secondary reinforcement purposes.

SUMMARY AND CONCLUSIONS

Short geosynthetic fibers have proven to be very effective in stabilization of more than 25 slopes in the US in recent years. These same fibers have tremendous potential in combination with planar reinforcement, for providing a long-term, virtually complete solution to steep slope stability problems. The example slope analysis included in this paper has indicated that the required effective length of the primary planar reinforcement may be reduced when used in combination with the fibers, and the planar secondary reinforcement can be eliminated. The fiber-reinforced veneer zone can provide full secondary reinforcement over the entire zone between the primary reinforcement layers, and in many cases may reduce the required length of the primary layers. The geotextile-fibers composite approach can provide project owners with a viable, long-term cost-effective solution for steep slopes, which previously was not available. Additional research, testing, and actual case histories are needed to further refine the geotextile-fibers composite solution.

APPENDIX: REFERENCES

Bishop, A.W., 1955. "The Use of the Slip Circle in the Stability Analysis of Slopes," *Geotechnique, 5(1)*, London, England, 7-17.

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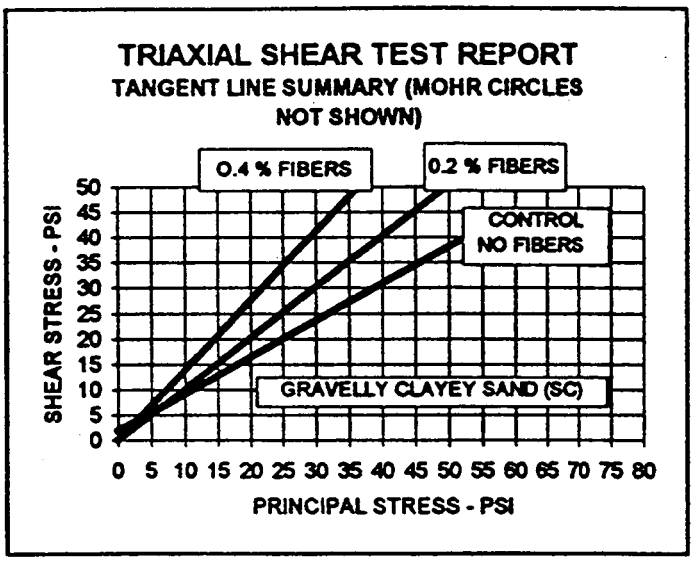
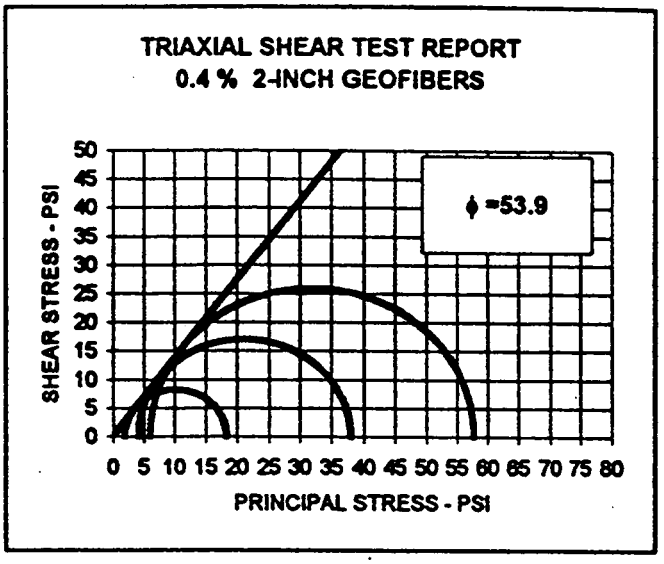
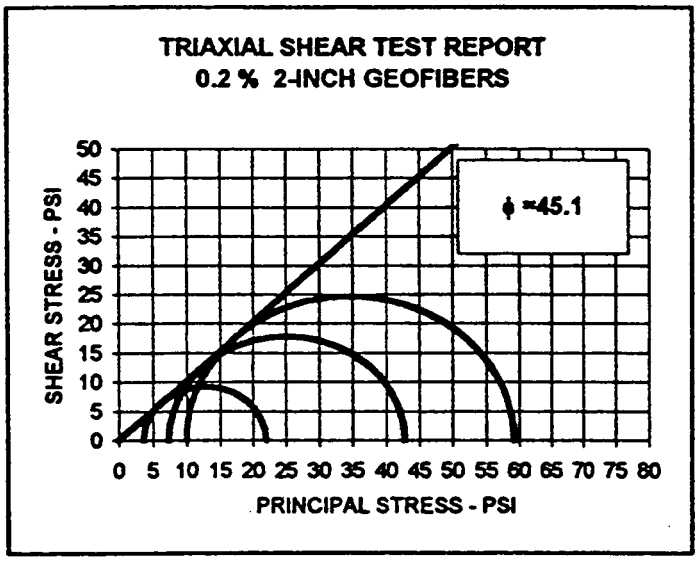
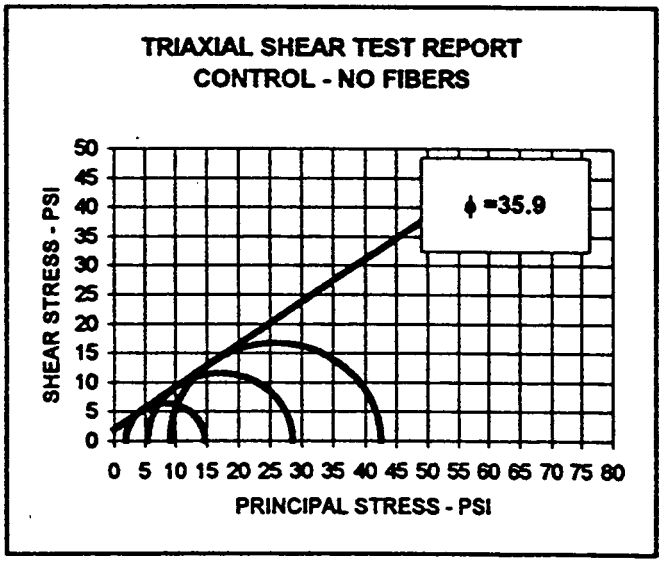
Sowers, George F., 1979. "Introductory Soil Mechanics and Foundations: Geotechnical Engineering," Macmillian Publishing Company, Fourth Edition.









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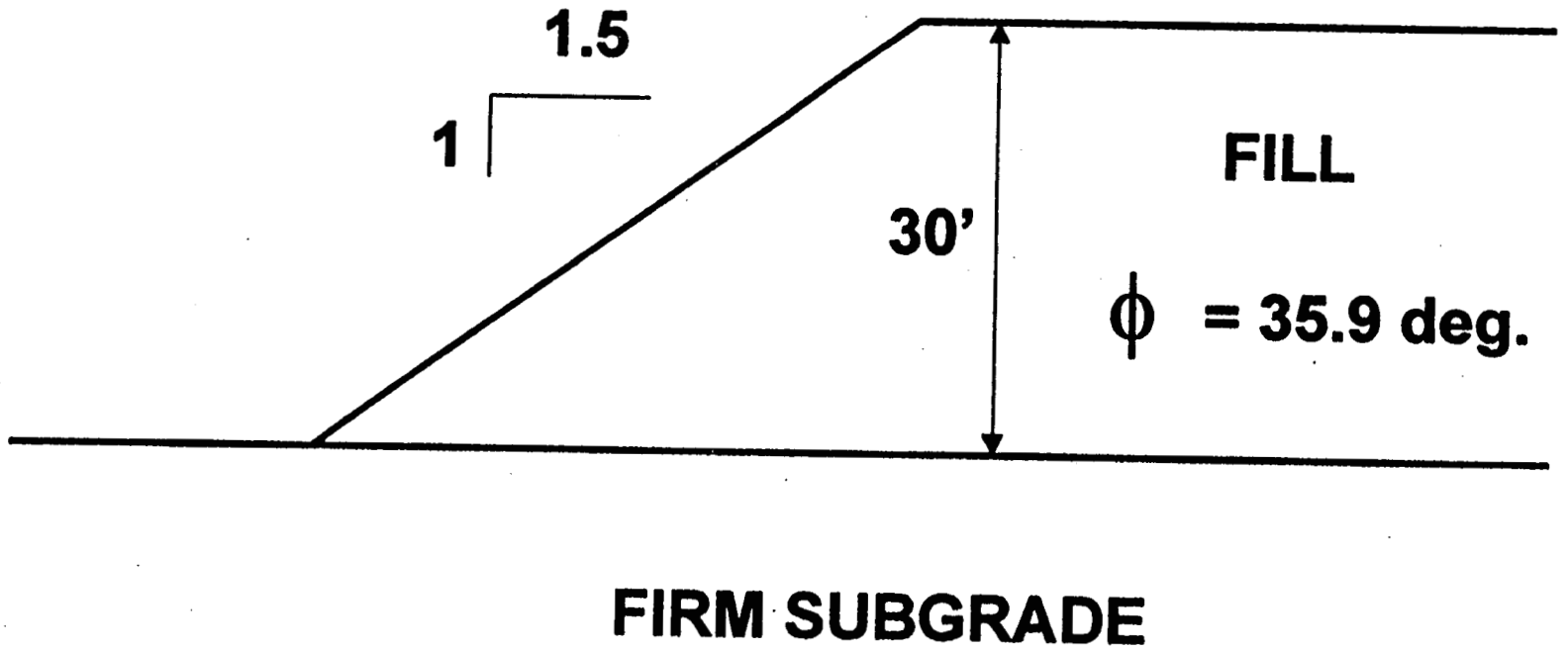
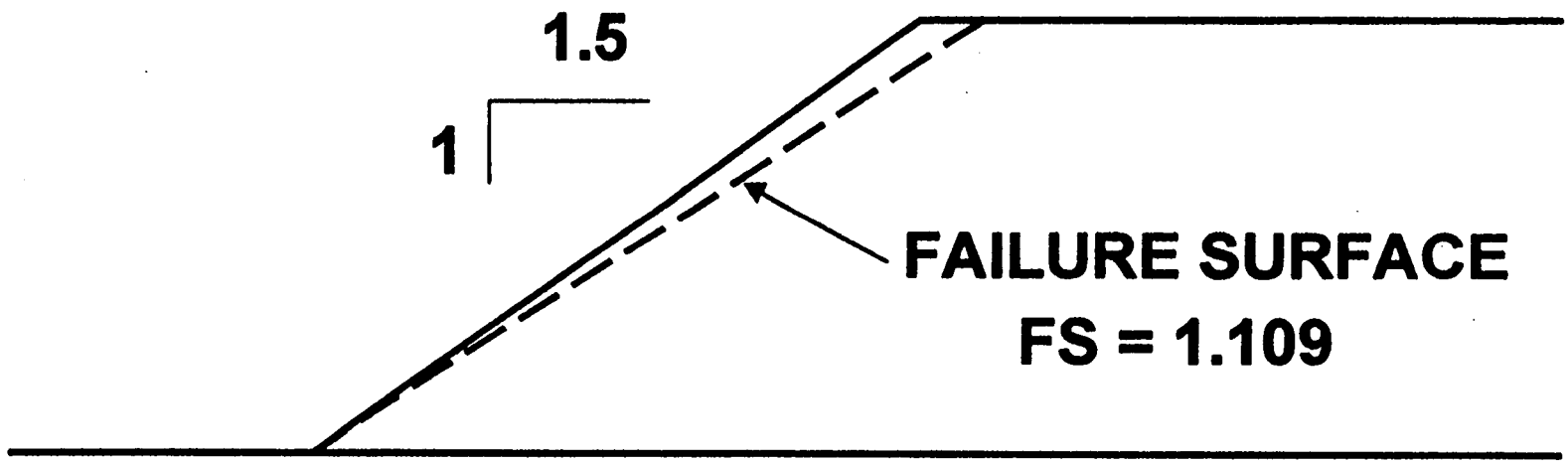
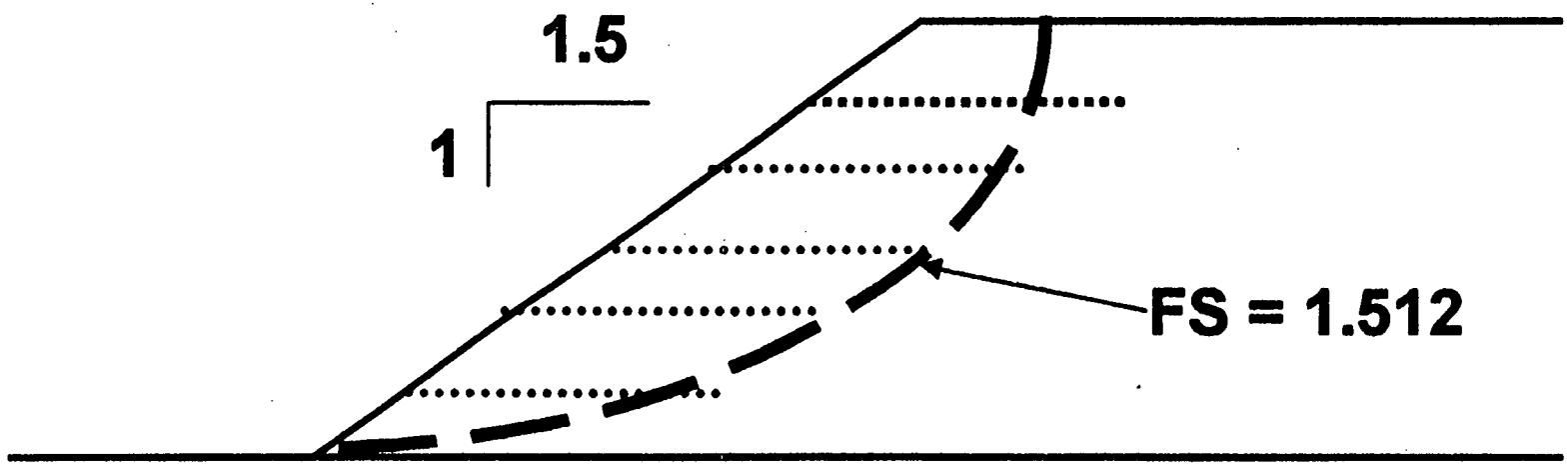
EXAMPLE EMBANKMENT SLOPE



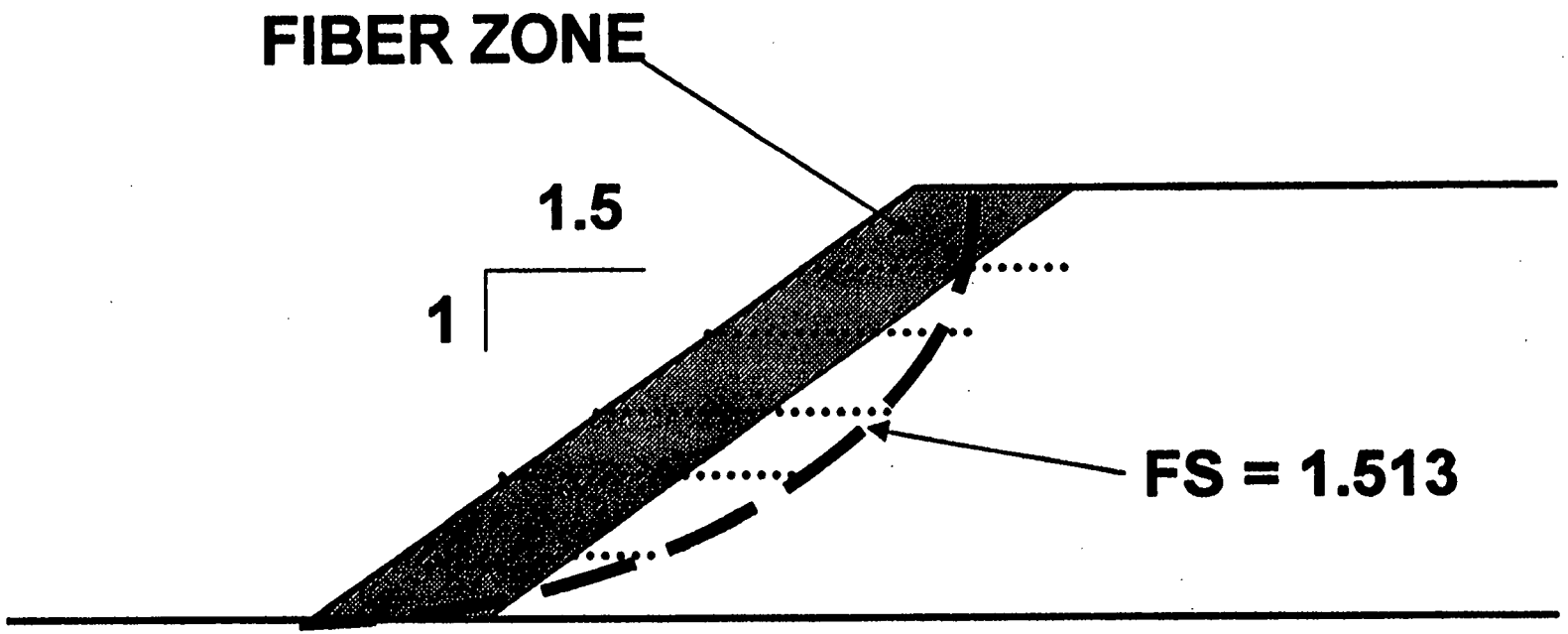
NON - REINFORCED SLOPE



GEOTEXTILE - REINFORCED SLOPE
18 FT LENGTH - 5 FT SPACING

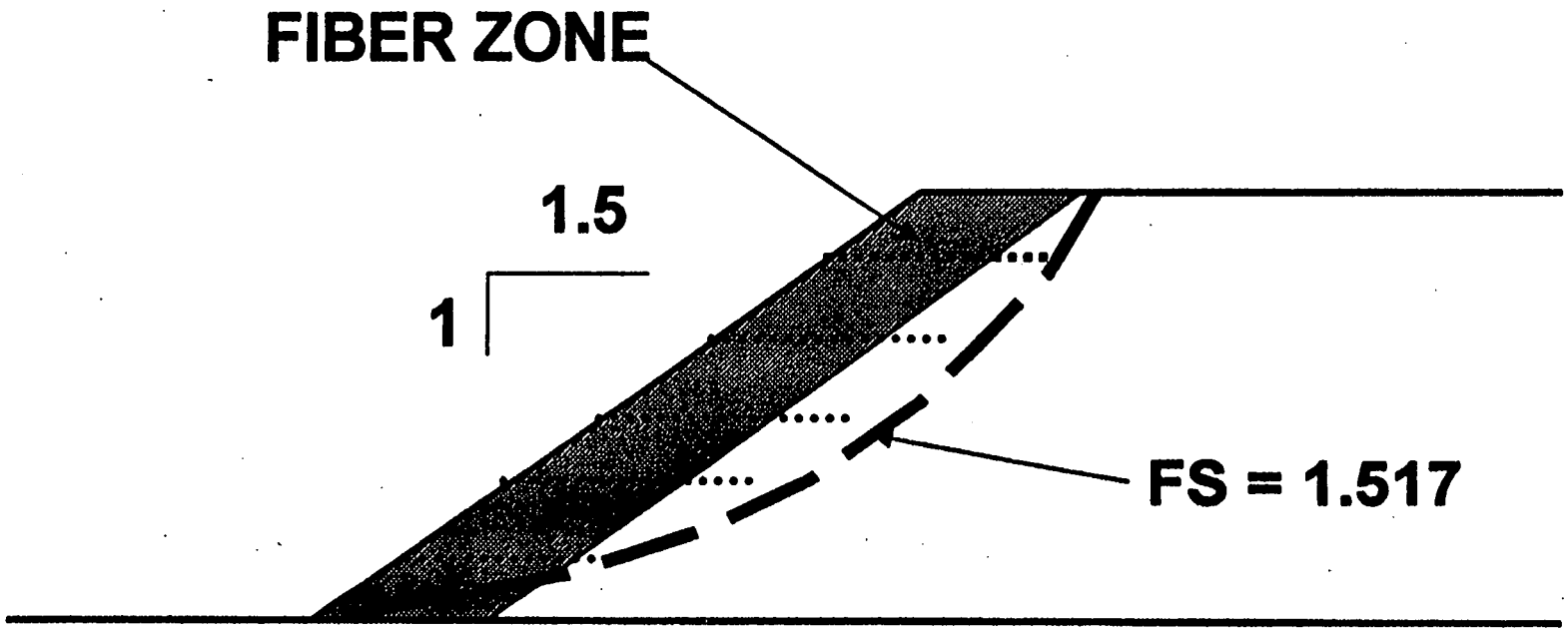


GEOTEXTILE - FIBER REINFORCED SLOPE
16.5 FT GEOTEXTILE & 0.2% FIBERS

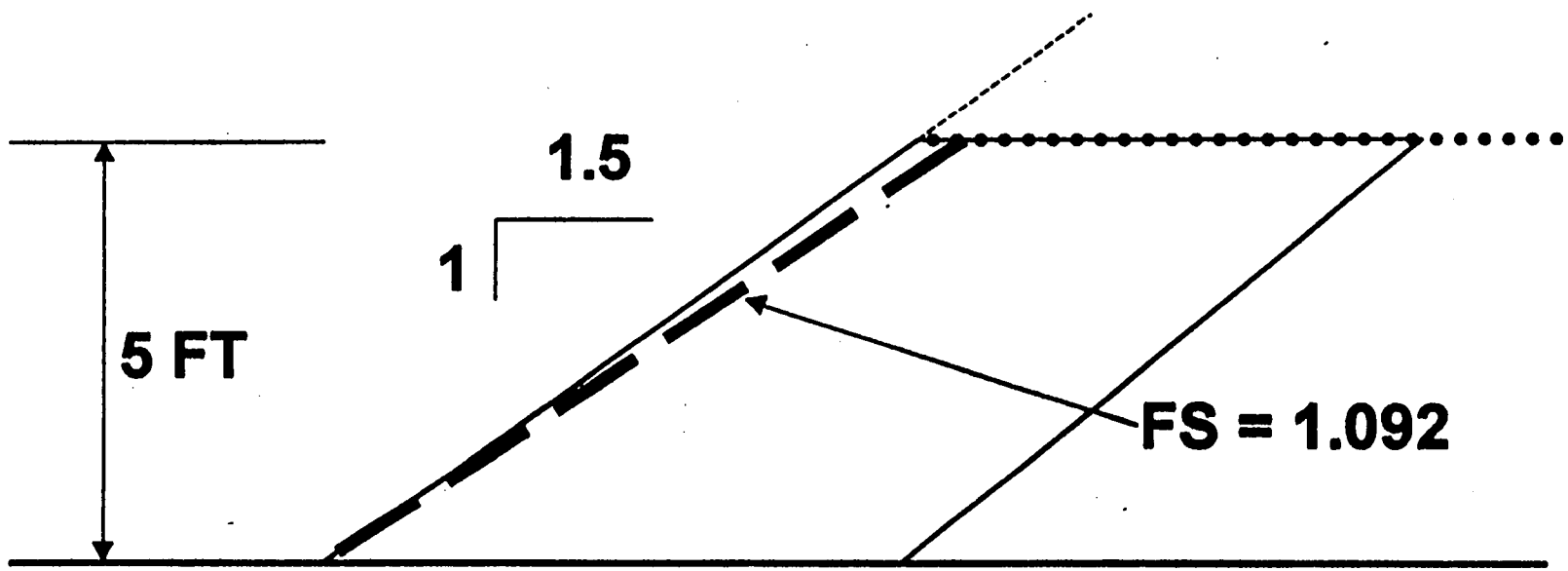


000228

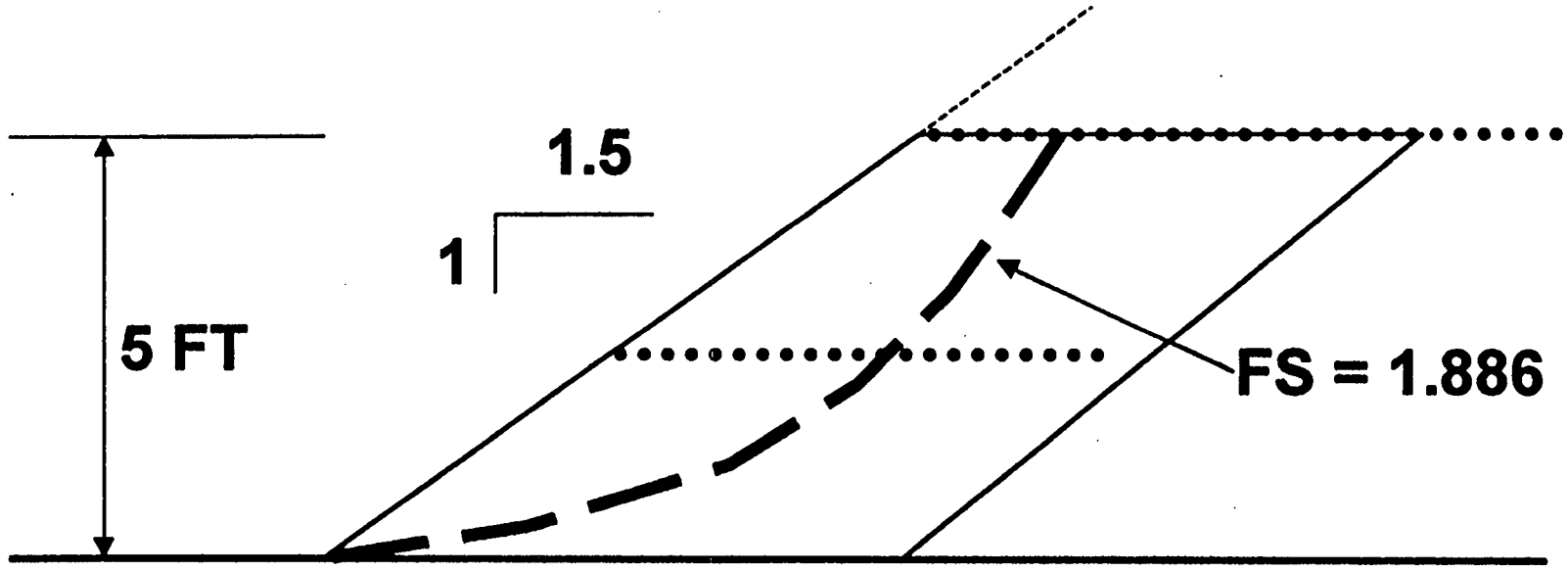
GEOTEXTILE - FIBER REINFORCED SLOPE
12.5 FT GEOTEXTILE & 0.4% FIBERS



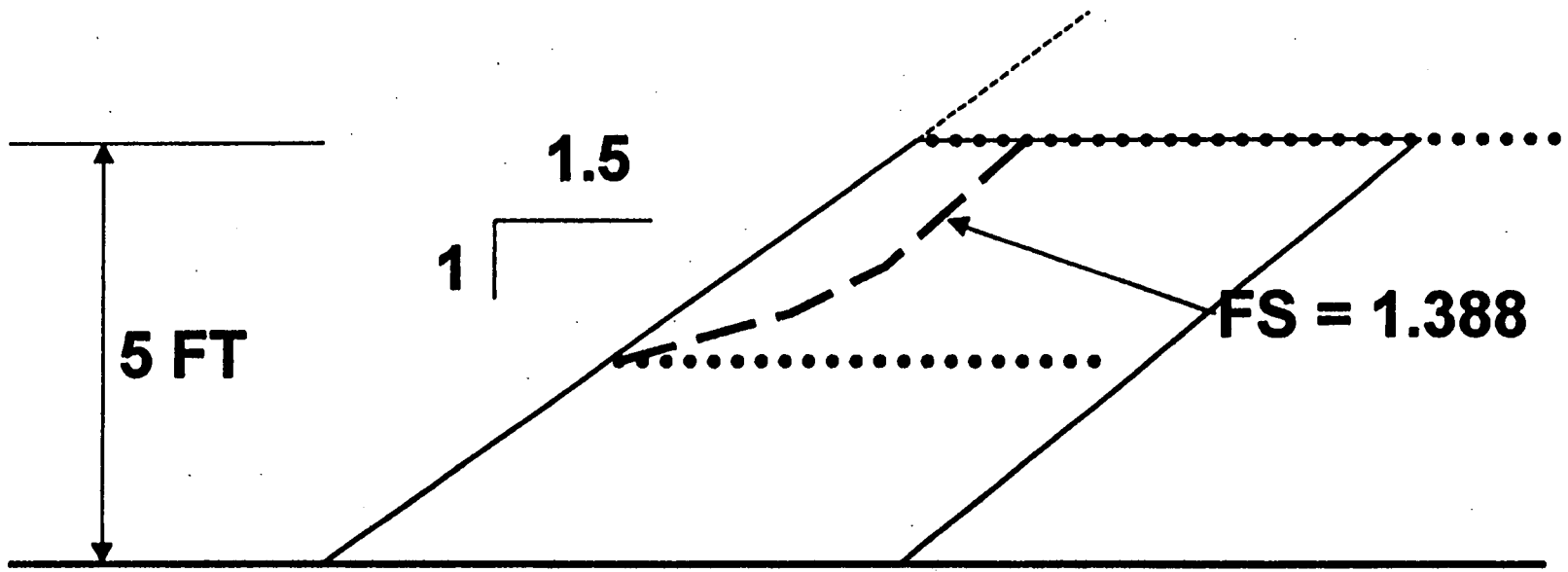
TRUNCATED SLOPE SURFACE ZONE
PRIMARY GEOTEXTILE ONLY



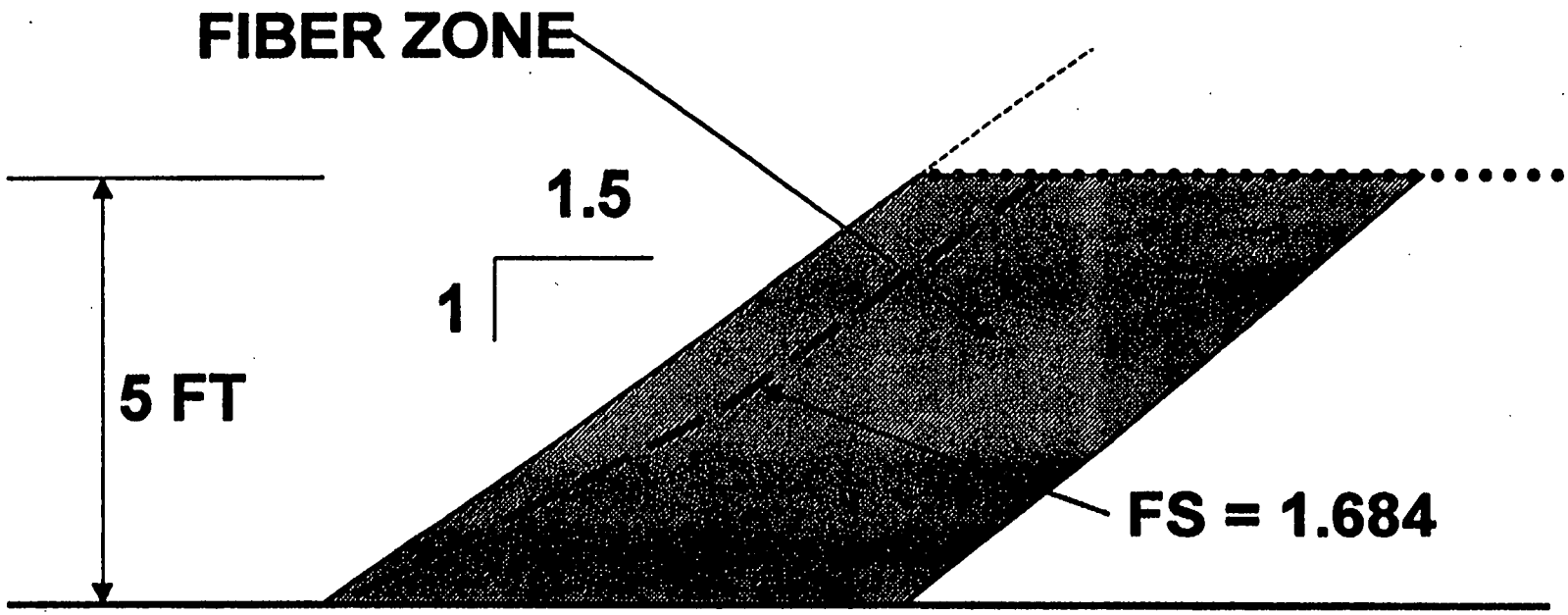
TRUNCATED SLOPE SURFACE ZONE
PRIMARY & SECONDARY GEOTEXTILE



TRUNCATED SLOPE SURFACE ZONE
PRIMARY & SECONDARY GEOTEXTILE

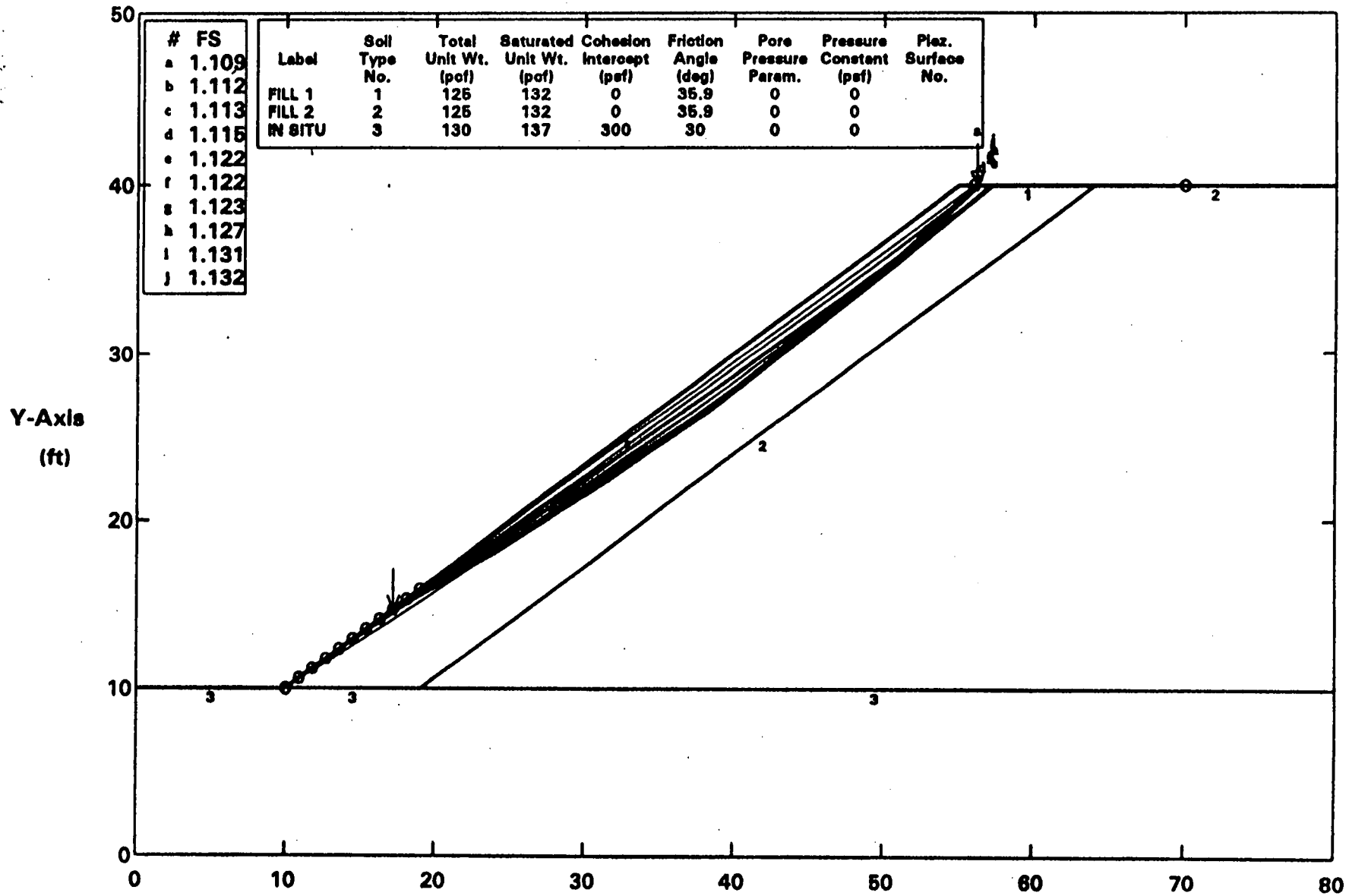


TRUNCATED SLOPE SURFACE ZONE
PRIMARY GEOTEXTILE & 0.2% FIBERS



NON-REINFORCED SLOPE - LONG TERM

Ten Most Critical. C:GTFI.PLT By: GHG



#	FS
a	1.109
b	1.112
c	1.113
d	1.115
e	1.122
f	1.122
g	1.123
h	1.127
i	1.131
j	1.132

Label	Soil Type No.	Total Unit Wt. (pcf)	Saturated Unit Wt. (pcf)	Cohesion Intercept (psf)	Friction Angle (deg)	Pore Pressure Param.	Pressure Constant (psf)	Piez. Surface No.
FILL 1	1	125	132	0	35.9	0	0	
FILL 2	2	125	132	0	35.9	0	0	
IN SITU	3	130	137	300	30	0	0	

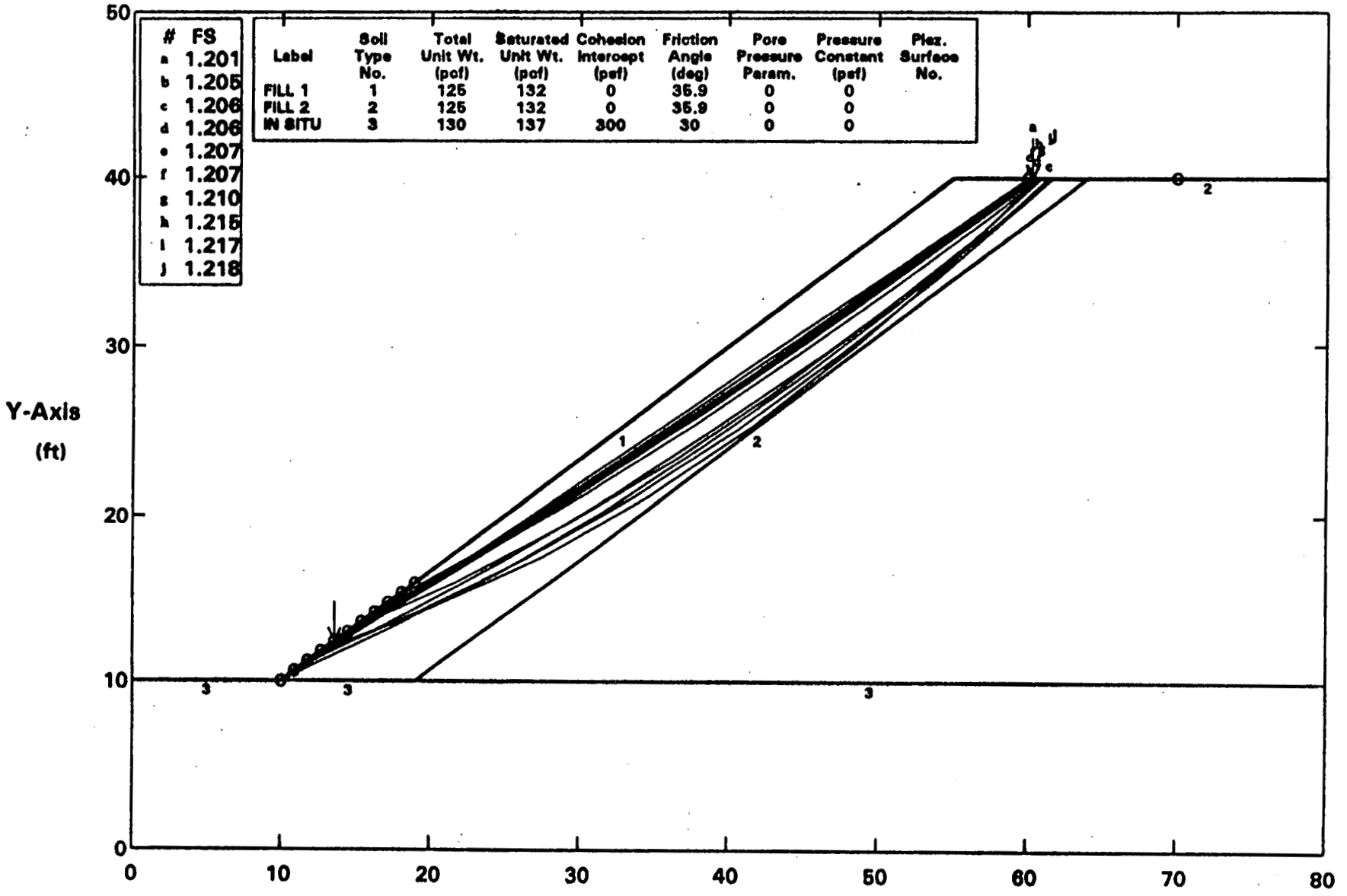
GSTABL7 FSmin = 1.109 X-Axis (ft)

Factors Of Safety Calculated By The Modified Bishop Method

000234

NON-REINFORCED SLOPE - LONG TERM

Ten Most Critical. C:GTFI1.PLT By: GHG



Label	Soil Type No.	Total Unit Wt. (pcf)	Saturated Unit Wt. (pcf)	Cohesion Intercept (psf)	Friction Angle (deg)	Pore Pressure Param.	Pressure Constant (psf)	Piez. Surface No.
FILL 1	1	125	132	0	35.9	0	0	
FILL 2	2	125	132	0	35.9	0	0	
IN SITU	3	130	137	300	30	0	0	

GSTABL7 FSmin = 1.201 X-Axis (ft)

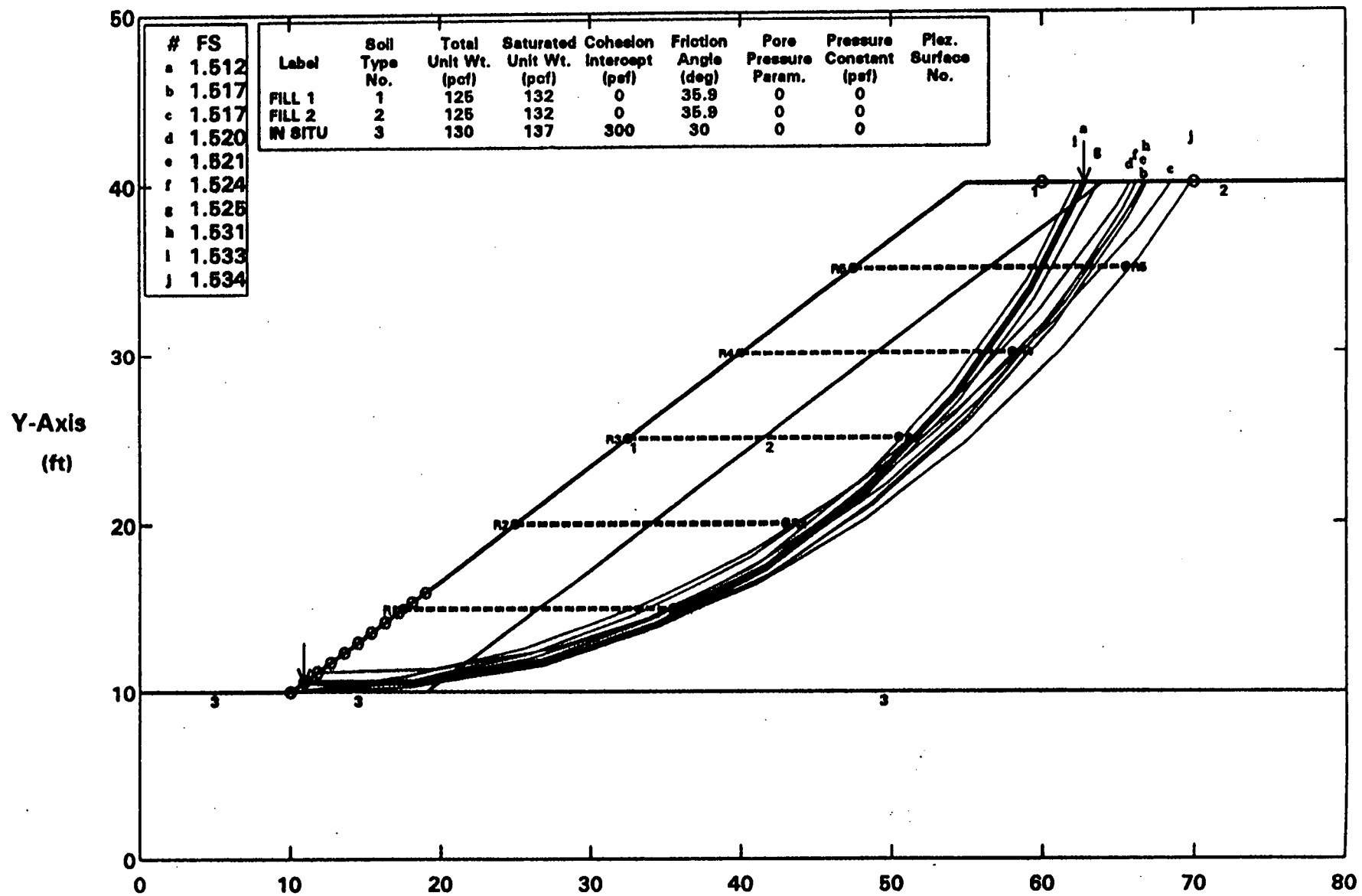
Factors Of Safety Calculated By The Modified Bishop Method

000235

3610

GEOTEXTILE-REINFORCED SLOPE - LONG TERM 18 FT GEOTEXTILE

Ten Most Critical. C:GTFI2.PLT By: GHG



#	FS
a	1.512
b	1.517
c	1.517
d	1.520
e	1.521
f	1.524
g	1.525
h	1.531
i	1.533
j	1.534

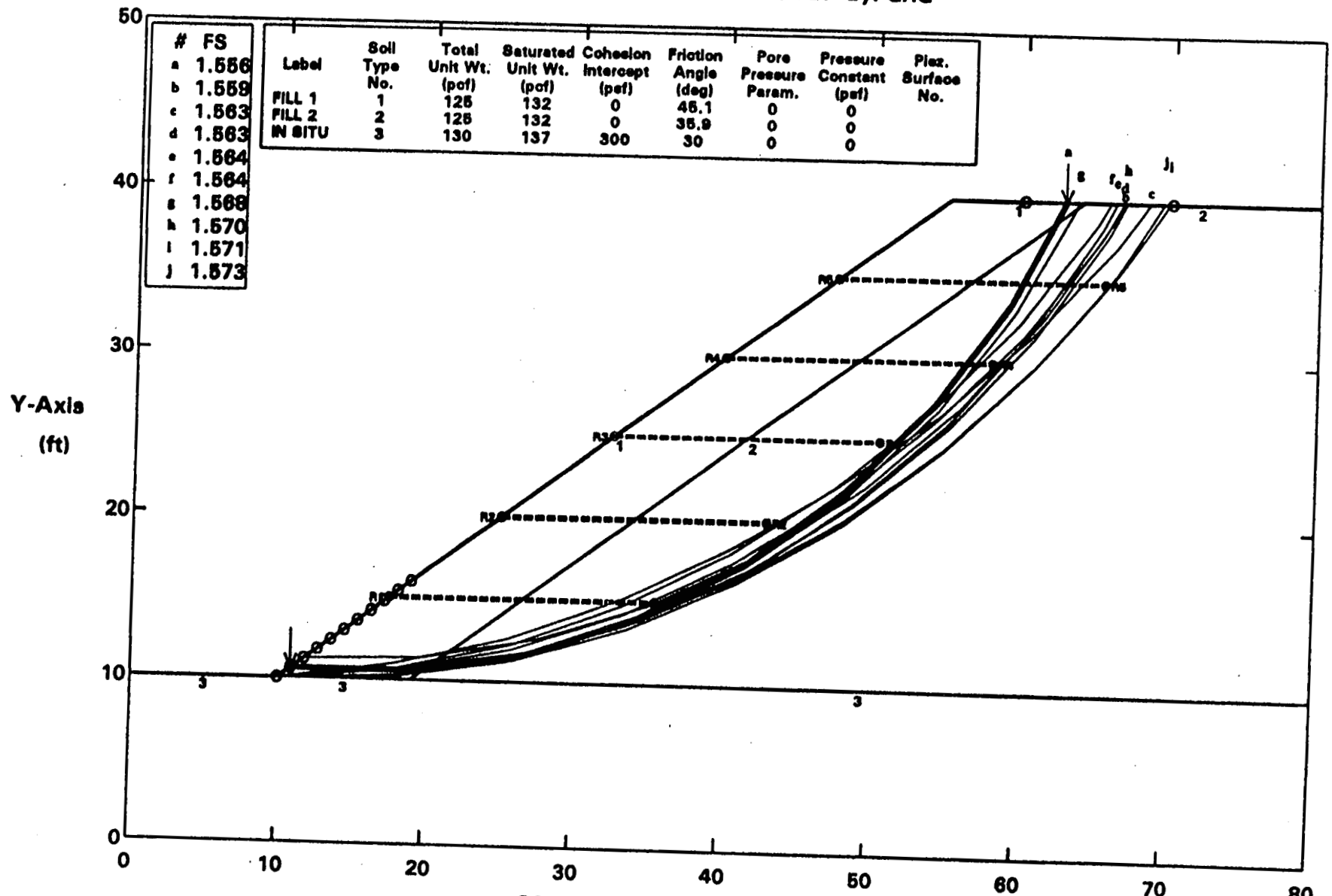
Label	Soil Type No.	Total Unit Wt. (pcf)	Saturated Unit Wt. (pcf)	Cohesion Intercept (psf)	Friction Angle (deg)	Pore Pressure Param.	Pressure Constant (psf)	Piez. Surface No.
FILL 1	1	125	132	0	35.9	0	0	
FILL 2	2	125	132	0	35.9	0	0	
IN SITU	3	130	137	300	30	0	0	

GSTABL7 FSmin = 1.512 X-Axis (ft)

Factors Of Safety Calculated By The Modified Bishop Method

000236

GEOTEXTILE-FIBER REINFORCED SL[illegible]- LONG TERM - 18 FT GEOTEXTILE & 0.2% FIBERS
Ten Most Critical. C:GTFI3.PLT By: GHG



#	FS
a	1.556
b	1.559
c	1.563
d	1.563
e	1.564
f	1.564
g	1.568
h	1.570
i	1.571
j	1.573

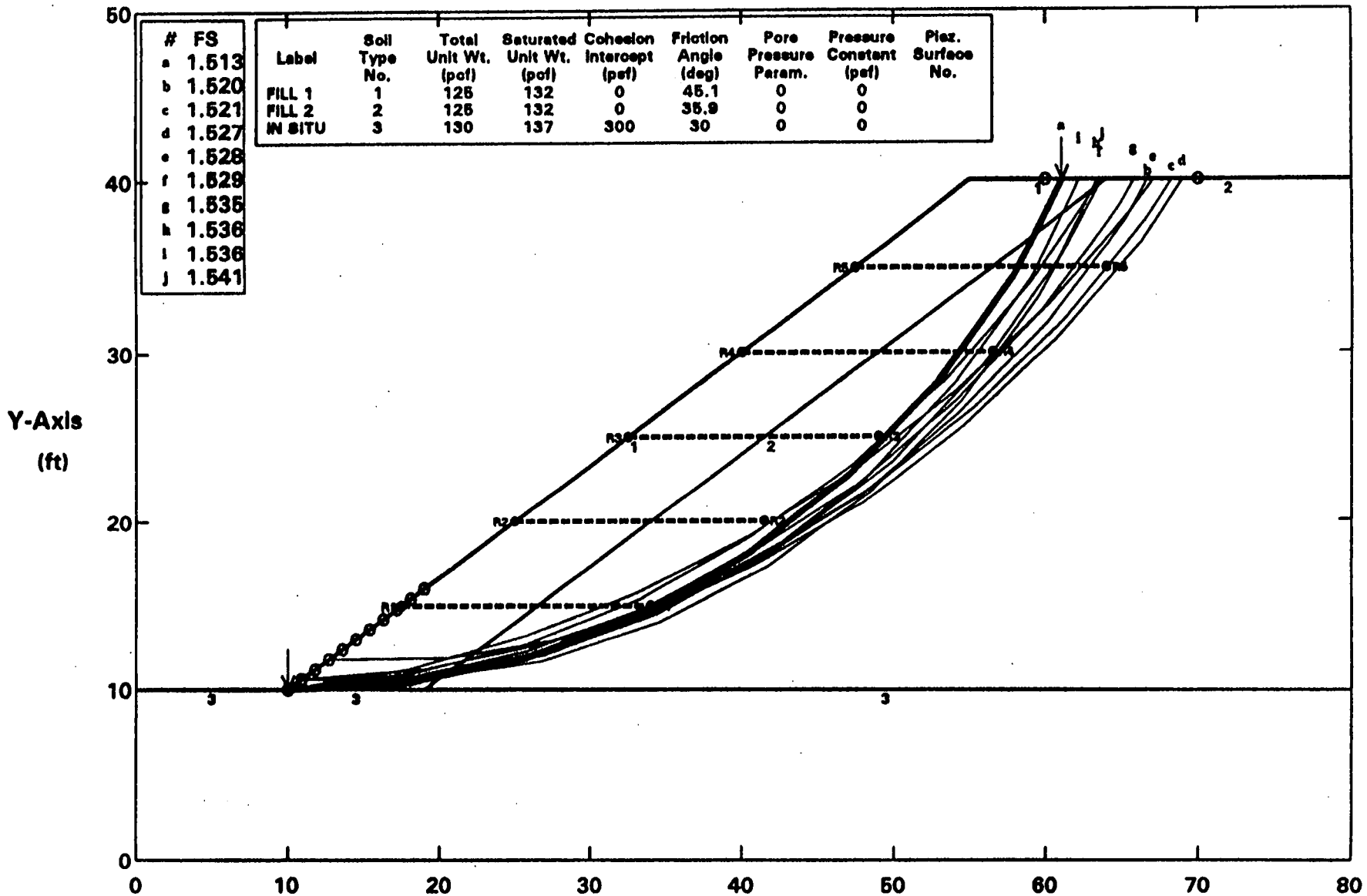
Label	Soil Type No.	Total Unit Wt. (pcf)	Saturated Unit Wt. (pcf)	Cohesion Intercept (psf)	Friction Angle (deg)	Pore Pressure Param.	Pressure Constant (psf)	Piez. Surface No.
FILL 1	1	125	132	0	45.1	0	0	
FILL 2	2	125	132	0	35.9	0	0	
IN SITU	3	130	137	300	30	0	0	

GSTABL7 FSmin = 1.556 X-Axis (ft)
Factors Of Safety Calculated By The Modified Bishop Method

000237

3610

GEOTEXTILE-FIBER REINFORCED SLOPE - LONG TERM - 16.5 FT GEOTEXTILE & 0.2% FIBERS
Ten Most Critical. C:GTFI4.PLT By: GHG



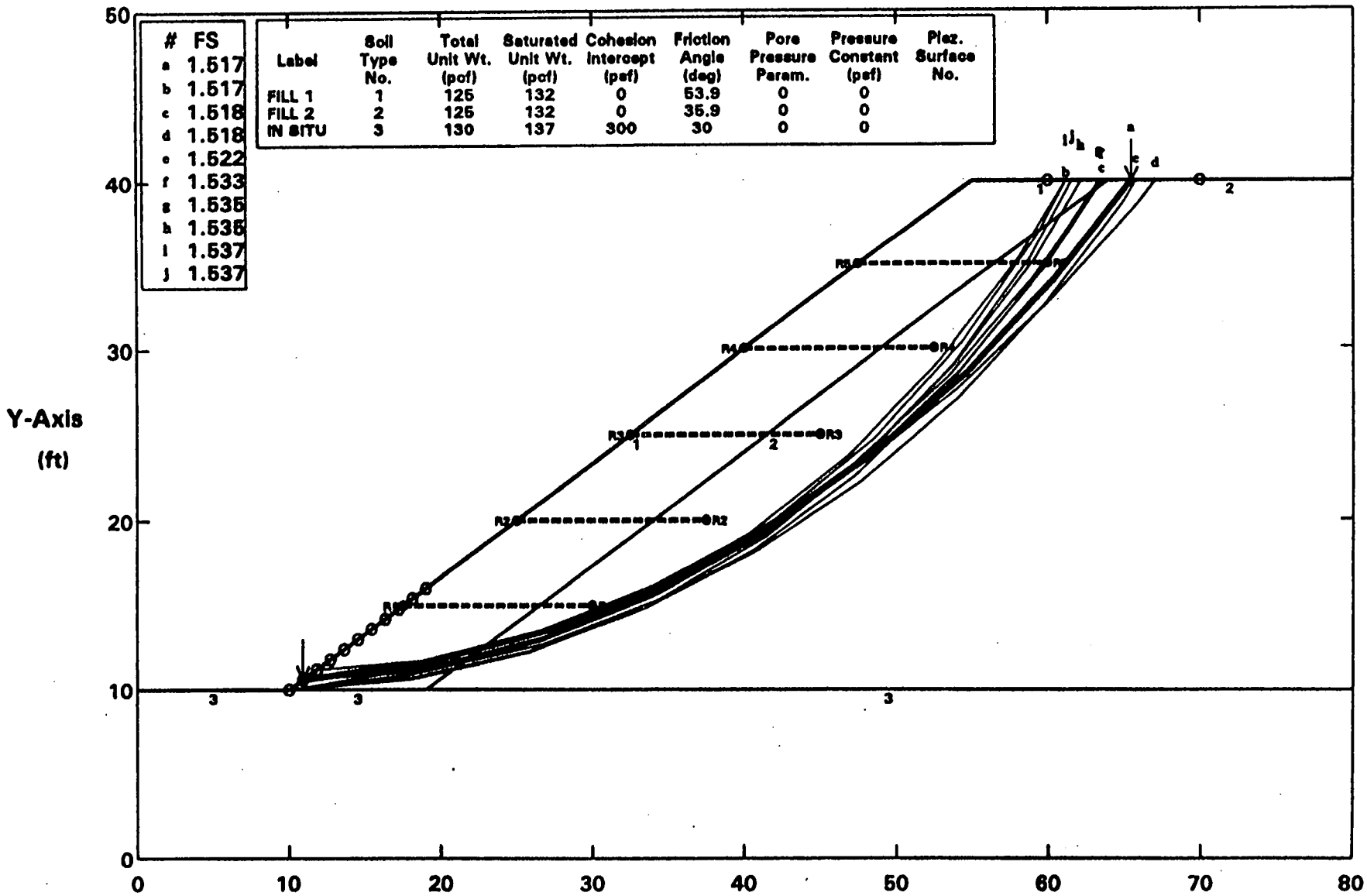
#	FS
a	1.513
b	1.520
c	1.521
d	1.527
e	1.528
f	1.529
g	1.535
h	1.536
i	1.536
j	1.541

Label	Soil Type No.	Total Unit Wt. (pcf)	Saturated Unit Wt. (pcf)	Cohesion Intercept (psf)	Friction Angle (deg)	Pore Pressure Param.	Pressure Constant (psf)	Piez. Surface No.
FILL 1	1	125	132	0	45.1	0	0	
FILL 2	2	125	132	0	35.9	0	0	
IN SITU	3	130	137	300	30	0	0	

GSTABL7 FSmin = 1.513 X-Axis (ft)
Factors Of Safety Calculated By The Modified Bishop Method

000238

GEOTEXTILE-FIBER REINFORCED SLOPE - LONG TERM - 12.5 FT GEOTEXTILE & 0.4% FIBERS
Ten Most Critical. C:GTFI5.PLT By: GHG



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FILL 1	1	125	132	0	53.9	0	0	
FILL 2	2	125	132	0	35.9	0	0	
IN SITU	3	130	137	300	30	0	0	

GSTABL7 FSmin = 1.517 X-Axis (ft)
Factors Of Safety Calculated By The Modified Bishop Method

000239

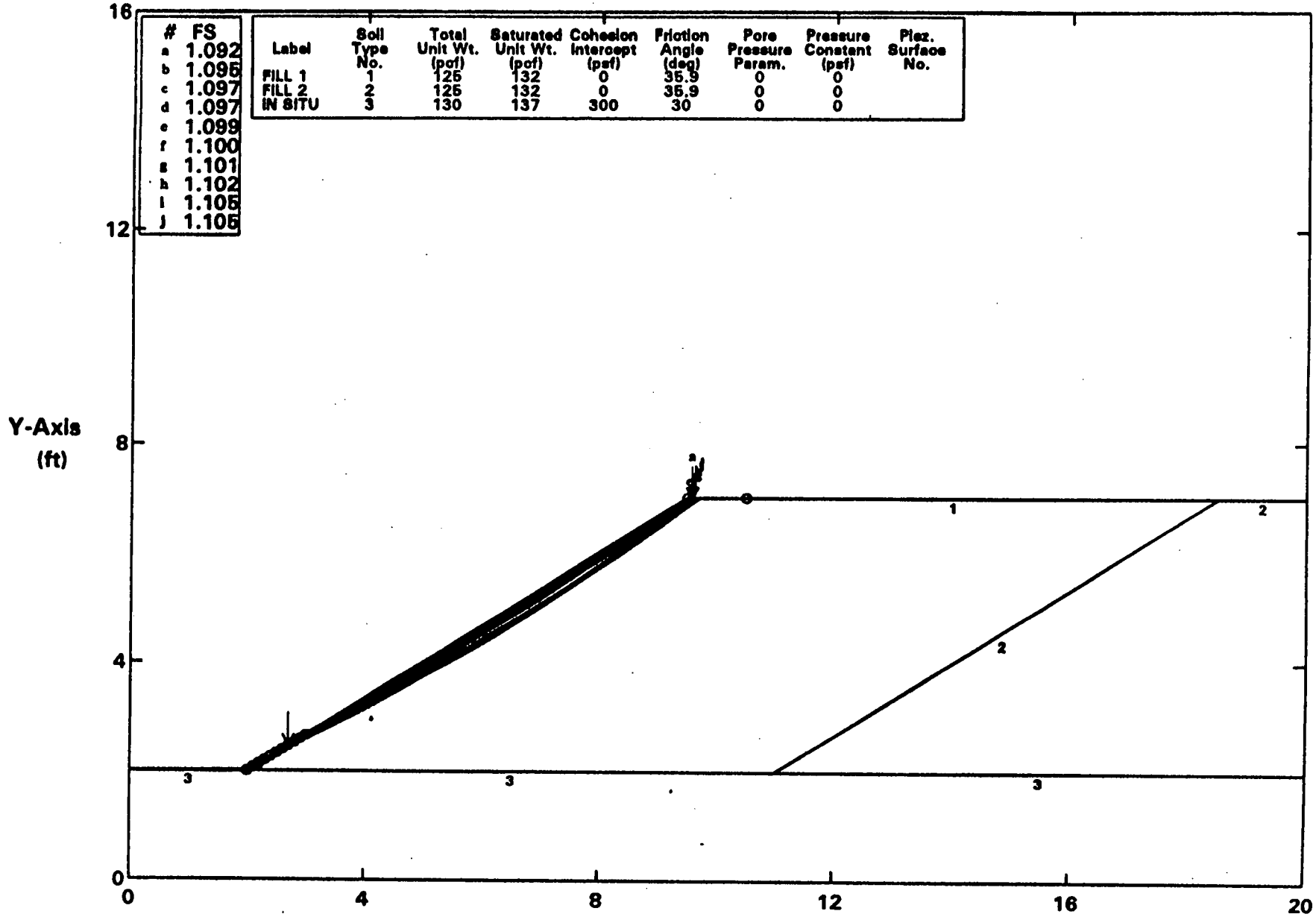
3610

TRUNCATED SLOPE - SURFACE ZONE PRIMARY GEOTEXTILE - NO SECONDARY

Ten Most Critical. C:GTFI6.PLT By: GHG

#	FS
a	1.092
b	1.096
c	1.097
d	1.097
e	1.099
f	1.100
g	1.101
h	1.102
i	1.105
j	1.105

Label	Soil Type No.	Total Unit Wt. (pcf)	Saturated Unit Wt. (pcf)	Cohesion Intercept (psf)	Friction Angle (deg)	Pore Pressure Param.	Pressure Constant (psf)	Piez. Surface No.
FILL 1	1	125	132	0	35.9	0	0	
FILL 2	2	125	132	0	35.9	0	0	
IN SITU	3	130	137	300	30	0	0	



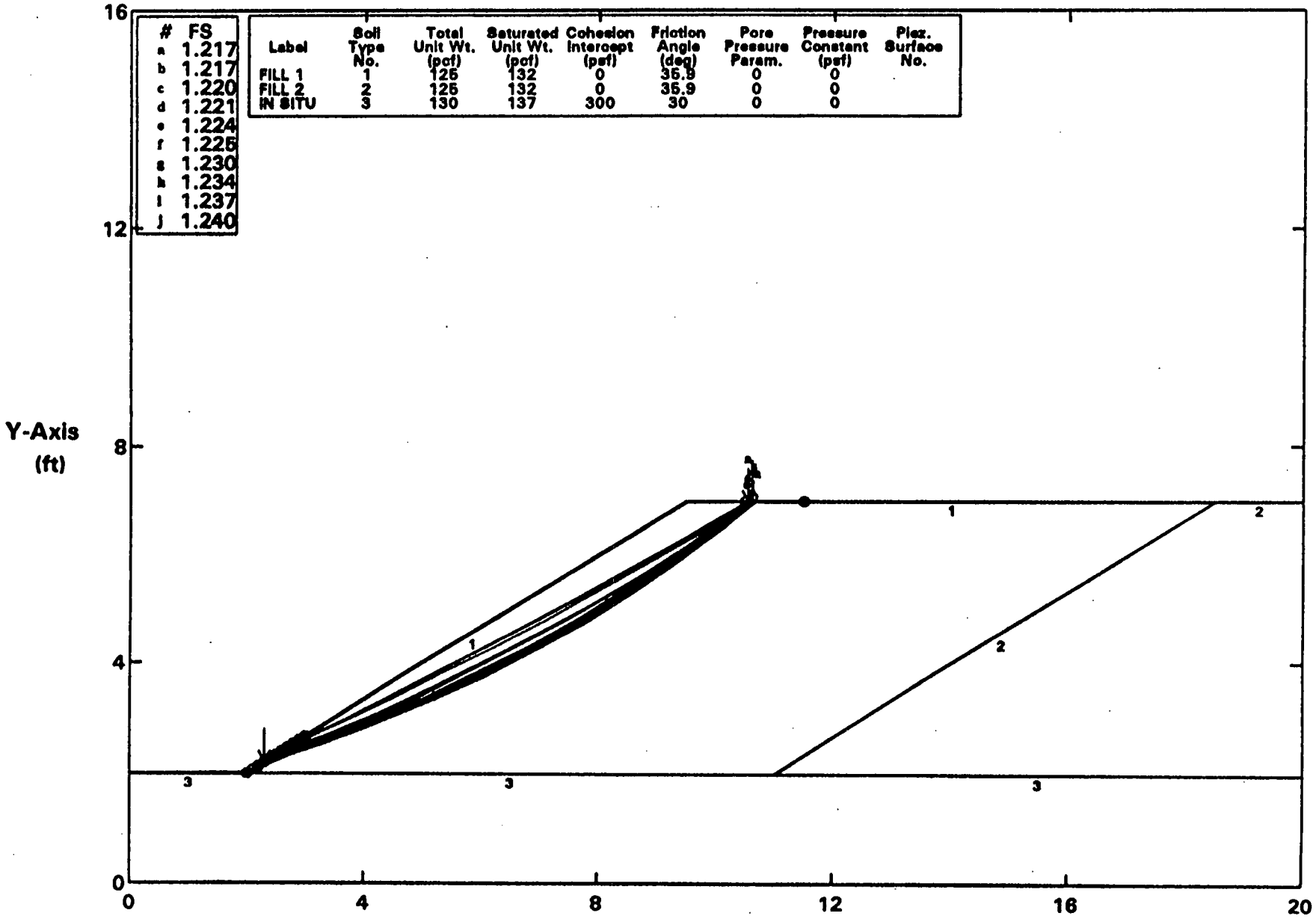
GSTABL7 FSmin = 1.092 X-Axis (ft)

Factors Of Safety Calculated By The Modified Bishop Method

000240

TRUNCATED SLOPE - SURFACE [illegible]E PRIMARY GEOTEXTILE - NO SECONDARY

Ten Most Cri[illegible]. C:GTFI7.PLT By: GHG



#	FS
a	1.217
b	1.217
c	1.220
d	1.221
e	1.224
f	1.225
g	1.230
h	1.234
i	1.237
j	1.240

Label	Soil Type No.	Total Unit Wt. (pcf)	Saturated Unit Wt. (pcf)	Cohesion Intercept (psf)	Friction Angle (deg)	Pore Pressure Param.	Pressure Constant (psf)	Piez. Surface No.
FILL 1	1	125	132	0	35.9	0	0	
FILL 2	2	125	132	0	35.9	0	0	
IN SITU	3	130	137	300	30	0	0	

GSTABL7 FSmin = 1.217 X-Axis (ft)

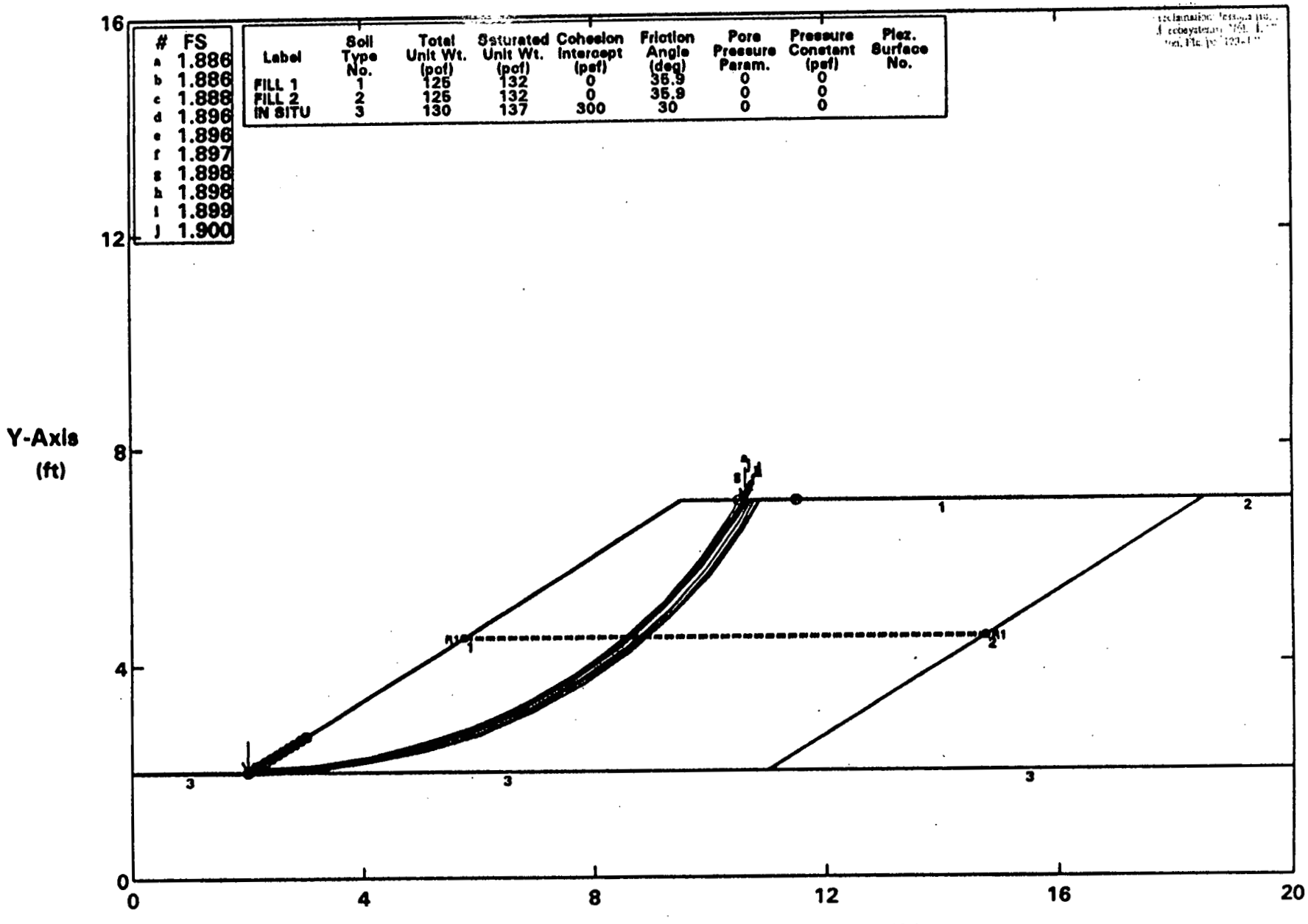
Factors Of Safety Calculated By The Modified Bishop Method

000241

3610

TRUNCATED SLOPE - SURFACE ZONE PRIMARY & SECONDARY GEOTEXTILE

Ten Most Critical. C:GTFI8.PLT By: GHG



#	FS
a	1.886
b	1.886
c	1.888
d	1.896
e	1.896
f	1.897
g	1.898
h	1.898
i	1.899
j	1.900

Label	Soil Type No.	Total Unit Wt. (pcf)	Saturated Unit Wt. (pcf)	Cohesion Intercept (psf)	Friction Angle (deg)	Pore Pressure Param.	Pressure Constant (psf)	Piez. Surface No.
FILL 1	1	125	132	0	35.9	0	0	
FILL 2	2	125	132	0	35.9	0	0	
IN SITU	3	130	137	300	30	0	0	

GSTABL7 FSmin = 1.886 X-Axis (ft)

Factors Of Safety Calculated By The Modified Bishop Method

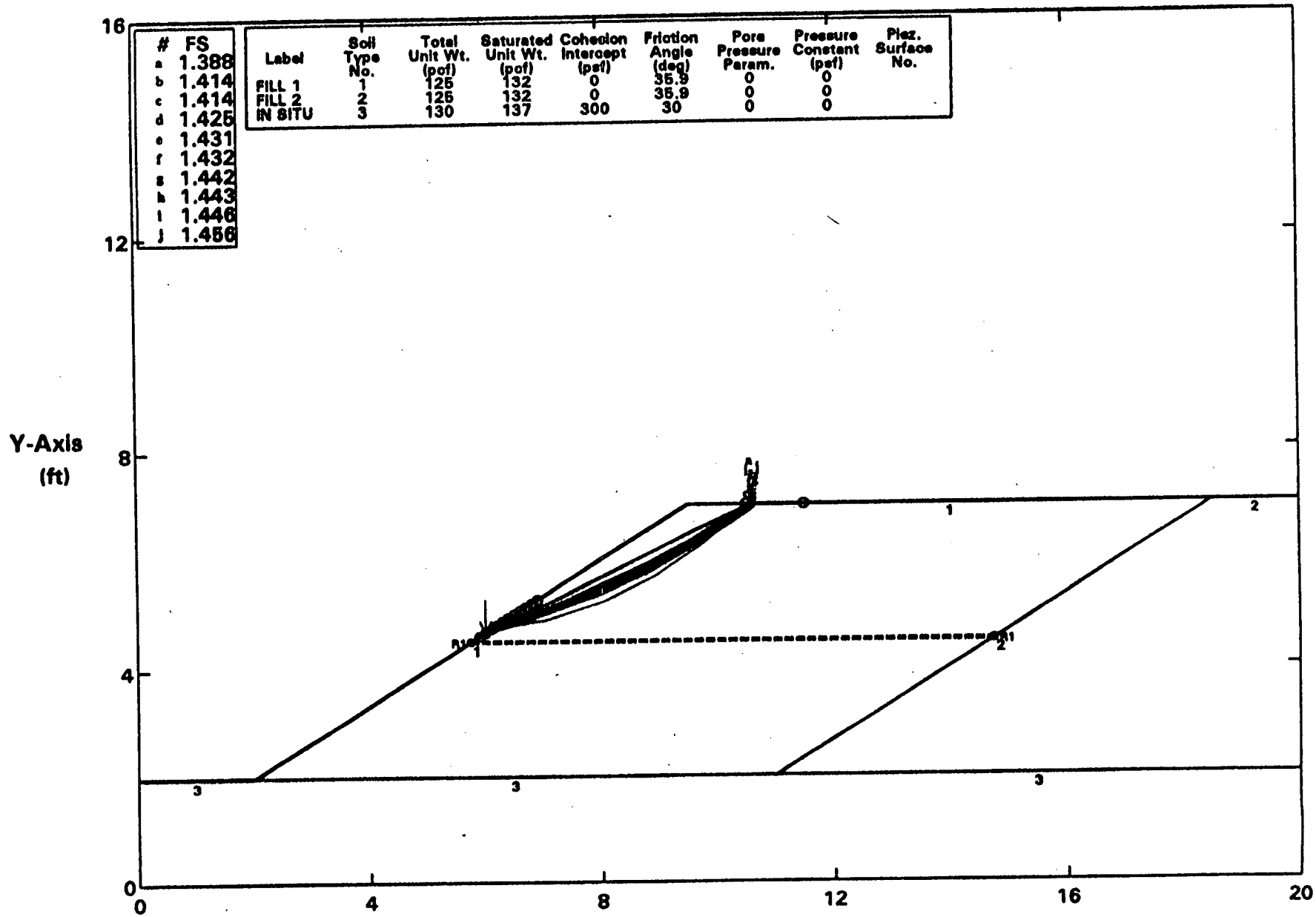
000242

TRUNCATED SLOPE - SURFACE ZONE PRIMARY & SECONDARY GEOTEXTILE

Ten Most Critical. C:GTFI9.PLT By: GHG

#	FS
a	1.388
b	1.414
c	1.414
d	1.425
e	1.431
f	1.432
g	1.442
h	1.443
i	1.446
j	1.456

Label	Soil Type No.	Total Unit Wt. (pcf)	Saturated Unit Wt. (pcf)	Cohesion Intercept (psf)	Friction Angle (deg)	Pore Pressure Param.	Pressure Constant (psf)	Piez. Surface No.
FILL 1	1	125	132	0	35.9	0	0	
FILL 2	2	125	132	0	35.9	0	0	
IN SITU	3	130	137	300	30	0	0	



GSTABL7 FSmin = 1.388 X-Axis (ft)

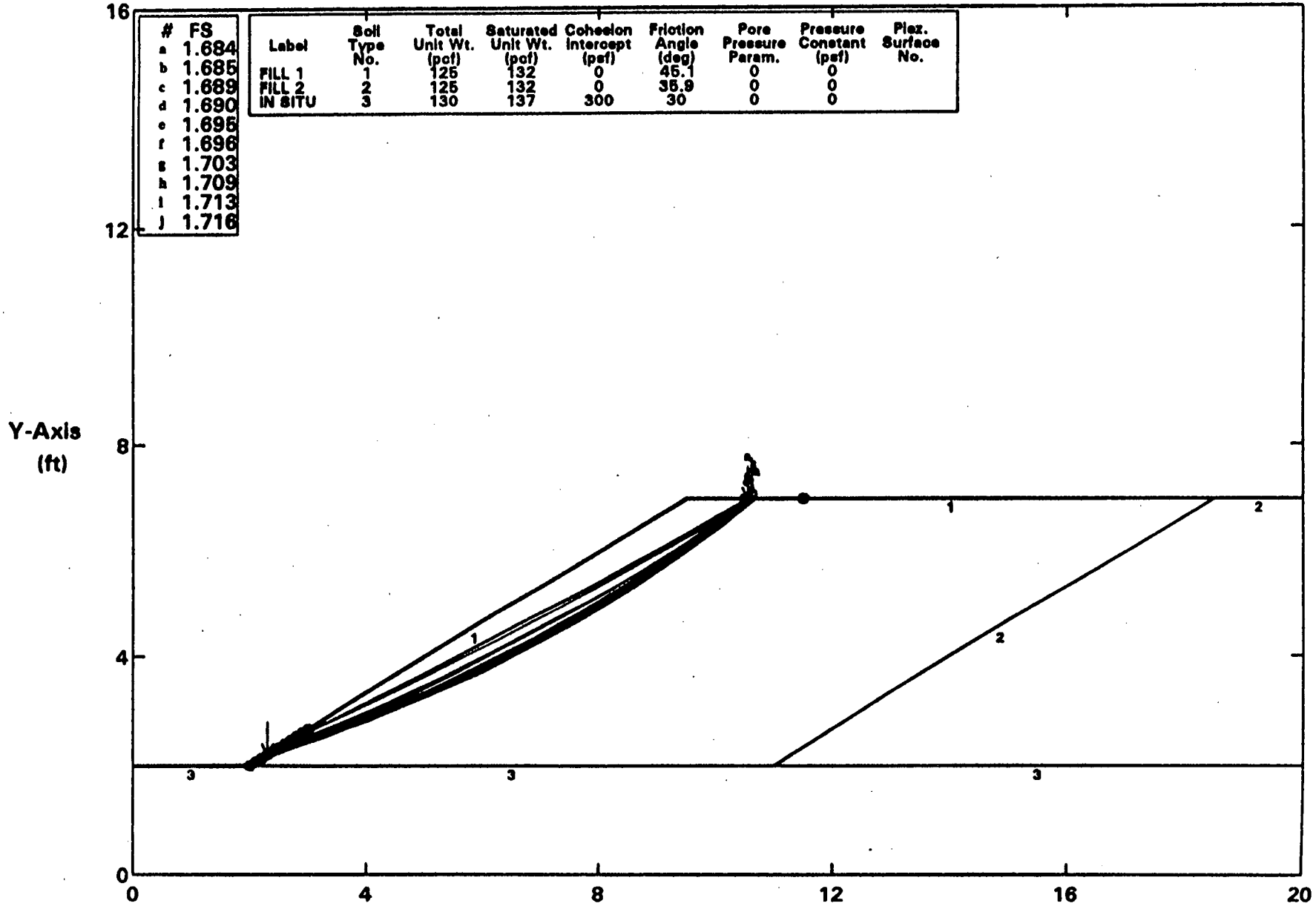
Factors Of Safety Calculated By The Modified Bishop Method

000243

3610

TRUNCATED SLOPE - SURFACE ZONE PRIMARY GEOTEXTILE & 0.2% FIBERS

Ten Most Critical. C:GTFI10.PLT By: GHG



#	FS
a	1.684
b	1.685
c	1.689
d	1.690
e	1.695
f	1.696
g	1.703
h	1.709
i	1.713
j	1.716

Label	Soil Type No.	Total Unit Wt. (pcf)	Saturated Unit Wt. (pcf)	Cohesion Intercept (psf)	Friction Angle (deg)	Pore Pressure Param.	Pressure Constant (psf)	Piez. Surface No.
FILL 1	1	125	132	0	45.1	0	0	
FILL 2	2	125	132	0	35.9	0	0	
IN SITU	3	130	137	300	30	0	0	

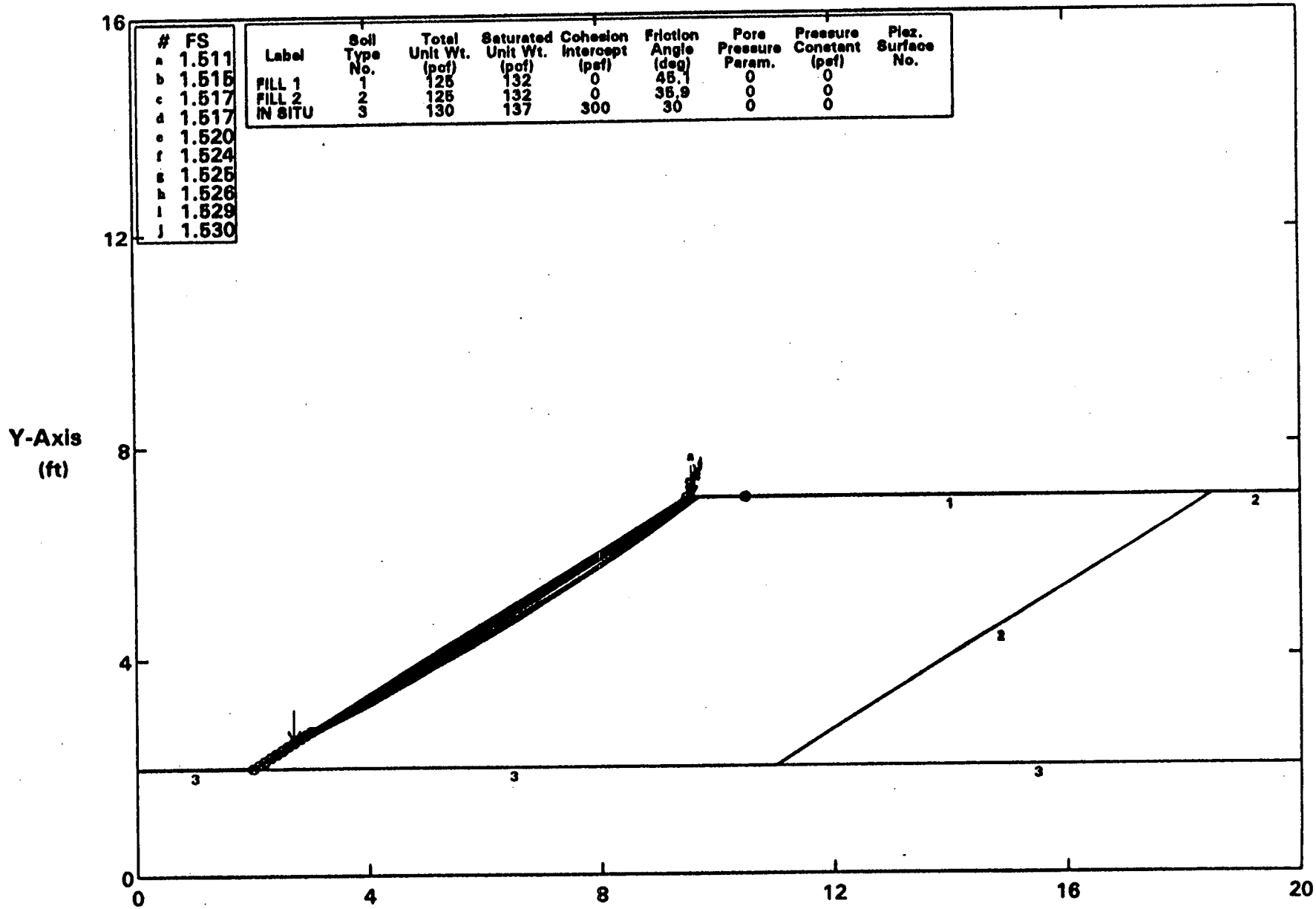
GSTABL7 FSmin = 1.684 X-Axis (ft)

Factors Of Safety Calculated By The Modified Bishop Method

000244

TRUNCATED SLOPE - SURFACE ZONE PRIMARY GEOTEXTILE & 0.2% FIBERS

Ten Most Critical. C:GTFI11.PLT By: GHG



#	FS
a	1.511
b	1.515
c	1.517
d	1.517
e	1.520
f	1.524
g	1.525
h	1.526
i	1.529
j	1.530

Label	Soil Type No.	Total Unit Wt. (pcf)	Saturated Unit Wt. (pcf)	Cohesion Intercept (psf)	Friction Angle (deg)	Pore Pressure Param.	Pressure Constant (psf)	Piez. Surface No.
FILL 1	1	125	132	0	45.1	0	0	
FILL 2	2	125	132	0	35.9	0	0	
IN SITU	3	130	137	300	30	0	0	

GSTABL7 FSmin = 1.511 X-Axis (ft)

Factors Of Safety Calculated By The Modified Bishop Method

000245

3610