ADDENDUM REVISION (8/5/83) TO COVER PAGE - NSF 83-57

PROPOSAL TO THE NATIONAL SCIENCE FOUNDATION
Cover Page

FOR CONSIDERATION BY NSF ORGANIZATIONAL UNIT (Indicate the most specific unit known, i.e. program, division, etc.)
Biotic Systems and Resources: Ecosystem Studies

IS THIS PROPOSAL BEING SUBMITTED TO ANOTHER FEDERAL AGENCY? Yes ___ No X ; IF YES, LIST ACRONYM(S):

PROGRAM ANNOUNCEMENT/SOLICITATION NO.: Long-Term Ecological Research Renewal

CLOSING DATE (IF ANY): April 10, 1987

NAME OF SUBMITTING ORGANIZATION TO WHICH AWARD SHOULD BE MADE (INCLUDE BRANCH/CAMPUS/OTHER COMPONENTS)
Regents, University of Minnesota

ADDRESS OF ORGANIZATION (INCLUDE ZIP CODE)
Office of Research Administration, 1919 University Avenue, St. Paul, MN 55114

TITLE OF PROPOSED PROJECT
Succession, Productivity and Dynamics in Temperate Mixed Ecosystems in Minnesota

REQUESTED AMOUNT $1,475,000

PROPOSED DURATION Four Years

DESIRED STARTING DATE January 16, 1987

PI/PD DEPARTMENT Department of Ecology and Behavioral Biology

PI/PD ORGANIZATION University of Minnesota

PI/PD PHONE NO. 612-373-2788

PI/PD NAME	SOCIAL SECURITY NO.*	SIGNATURE	MALE*	FEMALE*
G. David Tilman			X	
ADDITIONAL PI/PD				
ADDITIONAL PI/PD				
ADDITIONAL PI/PD				
ADDITIONAL PI/PD				

FOR RENEWAL OR CONTINUING AWARD REQUEST, LIST PREVIOUS AWARD NO.:

SUBMITTING ORGANIZATION IS: ☐ For-Profit Organization; ☐ Small Business; ☐ Minority Business; ☐ Women-Owned Business; (See cover page instructions, Page 3)

*Submission of social security numbers is voluntary and will not affect the organization's eligibility for an award. However, they are an integral part of the NSF information system and assist in processing the proposal. SSN solicited under NSF Act of 1950, as amended.

CHECK APPROPRIATE BOX(ES) IF THIS PROPOSAL INCLUDES ANY OF THE ITEMS LISTED BELOW:

☐ Animal Welfare
☐ Endangered Species
☐ Historical Sites
☐ Human Subjects
☐ Marine Mammal Protection
☐ Pollution Control
☐ National Environmental Policy Act
☐ Research Involving Recombinant DNA Molecules
☐ Proprietary and Privileged Information

PRINCIPAL INVESTIGATOR/ PROJECT DIRECTOR	AUTHORIZED ORGANIZATIONAL REP.	OTHER ENDORSEMENT (optional)
NAME G. David Tilman	NAME A. R. Potami	NAME Edward J. Cushing
SIGNATURE G. David Tilman	SIGNATURE	SIGNATURE Ed J Cushing
TITLE Professor, Dept. of Ecology and Behavioral Biology	TITLE Director, Office of Research Administration	TITLE Professor and Head, Dept. of Ecology and Behavioral Biology
DATE 3/25/86	DATE	DATE 3/25/86
TELEPHONE NO. Area Code: 612 373-2788	TELEPHONE NO. Area Code:	TELEPHONE NO. Area Code: 612 373-5177

APPENDIX IV

NATIONAL SCIENCE FOUNDATION

PROJECT SUMMARY

FOR NSF USE ONLY			
DIRECTORATE/DIVISION	PROGRAM OR SECTION	PROPOSAL NO.	F.Y.

NAME OF INSTITUTION (INCLUDE BRANCH/CAMPUS AND SCHOOL OR DIVISION)

Department of Ecology and Behavioral Biology
University of Minnesota

ADDRESS (INCLUDE DEPARTMENT)

Department of Ecology and Behavioral Biology
108 Zoology Building
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PRINCIPAL INVESTIGATOR(S)

G. David Tilman

TITLE OF PROJECT

Succession, Productivity and Dynamics in Temperate Mixed Ecosystems in Minnesota

TECHNICAL ABSTRACT (LIMIT TO 22 PICA OR 18 ELITE TYPEWRITTEN LINES)

The Cedar Creek LTER project has established and sampled over 1100 permanent experimental plots and 2300 permanent observational plots. The experiments are motivated by the belief that major advances in ecological understanding require a synthesis of "micro" studies of the direct and indirect mechanisms of population interactions with "macro" studies of ecosystem processes and feedback effects. Our research focuses on secondary succession because it is a long-term process that results from numerous direct, indirect, and feedback effects.

Our experiments, most replicated in four different successional fields, include (1) addition of various nutrients one at a time to determine which limit production; (2) addition of the major limiting soil resource, nitrogen, at various rates to establish experimental productivity gradients on natural vegetation within herbivore exclosures; (3) similar productivity gradients, except with herbivores present; (4) similar productivity gradients, except on newly disturbed soil; (5) different fire frequencies in large blocks of native oak savanna; (6) different fire frequencies in a 25 yr old field; (7) studies of rates of litter production, accumulation and decomposition; (8) in situ rates of nitrogen mineralization, leaching loss, and atmospheric input; (9) greenhouse and field studies of the nitrogen and light limited growth of major primary producer species; (10) selective removal of various herbivore guilds nested within large-scale experimental productivity gradients.

Our combination of long-term experimental and observational studies is providing the data needed to test numerous hypotheses concerning succession and ecosystem structure. Our experiments have already suggested that the usual short-term ecological field experiment may give results that can be the exact opposite of the long-term effect of the manipulation.

NSF Form 4 (7-83)

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I. RESULTS FROM PRIOR NSF SUPPORT

This is an application for renewal of an NSF grant (BSR-8114302) titled "LTER: Succession, Productivity, and Dynamics in Temperate Mixed Ecosystems in Minnesota." This project was funded for $1,426,172 for January 15, 1982 through January 15, 1987.

Our research was, and still is, motivated by the belief that major advances in ecological understanding require a synthesis of "micro" studies of population processes with "macro" views of whole system functioning. We have established a series of interdependent, replicated field experiments to determine the mechanistic bases for the direct, indirect and feedback effects of major species, functional groups, and processes on each other. We framed our hypotheses within the context of secondary succession because it is a long-term process that is likely to result from numerous short-term, direct, indirect, and feedback processes.

One measure of the results of the first four field seasons of the Cedar Creek LTER project is the number of long-term experimental and observational plots that we have established and sampled. As detailed in this proposal, these includes (1) 2300 permanent plots in an old field successional chronosequence (Inouye et al. 1986) and (2) a total of 1104 permanent experimental plots representing 10 major experiments, many of which are replicated in four fields of differing successional ages.

Another measure of our accomplishments to date is provided by the insights that have already come from our work. These are all discussed in detail later in this proposal. First, we have found that the initial response (first or second year) to many of our field manipulation experiments is often the exact opposite of the response we see by the fourth year. If this trend continues, it would suggest that the usual short-term ecological field experiment may often give results that are either unrelated to or even the exact opposite of the ultimate effect of the manipulation (Tilman 1986a). Second, in the first two or three years of our work, we observed divergence of initially disturbed versus initially undisturbed plots that otherwise received the same treatments, but found them to be converging by the fourth year. Because these plots differed greatly in initial soil chemistry and plant abundances, this convergence, if it continues, would suggest that old field ecosystems do not have multiple stable equilibria (Tilman, in review). If multiple stable equilibria are common in nature, all future states of an ecosystem will be determined by the past history of its species composition. However, if multiple stable equilibria are rare, ecosystems should converge on species compositions that reflect major physical constraints, not historical differences. Third, our experimental manipulations of herbivore densities suggests that herbivores are having little total effect on the dynamics and pattern of secondary succession, although herbivores do influence the abundance of some species. We hypothesize that herbivores have little effect on vegetation in unproductive habitats, such as Cedar Creek, and that the main effect of herbivores on plants is through resource resupply (Tilman 1982; Sterner 1986). Fourth, our results suggest that increased productivity may lead to oscillating plant succession because of litter feedback effects. It will be several years before we know if the oscillations we have observed during the first four years are sustained oscillations or transient effects that will be eventually damped. Fifth, our work has lead to a new theory of primary and secondary succession, the resource ratio hypothesis of succession (Tilman 1985). Sixth, our results to date strongly suggest that plant competition for nitrogen and light is the main cause of the secondary successional sequence at Cedar Creek, and that point-to-point variation in nitrogen mineralization within a landscape is a major cause of spatial variation in plant species abundances.

Our publication list (Appendix A) provides another measure of our accomplishments. To date, 16 papers largely attributable to the Cedar Creek LTER project have been published or accepted for publication. Eleven more papers are currently in review in major, refereed journals. In addition, we have collected the necessary data and started data analysis and writing on another 17 papers and one book that will be ready for submission before the end of 1986.

II. PROJECT DESCRIPTION

A. INTRODUCTION

We believe that the field of ecology is at a crossroads. During the past 20 years our knowledge of primary production, population growth, pairwise interspecific interactions, evolutionary ecology, optimal foraging, energy flow, nutrient budgets and cycling, and species diversity patterns has increased greatly. However, each of these advances has been gained by ignoring or greatly simplifying either higher or lower level phenomena. One portion of an ecosystem has been studied in great depth and other portions, even though they impinge on it, have been treated as if they were constant or have been ignored. We believe that the next major synthesis in ecology will be the integration of the principles, processes and mechanisms of population and community ecology into the framework of the whole ecosystem. Such a synthesis will require long-term experimental and observational studies of the mechanisms of interspecific interactions and of the various indirect, feedback effects that link together the biotic and physical components of ecosystems.

We believe that a major reason that this synthesis has been slow to materialize is that most ecological theories attempt to understand the long-term implications of processes, whereas most experimental studies have been short-term. Short-term studies demonstrate the immediate response to manipulations. However, because of time lags in feedback effects and differences in maximal growth rates, the immediate response to a manipulation may be a transient response that is the opposite of the long-term response. During the first four years of the Cedar Creek LTER project, we have observed numerous cases in which responses in the first or second year differed greatly from those in the third or fourth year.

Most of current population ecology theory is based on the demography and genetics of single populations and on pairwise interactions between species - interactions such as competition, predation, herbivory, parasitism and mutualism. The mechanisms inherent in these theories are potentially important elements of a general theory of ecosystem structure and function. However, there is little reason to believe that these elements, by themselves, will be able to describe the dynamics and functioning of natural communities. Each species in an ecosystem is imbedded in a matrix of other species with which it can interact both directly and indirectly. A change in any one element of an ecosystem can lead, eventually, to a change in any other element. Thus, the total effect that one species has on another depends not just on the mechanism of the direct pairwise interaction, but also on the various indirect, feedback effects mediated through other species and through elements of the abiotic environment.

The importance of such linkages and feedback effects has been highlighted by recent theoretical (e.g., Levine 1976; Holt 1977; Lawlor 1979; Vandermeer 1980) and experimental (Lynch 1978; Tilman 1983; Brown et al. 1986; Sterner 1986) studies. For instance, consider two herbivore species that directly compete with each other because both consume the same two plant species (Fig. 1A). The total effect of the herbivores on each other can switch from "competition" to "mutualism" as the intensity of the competition between the two plants increases. The interaction can behave as a "mutualism" if an increase in the density of Herbivore 1 decreases its preferred resource, Plant 1. This frees Plant 2 from competition, causing it to increase, and thus favor Herbivore 2, which feeds preferentially on Plant 2. Thus, the total effect of one species on another depends on both direct and indirect effects. If we are to achieve a mechanistic, potentially predictive understanding of the functioning of natural ecosystems, we must integrate the mechanisms of interspecific interactions into the framework of the entire ecosystem.

In an ecosystem there are numerous ways in which one species can indirectly affect another species. Consider, for instance, a diagram of some of the major foodweb and environmental linkages for an old field at Cedar Creek Natural History Area, Minnesota (Fig. 1B). Every line shows a direct mechanism of interaction. However, the total effect of one species on another can be understood only when both direct effects and various indirect effects (all of the possible feedback loops) are considered. At first sight, a

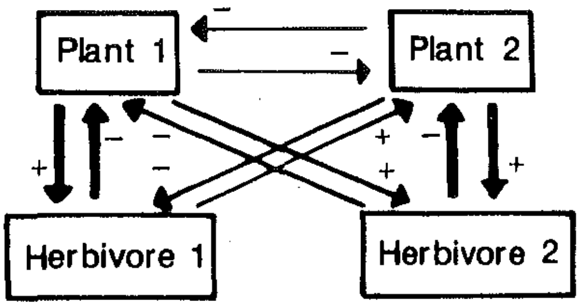


Figure 1A. Although Herbivore 1 and 2 directly compete for food, the total effect of Herbivore 1 on Herbivore 2, and vice versa, can be positive (i.e. mutualistic) because of indirect effects mediated through plant competition (see Vandermeer 1980).

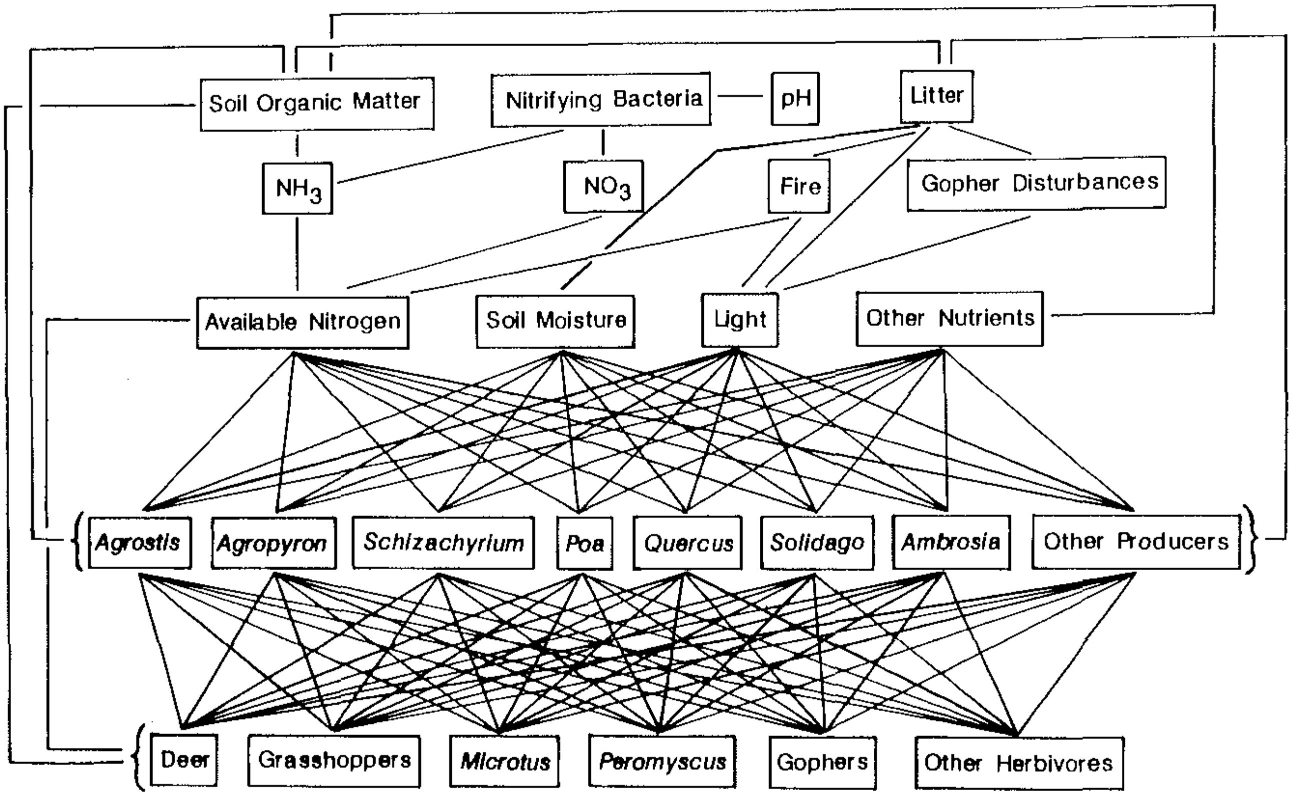


Figure 1B. A greatly simplified diagram of foodweb linkages in a Cedar Creek old field. The Cedar Creek LTER project includes studies of all the processes indicated by the arrows linking the boxes.

diagram like Figure 1B may make ecosystem ecology look hopelessly complex. However, the large number of lines linking together the various species and abiotic elements of Figure 1B represent just three distinct types of processes: (1) consumer-resource interactions; (2) nutrient resupply for the primary producers; and (3) disturbance. Our research at Cedar Creek is a highly experimental attempt to integrate these three elements into a foodweb-based theory of ecosystem function and dynamics. Figure 1B includes many of the types of processes upon which we have focused our first four years of research at Cedar Creek. Our research, though, goes well beyond description of such linkages. We have established long-term experimental manipulations, replicated in 4 different fields, that are allowing us to quantify various links and to establish the relative importance of various direct and indirect effects in structuring these ecosystems.

Most ecologists readily admit that natural ecosystems are quite complex. For instance, a mathematical model that included but a single equation for each species in an ecosystem would require hundreds of equations. Does this mean that we must quantify all the mechanisms of all foodweb interactions in order to understand how an ecosystem functions? Must we use systems of hundreds or thousands of simultaneous, non-linear differential equations to make an acceptable model of ecosystem dynamics? Or, is it possible to predict ecosystem dynamics using a few summary variables? If so, what are the variables that can be ignored and what are the variables that must be included? There are no clear answers yet available to these questions. Although mathematics might provide some insights (e.g., Schaffer 1981), the ultimate answers can come only from careful field observation and experimentation.

We have some reason to believe that simplicity may exist. In any system which has the structure of an ecosystem - i.e., linkages determined by the flow of energy and the cycling of nutrients - a few steps may become rate limiting. If this occurs, a complex system may have simple dynamics. For instance, mathematicians have found that models of cellular biochemical physiology that include hundreds of equations can often be reduced to 3 or 4 equations because a few steps eventually take predominance. Such "reduced dimensionality" (Schaffer 1981) may lead to the major, predictable elements of ecosystem dynamics, whereas the rest of ecosystem dynamics may remain forever in the realm of unexplainable noise. The only way to determine if this is so is through experimentation. By exploring, experimentally, the importance for succession of a variety of potentially important processes, we should be able to determine to what extent the complexity of nature can be simplified. Although our work stresses the possible importance of complexity, ultimately we are seeking simplicity, if it exists.

The LTER research that we have already initiated, and the extensions that we propose for the next four years, will help provide a synthesis of what have all too often been disparate views of the natural world. Evolutionary ecology, population ecology, community ecology and ecosystem ecology represent different perspectives that we take in trying to understand the patterns we see in the natural world. Each of these is a simplification -- an attempt to hold most elements constant so that the importance of one or a few elements can be rigorously explored. Ultimately, however, these approaches must be compatible. Organisms do not live in four separate worlds, each governed by the different perspectives of evolution, population, community or ecosystem ecology. Ecology has reached the point where a sufficient amount is known about each of these areas that syntheses must now be attempted. Population ecology can be greatly strengthened by consideration of the long-term effects, the indirect effects and the feedback effects that the ecosystem approach emphasizes. Similarly, ecosystem ecology can be strengthened by detailed studies of the dynamics of interactions among the individual species that play such a key role in the processes of productivity, energy flow and nutrient cycling. We believe that such a synthesis will only be possible if long-term research combines population, community and ecosystem perspectives.

This synthesis will require a marriage of what Orians (1980) has called the micro and macro approaches in ecology. Orians (1980) stated: "We have been slow to develop better ways of integrating the two areas because, until very recently, we had little microecology worth using as building blocks for imaginative macroecological models. This is no longer true, and much is to be done." The research program that we have established at Cedar Creek includes long-term studies of both large-scale and small scale unmanipulated and manipulated plots. Our large plots, which we call our "macroplots," are providing information on whole system responses to manipulations and to natural environmental change. The small scale plots, our "microplots," are providing detailed experimental information on the direct effects of various underlying processes, especially plant competition for resources (mainly nitrogen and light), plant-herbivore interactions, nutrient resupply processes, and biotically-caused disturbance. One way that we are analyzing and synthesizing our results is through the use of a theory of multispecies consumer-resource interactions (Tilman 1980, 1982, 1985, 1986a,b,c). Because this theory incorporates the direct mechanisms of consumer-resource (i.e., inter-trophic level) interactions, it is easily expanded to include the various foodweb links shown in Figure 1B. This theory can easily incorporate spatial and temporal variability, species' differences in above and below ground allocation of production, and disturbances such as fire or gopher mound production. However, we must point out that we are using such theory to develop a mechanistic understanding of the direct and indirect effects that are of major importance in structuring these old field ecosystems. Thus, we continually apply Ockham's Razor - asking, through our experimental and observational studies, if each element added to the model can, indeed, explain a significantly greater portion of the observed variance. We do this because it is a trivial matter to observe potentially complex interactions in nature - but much more difficult to demonstrate that they are of importance. Our field needs the simplest theoretical approach that can actually predict the dynamics of natural and perturbed ecosystems. We are sure that such models will be more complex than classical population models -- and hope they will be simpler than most current ecosystem models.

Our research is being performed within the context of the natural secondary successional sequence that occurs at Cedar Creek Natural History Area. (See Appendix B for a description of Cedar Creek.) We believe that a long-term, detailed, experimental study of succession is an ideal framework within which a synthesis of population and ecosystem approaches can develop. Succession is a long-term process that results from numerous short-term changes. Succession is likely to result from both direct and indirect effects. It is impossible to divorce succession from a consideration of plant life history characteristics, from the population processes of competition and herbivory, or from the ecosystem processes of soil development, decomposition, nutrient cycling, and disturbance. The patterns and causes of the process of succession are the major theme unifying the work that we propose. Our experiments and detailed observations are designed to provide a multi-faceted view of succession from evolutionary, population, community and ecosystem perspectives. We will explore in especially great depth any areas for which these different perspectives seem to make conflicting predictions, for it is in these areas that we are likely to find the greatest opportunities for new syntheses.

Although succession has long been of interest to ecologists (e.g., Cowles 1899; Cooper 1913; Clements 1916; Gleason 1917), there is still considerable disagreement as to which processes are most important in controlling the dynamics of ecosystem components and population densities following disturbance (e.g., Connell and Slatyer 1977; Peet and Christensen 1980; McIntosh 1981; Horn 1981; Tilman 1984). There are comparable disagreements as to the importance of physical and biotic processes in determining the spatial variation in species composition and diversity within undisturbed habitats. These disagreements may partially result from the unique features and past history of particular habitats, but a larger problem is the paucity of field experiments, especially long-term experiments. Only experimentation can distinguish mere correlates of observed patterns from causes. However, because of the multiple paths of causation, the different response times of these paths, and the long life spans of many organisms, it is imperative that such experiments be allowed to proceed for a long time. For instance, dynamic models of ecosystem change predict that it can take forests 100 or more years to come to a new equilibrium after a 2°C reduction in mean annual temperature (Davis and Botkin 1985; Davis 1986). Although a 100 year experiment is hard to imagine, the Park Grass Experiments in Rothamsted, England, are now in their 132nd year, and have become of increasingly greater value with each sampling period (e.g., Lawes and Gilbert 1882; Brenchley 1924; Brenchley and Warington 1958; Tilman 1982).

Because the life spans of most primary producers in the secondary successional sequence at Cedar Creek are much shorter than those of forest canopy trees, we should observe a more rapid response to natural disturbances or experimental manipulations than suggested by Davis and Botkin (1985) for forests. However, even for herbaceous vegetation, dynamic models predict that it can take 10 to 15 years for the vegetation to attain a new equilibrium after a disturbance or a major change in the supply rate of a limiting resource (Tilman 1985, 1986a). More importantly, these models predict that during the first 5 years, much of the observed response to a disturbance or experimental manipulation can be a transient response determined more by differences in the maximal growth rates of species than by the long-term outcome of their various pathways of interaction. This theory predicts that, at least in successional vegetation, such transient responses are often the opposite of the true long-term effect of the experiment. To understand how ecosystems are structured and to make intelligent decisions concerning ecosystem management, will require that we understand the causes of both their short-term and their long-term dynamic responses to perturbations.

B. THE CEDAR CREEK LTER RESEARCH PROGRAM

1. Objectives

The main purpose of our project is to understand the various direct and indirect ecosystem and population processes that cause secondary succession. The processes we have focused on are (1) the dynamics and control of soil nutrient cycles and availability, especially for nitrogen; (2) the pattern of disturbance and the effects of disturbance on succession; (3) the mechanisms of plant competition for soil resources and light; (4) the direct effects of herbivore feeding on plants; and (5) various indirect effects of herbivores, such as through disturbance or soil modification. Figure 1B, which schematically illustrates the major foodweb linkages that we are exploring, shows that we are concentrating our efforts on the decomposer, the primary producer and the herbivore trophic levels, and on interactions within and among these levels. Although it is not always feasible, to the greatest extent possible we are quantifying the responses of each species in our experimental and observational plots. Although this entails much more effort than lumping species by functional groups, this information is critical if we are to achieve a synthesis of evolutionary, population and ecosystem perspectives.

We are focusing our study on various interactions within and among the decomposer, primary producer and herbivore levels because each of these may be an important determinant of succession. Numerous studies of succession have reported correlations between plant abundances and the availability of various resources, especially soil nitrogen. These correlations have been strongest for cases of primary succession (Crocker and Major 1955; Lawrence 1958; Olson 1958; Walker et al. 1981) and secondary succession on poor soils (Rice et al. 1960; Odum 1960; Inouye et al. 1986). Such observations have led to one view of succession, that it is caused by a gradient through time in soil nutrient availability (e.g., Drury and Nisbet 1973; Tilman 1982). The most recent extension of these ideas is the resource ratio hypothesis of succession (Tilman 1985). Similarly, several studies have suggested that much of the point-to-point spatial heterogeneity in vegetation composition might be understood as change along gradients in various physical or biotic factors (e.g., Zedler and Zedler 1969; Harper 1969; Whittaker and Niering 1975; Tilman 1984). Although these observations and theory (Tilman 1980, 1982, 1985) suggest that both successional patterns and local spatial heterogeneity may be explained as resulting from plant differentiation along temporal or spatial gradients, there have been no direct experimental tests of these ideas.

If this view is found to have merit, though, it would provide but a partial explanation of succession. A full explanation of succession must also include the various processes that cause the temporal gradient in soil characteristics. Why is it that, starting with a bare, mineral substrate, soil organic matter and nitrogen tend to increase for a period of from 100 to 200 years (i.e., Crocker and Majors 1955; Olson 1957)? Why do comparable changes occur during secondary succession on nitrogen poor soils (Rice et al 1960; Odum 1960; Inouye et al. 1986)? Are the often cited patterns of "soil development" during the first few hundred years of primary succession or secondary succession merely an initial stage of longer-term soil dynamics, as is suggested by the Walker et al. (1981) study of soils and vegetation in the sand dunes of eastern Australia? Although short-term experiments (Abul-Fatih and Bazzaz 1979; Hils and VanKat 1982) lead to the clear rejection of Clement's "facilitation hypothesis" of succession, might long-term studies reveal an element of "facilitation" in succession? If so, we must be sure that it can be explained within the current framework of evolution by natural selection. If it cannot be, then we must explore all the underlying assumptions of both the evolutionary and ecosystem perspectives to seek a resolution.

It has long been thought that herbivores could have a great effect on succession (e.g., Moore 1933; Summerhayes 1941; Tansley 1949; Connell and Slatyer 1977; Tilman 1983; Inouye et al 1986; Sterner 1986). In England, for example, areas open to sheep or cattle grazing remain grasslands whereas areas from which these herbivores are excluded often become forest (Grubb 1986). However, it is not known what aspects of herbivory (i.e., selective feeding, local disturbance, nutrient cycling, etc.) actually cause the observed effects or if herbivores would be important at their natural densities in unmanaged ecosystems. To understand the role of herbivores at their natural densities during succession will require long-term experimental and observational studies of both their direct and indirect effects. We are performing such studies at Cedar Creek.

2. Approach

Our study of the mechanisms controlling secondary succession uses broad-scale, comparative studies of ecosystem patterns, long-term experimental manipulations, and shorter-term studies of various underlying mechanisms and processes. During the past four years doing our research, we have established the following permanent field plots:

(1) 2300 observational quadrats (distributed among 22 old fields) to provide detailed information on spatial variation within and among old fields and to document long-term changes in natural vegetation.

(2) 33 experimental 20m x 50 m plots to determine the long-term, interactive effects of herbivores and primary productivity (manipulated with N addition) on ecosystem dynamics.

(3) 162 experimental 4m x 4m plots to determine the joint effects of disturbance (via discing) and primary production (manipulated through N addition) on succession in the absence of herbivores.

(4) 207 experimental 4m x 4m plots to determine the effects of nitrogen addition on succession in the absence of disturbance and herbivory.

(5) 162 experimental 4m x 4m plots to determine herbivore microhabitat choice and the effects of herbivores on the dynamics of succession.

(6) 168 herbivore removal experimental plots to determine the long-term effects of exclusions of various herbivore species or functional groups and how these effects depend on the rate of primary productivity.

(7) 24 experimental 8m x8m plots to determine the effects of different fire frequencies on secondary successional plant dynamics and soil development.

(8) 288 sampling sites (24 sites in each of 12 compartments) in native oak savanna stands that have been subject to different fire frequencies for the past 20 years.

(9) 48 experimental 4m x 4m plots to determine the joint effects of soil pH (experimentally manipulated) and nitrogen (experimentally manipulated) on the dynamics of nitrifying bacteria, litter decay, nitrogen cycling and plant dynamics.

(10) 12 10m x 30m deer exclosures and controls in two early successional fields to determine effects of deer browsing on old field succession.

In addition to the above on-going experimental and observational studies, we have performed a variety of short-term observational and experimental studies on a variety of ecosystem and population processes, including: (1) rates of nitrogen mineralization; (2) rates of litter decay; (3) rates of atmospheric nitrogen inputs and soil leaching losses of nitrogen in fields of different successional ages; (4) rates of nitrogen fixation by associative bacteria; (5) greenhouse studies of nitrogen and light limited growth of major plant species; (6) gopher feeding preference studies; (7) gopher habitat use patterns; (8) grasshopper habitat use; and (9) seasonal patterns of below-ground and above-ground primary production in an old field chronosequence.

The research proposed for the next four years of the Cedar Creek LTER project is described in the remainder of this document. About 2/3 of the research represents a continuation of the detailed, long-term experimental and observational studies that we have already initiated. The remainder of our proposed research is equally divided between efforts at intersite and theoretical syntheses and detailed, shorter-term studies of the factors controlling processes such as litter dynamics, soil spatial heterogeneity, carbon and nitrogen interactions in soils and local disturbance frequencies. We want to stress that the vast majority of our studies were designed to be long-term studies. We have invested considerable energy in initiating a uniquely thorough series of experiments that may not give us their greatest payback for another 5 or 10 years. We have been willing to make these investments because we believe that such long-term experiments are the only way in which we can answer fundamental ecological questions.

3. The Five Core Topics for LTER Projects: In addressing our central research questions, we established a sufficiently broad research program that it addressed, in considerable detail, all five of the core research topics that were specified by the National Science Foundation as being unifying elements among all the LTER sites. Table 1 lists these five core topics and, for each topic, names the Cedar Creek experiments that contribute to each area. The names used to describe each experiment are the same as those used in the remainder of this grant proposal. Although we feel that these five core areas are important in establishing a common ground among the LTER sites and in assuring that the research at each site takes a broad, ecosystem-oriented approach, the five core areas, by themselves, do not specify the major hypotheses that are likely to motivate any given research project. Because we wish to discuss how our research addresses the specific research questions we have raised above, we will not discuss in detail greater than that given in Table 1 how our work relates each of the five core areas.

C. OLD FIELD SUCCESSIONAL CHRONOSEQUENCE

At the time of European settlement in the 1880's, most upland areas of Cedar Creek

TABLE 1. SUMMARY OF CEDAR CREEK RESEARCH IN THE FIVE CORE AREAS

Topic 1: Pattern and Control of Primary Production

A. Old Field Successional Chronosequence (within and between field comparisons of standing crop and soil nutrients in 2300 permanent quadrats).

B. Nitrogen-Gradient Microplot Experiments (year-by-year information on primary production in 36 control plots in each field; role of nitrogen in primary production; replicates with and without mammalian herbivores).

C. Seasonal Productivity Patterns (biweekly sampling of above ground biomass to species throughout the growing season).

D. Macroplot Nitrogen Gradient Experiments (standing crop and plant species abundances at various nitrogen levels; effects of grasshoppers, other insects and various small mammal functional classes on productivity).

E. Long-Term Monoculture Experiments (monocultures of the five major primary producer species, with each monoculture replicated on 10 different soil types in the field; within season and year-to-year dynamics of production).

F. Dynamics of Below and Above Ground Production (biweekly samples of root biomass by depth and of above ground biomass in relation to soil nutrients and water availability).

Topic 2: Spatial and Temporal Distributions of Selected Populations

A. Old Field Successional Chronosequence (spatial abundance patterns for major plant species; temporal patterns inferred from a chronosequence).

B. Macroplot Nitrogen Gradient Experiments (small mammal and grasshopper population densities in control and nitrogen addition plots).

C. Nitrogen-Gradient Microplot Experiments (dynamics of invasion and habitat use by small mammals on a grid of plots that differ in their rate of primary production).

D. Nitrogen-Gradient Microplot Experiments (biweekly and year-to-year dynamics of major plant species).

E. Gopher Habitat Use (continuous recording of below ground habitat use by gophers).

F. Gopher Feeding Experiments (studies of gopher foraging in relation to plant density and plant tissue N levels).

Topic 3: Pattern and Control of Organic Matter Accumulation

A. Litter Dynamics (experimental study of litter decomposition and the influence of nitrogen availability on decomposition).

B. Oak Savanna Burn Experiments (survey of vegetation and soils, including litter and soil organic matter, in the 20th year of prescribed burning).

TABLE 1. (continued)

C. Nitrogen Mineralization and Nitrification (interrelations of organic carbon, total nitrogen and nitrogen mineralization).

D. Nitrogen-Gradient Microplot Experiments (annual and biweekly litter samples show dynamics of litter accumulation in relation to primary production).

E. Long-Term Monoculture Experiments (litter accumulation in monocultures of five dominant grass species grown on 10 different soil mixtures; litter quality feedback effects on nitrogen dynamics).

Topic 4: Patterns of Inorganic Inputs and Nutrient Movements

A. Macroplot Lysimeters (a total of 66 modified porous cup lysimeters provide periodic information on nitrogen loss from intact soil/vegetation cores in 22 control plots and 44 N addition plots).

B. Precipitation collectors (rainbuckets; wet/dry fall collectors; atmospheric nutrient inputs).

C. Nitrogen Mineralization and Nitrification (buried bag experiments throughout the growing season replicated in 4 fields).

D. N-15 Addition Experiments (N-15 injections to various soil depths at different times in growing season; N-15 accumulation in plants, soil fractions).

E. Nitrification and Soil pH (experimental plots to determine effects of soil pH on dynamics of nitrifying bacteria).

F. Long-Term Monoculture Experiments (changes in soil nutrients in response to plant growth; feedback effects of litter production by different species).

Topic 5: Patterns and Frequency of Disturbance

A. Old Field Successional Chronosequence (gopher mounds and other small scale disturbances in 22 old fields; relations between disturbance, field age and soil chemistry).

B. Windstorm Forest Disturbance (permanent quadrats on forested areas that suffered or did not suffer extreme adult tree mortality from a major wind storm; seedling and sapling survival patterns will be followed for next 10+ years).

C. Macroplot and Microplot Experiments (annual or more frequent surveys of small-scale disturbance).

D. Oak Savanna Burn Experiments (20 years of burning native oak savanna vegetation at different frequencies).

E. Fire and Secondary Succession (replicated compartments burned at different frequencies).

contained an oak savanna - prairie vegetation. By about 1910, many of these areas had been clearcut and cultivated (Pierce 1954). The well-sorted, excessively well-drained fine sands of Cedar Creek were poor in nitrogen, and were further depleted by agriculture. Starting in about 1930, farmers began abandoning fields from agriculture. Secondary succession in these fields thus began under conditions of significant nitrogen limitation. From 1930 to the present time, 78 different fields, ranging in size from 1 to more than 40 ha, have been abandoned on the land that is now Cedar Creek Natural History Area. Additional fields at Cedar Creek are still farmed so that they may be abandoned over the next 50 years to provide Cedar Creek with a rich array of old fields for comparative and experimental research.

At the start of our LTER research, we chose 22 of these 78 fields to form a successional chronosequence. In each field we established 100 permanent 1.0m x 0.5m quadrats (150 quadrats in Fields A and B). We collected a soil sample from the center of each quadrat and estimated vegetative cover, to species, of all plants in each quadrat. We also determined the abundances of several major herbivores in each field. In addition, we recorded if a given sampling quadrat happened to fall on a recently disturbed area. The results of this survey are described in detail in Inouye et al. (1986).

We found that total soil nitrogen increased significantly with field age (Fig. 2A), and that total cover by vascular plants (Fig. 2B) and litter (Fig. 2C) increased significantly with total soil nitrogen. Light penetration to the soil surface was negatively correlated with total plant biomass. The total species richness of a field (Fig. 2D) and the quadrat-to-quadrat heterogeneity in species composition within a field increased significantly with field age. In contrast, the species richness of individual quadrats **decreased** with increasing soil nitrogen. Thus, the greater species richness of older fields was not caused by an increased number of species within small areas (quadrats), but by increased quadrat-to-quadrat heterogeneity within older fields. This greater vegetation heterogeneity corresponded with the greater spatial heterogeneity in

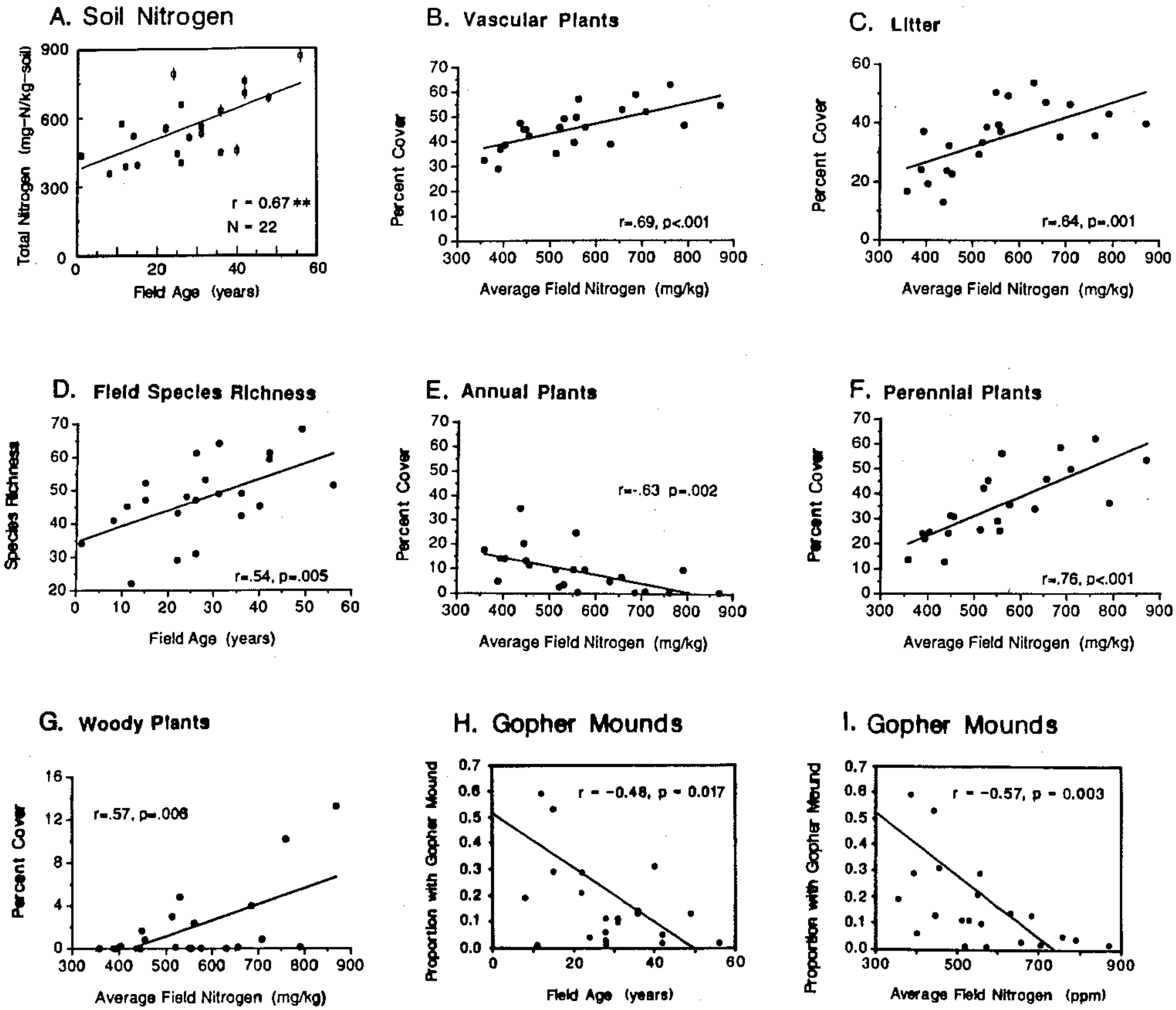


Figure 2. Relations among various parameters measured in the Old Field Successional Chronosequence. Each point in each figure is an average over all samples (100 or 150) collected in a particular field. See Inouye et al. (1986) for further details.

nitrogen within older fields.

Cover of annual plants (Fig. 2E) and of species of European origin decreased significantly with field age and nitrogen, but annuals still comprised more than 20% of the vegetation of 25 year old fields. Cover of perennials (Fig. 2F) and of woody plants (Fig. 2G) increased with field age and nitrogen, but woody plants were less than 15% of total vegetative cover in even the oldest fields. Soil disturbances, most often caused by the plains pocket gopher, *Geomys bursarius*, were most common in young fields and declined significantly with field age and field nitrogen (Fig. 2 H and I). We also analyzed the results of our observations in the 2300 permanent quadrats on a species-by-species basis, for the 15 most abundant species during secondary succession (Fig. 3). These results have shown that the abundance of each major plant species is strongly correlated with total soil nitrogen. Each species seems to have a fairly individualistic, approximately Gaussian distribution along the temporal nitrogen gradient of secondary succession. Early successional species (*Rumex acetosella*, *Ambrosia artemisiifolia*, *Agrostis scabra*, and *Hedeoma hispida*) reach their peak abundance at low soil nitrogen, and decline in abundance in more nitrogen-rich quadrats. These patterns hold both within individual fields and among all fields, combined. Similarly, late successional species (*Schizachyrium scoparium*, *Sorghastrum nutans*, *Poa pratensis*, and *Artemisia ludoviciana*) reach their peak abundance at high soil nitrogen, both within individual fields and for all fields combined (Fig. 3).

These patterns have led us to formulate a series of hypotheses concerning the forces structuring these old field ecosystems. Much of our experimental and observational work is testing these hypotheses. The major questions raised by our old-field survey are:

1. Is nitrogen the main soil resource limiting plant productivity in Cedar Creek old fields and in native vegetation?

2. Is the rate of nitrogen mineralization in Cedar Creek soils proportional to total soil nitrogen?

3. Is the apparent increase in soil nitrogen suggested by the old field survey really an

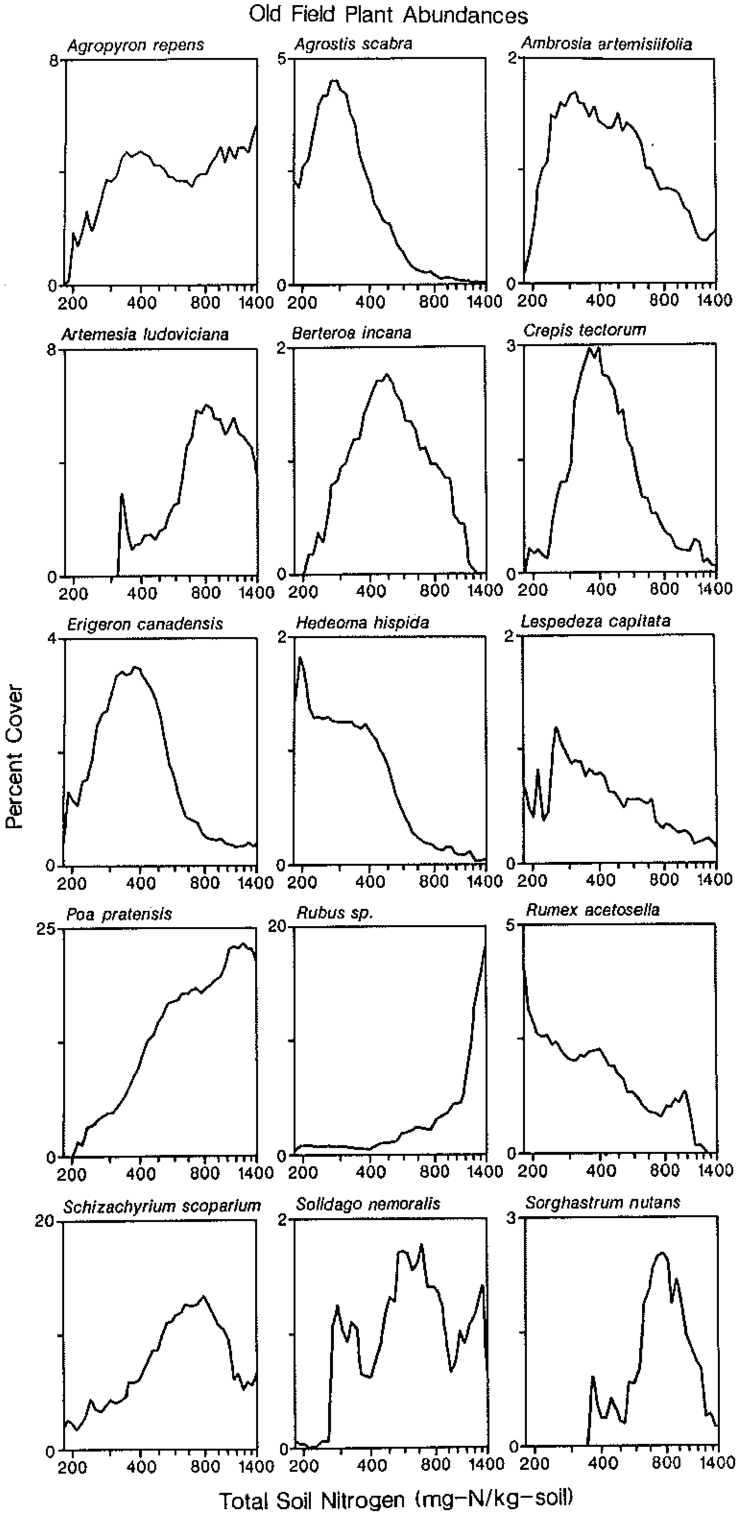


Figure 3. These figures show the dependence of plant abundance on soil nitrogen in the old field survey. These are based on all 2300 plant and soil samples. To obtain these curves, the observed total soil nitrogen levels were divided into 40 classes of equal size on a natural log scale. The average percent cover of each plant species was then calculated for all quadrats falling in each soil nitrogen interval. These averages were then smoothed once using running averages to get the figures above.

increase in nitrogen through time, or were the fields abandoned 50 years ago more nitrogen rich than those abandoned recently?

The old field survey provided us with strong correlations, but correlations need not be indicative of causation. If nitrogen does increase through time, we should be able to detect these increases when we re-sample our 2200 permanent old field quadrats after a 7 year interval. The slope of the observed regression predicts that there should have been an average increase of 6.8 ppm of N per year. After 7 years, this should thus give an increase of almost 50 ppm of N. Because we have archived the dried soil samples we originally collected, upon resampling these 2200 quadrats in 1990 we will be able to directly calculate the differences in total soil nitrogen for each quadrat without having to allow for any change that may have occurred in our chemical technique during that interval.

4. Assuming that soil nitrogen does increase during secondary succession, what causes this increase? Is it caused by nitrogen fixation by legumes, blue-green soil algae, or various associative N-fixing bacteria in the rhizosphere? Or, is it caused by a slow accumulation of fixed nitrogen that enters via wet and dry fall, and which is not lost from the soil? To what extent can the accrual of soil nitrogen be explained by a simple model of atmospheric inputs and atmospheric and soil leaching losses?

5. How do litter accumulation and decomposition influence soil change during succession? Why does litter accumulate during succession? Do later successional species produce low-quality litter (high C:N ratios, high lignin content) that effectively causes soil development to cease at a point at which those species are favored?

6. Is the observed sequence of plant species dominance during secondary succession at Cedar Creek caused by changes in soil nitrogen and associated changes in light interception?

a. If so, then each species should be a superior competitor at a particular rate of nitrogen supply (Tilman 1982).

b. If so, then experimental changes in the rate of nitrogen supply should cause species composition to change in a manner consistent with the patterns shown in Figure 3.

c. If so, then pairwise competition experiments should be consistent both with species responses to experimental N gradients and with species distributional patterns during succession (Fig. 3).

d. If so, the physiology, morphology, and growth allocation patterns of each species should be consistent with its position of peak abundance along the temporal nitrogen gradient of succession (Tilman 1982, 1985, 1986a).

7. Is the observed successional sequence at Cedar Creek caused by herbivory?

a. If so, then herbivore removal or addition experiments should lead to changes in the plant community composition. Specifically, the patterns we observed in our old field survey predict that (1) removal of gophers should increase the rate of succession, since gopher activity declined during succession in our old field survey; (2) gopher addition should favor early successional plant species.

b. Alternatively, it may be that vegetation change, whatever its cause, is the cause of changes in herbivore density during succession. Specifically, it may be that gopher densities decline during succession because later successional plants are poorer foods for gophers. If this is so, feeding trials should reveal that gophers feed preferentially on early successional plants.

8. Is Cedar Creek succession determined by both direct and feedback effects involving soils, plants and herbivores? If it is, the concept of cause and effect, itself, becomes of limited utility and a systems approach would provide the only explanation for the observed patterns.

9. Compared to many other ecosystems, herbivore densities are low in the low-productivity, nitrogen poor fields of Cedar Creek. Might herbivory be less important in unproductive habitats, especially those with nitrogen-poor soils, because herbivores would be protein-limited and kept to lower population densities than in more productive ecosystems?

10. Do the short-term dynamic responses of ecosystems to disturbances differ from their long-term responses?

If transient effects are common, short-term experiments may give misleading information on the true long-term role of various processes in structuring natural communities. Only long-term observational and long-term experimental studies will be able to determine which responses are transients and which are indicative of the long-term effects of a manipulation. However, if ecosystems do show transient effects, experimental manipulations of ecosystems must be performed over sufficiently long periods of time to observe both the transient and the long-term change in the ecosystem caused by a given manipulation. If experiments are performed on too short a time scale, valid hypothesis may be rejected and incorrect hypotheses may be supported. This is an especially great danger because so many ecological hypotheses are qualitative statements of the likely long-term outcome of a process, not detailed, mechanistic models of short-term dynamics.

D. CEDAR CREEK LTER EXPERIMENTAL FIELDS

From among the 22 fields forming the old field chronosequence, we chose four fields in which to perform most experiments. Some work is also being done in a fifth field. We are restricting our experiments to these five fields because we wish to obtain detailed information on a variety of ecosystem processes, and their underlying mechanisms, in the same localities so that we may directly compare them one to the other. The four fields represent a successional gradient, from a 14 yr old field (Field A), to a 25 yr old field (Field B), to a 48 yr old field (Field C) and finally to native oak savanna (Field D). By replicating most of our long-term experiments in each of these four fields we are able to determine if the effect of a process changes during succession and test a variety of ideas concerning convergence, divergence and multiple stable equilibria. The general characteristics of the five fields are given below.

Field A (Fig. 4B) was last cultivated and planted, to soybeans, in 1968. It had been abandoned 14 years when this work began in 1982. It has a Sartell fine sand soil, an

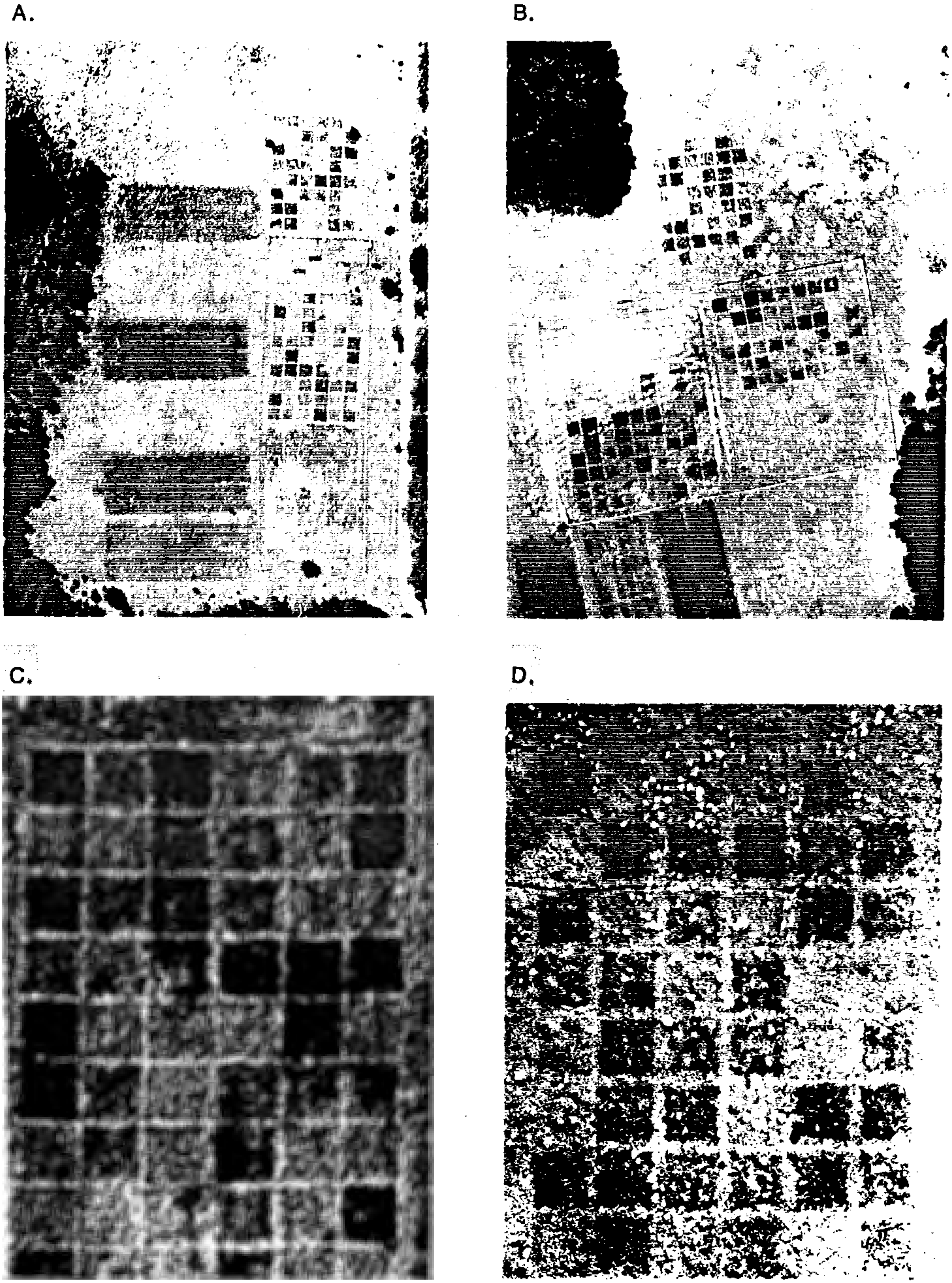


Figure 4

excessively well-drained soil formed in sandy outwash and aeolian sediments (Grigal et al. 1974). The dominant species in Field A are Agropyron repens, Berteroa incana, Agrostis scabra, Achillea millefolium, Erigeron canadensis, Aristida basiramea, Ambrosia artemisiifolia, Poa pratensis, and Potentilla recta.

Field B was last farmed in 1957 (last crop: soybeans). It was 25 years old in 1982. It has a Zimmerman fine sand soil, similar to the Sartell sand except for a thicker B2t than the Sartell soil (Grigal et al. 1974). Its dominant plant species are Schizachyrium scoparium, Poa pratensis, Panicum oligosanthes, Lespedeza capitata, Cyperus filiculmis, Rosa arkansana, Solidago rigida, and S. nemoralis.

Field C, the oldest of the abandoned fields (Fig. 4A), was last farmed, to corn, in 1934. It was 48 years old in 1982. Its soil is a fine Zimmerman sand. Its dominant plants are Schizachyrium scoparium, Artemisia ludoviciana, Poa pratensis, Stipa spartea, Sorghastrum nutans, Solidago nemoralis, Aster azureus, Ambrosia coronopifolia, and Carex sp. Field C contains many seedlings and a few scattered saplings of Quercus macrocarpa, Q. ellipsoidalis, and Q. borealis, especially at the field edges, but no mature trees.

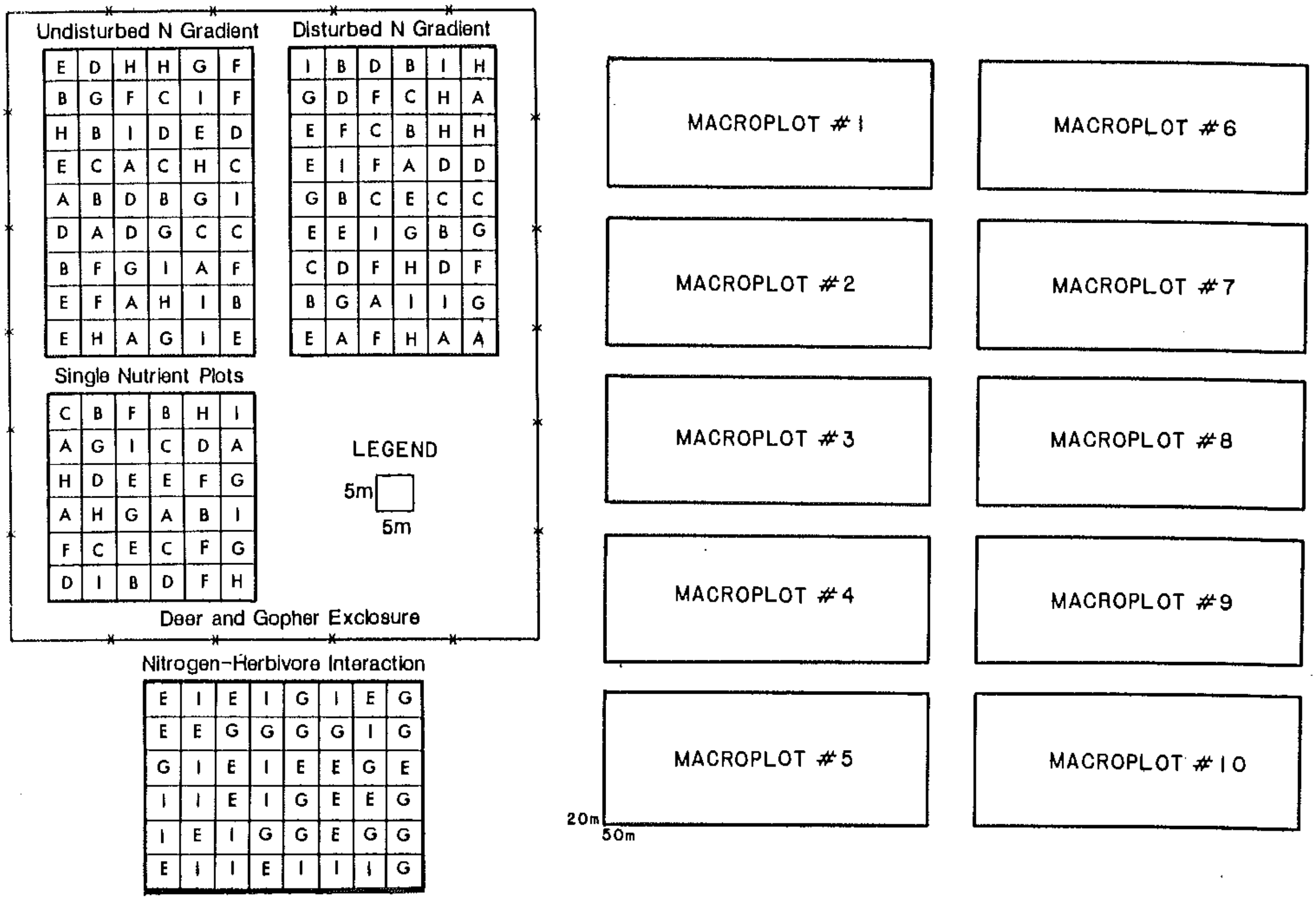
Field D, native oak savanna, has never been clear-cut or plowed, although it was possibly grazed prior to 1940. Its soil is a Sartell fine sand. It is one of several compartments in a prescribed burn experiment (White 1983). Since 1966 it has been burned, generally in late April or early May, for 2 years in succession followed by one year without burning. The entire field, including the experimental plots, was burned on April 27, 1982, April 17, 1984, and April 11, 1985, but not burned in 1983. The dominant herbaceous species are Carex muhlenbergii, Andropogon gerardi, Sorghastrum nutans, Artemisia ludoviciana, Carex pensylvanica, Solidago graminifolia, Poa pratensis, Schizachyrium scoparium, Stipa spartea, Panicum perlongum, Rubus sp., Helianthemum bicknellii, and Liatris aspera. In addition, it contains scattered oaks (Quercus macrocarpa, Q. ellipsoidalis, Q. borealis).

Field E, our fifth field, is the youngest and most nitrogen poor of all the fields. Last farmed (to rye) in 1975, it was 7 years old in 1982. Its Sartell fine sand soil is dominated by Agrostis scabra, Agropyron repens, Ambrosia artemisiifolia, Chenopodium album, Berteroa incana, and Crepis tectorum.

E. LONG-TERM EXPERIMENTS

The basic layout of our on-going field experiments is illustrated in Figure 5. The actual layout of plots in Fields C and A are shown in the aerial photographs of Figure 4A and 4B, respectively. Note that some macroplots are not included in these pictures. Parts C and D show closeups aerial photographs of nitrogen-gradient microplots without mammalian herbivores (Fig. 4C) and with them (Fig. 4D). The small dots are gopher mounds. Because of limited space in the field of native oak savanna and because of the permanent damage to oaks that could have resulted from trenching to bury fence to exclude gophers, some experiments were performed just in Fields A, B and C. Each experiment was designed to test a different, though interrelated, hypothesis. Each has a different time

LAYOUT OF FIELD EXPERIMENTS



Undisturbed N Gradient

E	D	H	H	G	F
B	G	F	C	I	F
H	B	I	D	E	D
E	C	A	C	H	C
A	B	D	B	G	I
D	A	D	G	C	C
B	F	G	I	A	F
E	F	A	H	I	B
E	H	A	G	I	E

Disturbed N Gradient

I	B	D	B	I	H
G	D	F	C	H	A
E	F	C	B	H	H
E	I	F	A	D	D
G	B	C	E	C	C
E	E	I	G	B	G
C	D	F	H	D	F
B	G	A	I	I	G
E	A	F	H	A	A

Single Nutrient Plots

C	B	F	B	H	I
A	G	I	C	D	A
H	D	E	E	F	G
A	H	G	A	B	I
F	C	E	C	F	G
D	I	B	D	F	H

Nitrogen-Herbivore Interaction

E	I	E	I	G	I	E	G
E	E	G	G	G	G	I	G
G	I	E	I	E	E	G	E
I	I	E	I	G	E	E	G
I	E	I	G	G	E	G	G
E	I	I	E	I	I	I	G

Figure 5. Typical layout of some of the major experiments within a field. The smaller plots are microplots whereas the larger plots are macroplots. The letters A through I refer to treatments. Note that all experiments include from 3 to 6 replicates of each treatment. Most experiments are replicated in all four experimental fields. A completely randomized experimental design was used in each experiment. For sampling frequencies for various experiments, see Table 2. See Figure 4A and B for aerial photographs of actual plot layouts in Fields A and C.

scale on which it is likely to show its response. For example, our study of above- and below-ground productivity uses biweekly sampling throughout the entire growing season. The fenced microplot experiments are being sampled once each year to detail year-to-year plant and litter dynamics. Most other experiments were designed to determine the long-term, total effect of a given manipulation. These are sampled every other year on a rotating basis, or more frequently, if possible.

1. SINGLE-NUTRIENT ADDITION EXPERIMENTS

In 1982 we established 36 plots in each of the four main experimental fields. These 36 plots were randomly assigned to receive one of 9 treatments, with 4 replicates of each treatment in each field. The treatments consist of addition of various potentially limiting soil resources, each added singly, as well as a control. The nutrients, added twice a year, are N, P, K, Ca, Mg, S, a trace metal mixture, water (2.5 cm/wk throughout the growing season). In the past four years, we have harvested above-ground biomass in these plots four times. ANOVA of the results of these experiments, and contrasts using Dunnett's t (Steel and Torrie 1980), showed that **nitrogen** addition led to significant increases in above-ground plant biomass compared to controls in 10 of the 16 possible cases. Phosphorus, magnesium and water were each significant in only 1 of 16 possible cases each. No other treatment was significant for any field or in any year. Similar results have been obtained in separate experiments in Field E (Tilman 1983, 1984). Thus, of all the soil resources added, nitrogen is far and away the most important in limiting primary production throughout succession at Cedar Creek. For this reason, we have focused on nitrogen as the most important soil factor likely to influence primary productivity, plant community composition, and successional dynamics. Because we will continue these experiments indefinitely, we will be able to determine if year-to-year climatic variation affects the pattern of resource limitation at Cedar Creek.

2. NITROGEN-GRADIENT MICROPLOT EXPERIMENTS

Several of our major, long-term experiments at Cedar Creek involve manipulation of primary productivity via nitrogen fertilization. Most of these experiments are performed in what we call "microplots." Each microplot is a 4m x 4m plot separated from other plots in the same experiment by 1m wide buffers that serve as walkways and prevent plants in one plot from receiving nutrients supplied to another plot. In general, our nitrogen-gradient microplot experiments contain 9 different treatments, with 6 replicates of each treatment for each experimental type within a field. The treatments consist of a completely unmanipulated control as well as 8 other treatments that receive the same background mixture of P, K, Ca, Mg, S, Cu, Mn, Co, Cu, and Zn but differ in the amounts of nitrogen added (Fig. 6). A completely randomized experimental design was used in each field, with treatments assigned to plots at random. Nutrients are applied twice each year, starting in 1982, with half applied in mid-May and half in late June.

This experimental design establishes a primary productivity gradient with numerous replicates of each productivity level (Figs. 4 and 5). Many studies have suggested that along productivity gradients there are major changes in above-ground versus below-ground allocation (e.g., Chapin 1980; Grime 1977), species diversity (Beadle 1966; Holdridge et

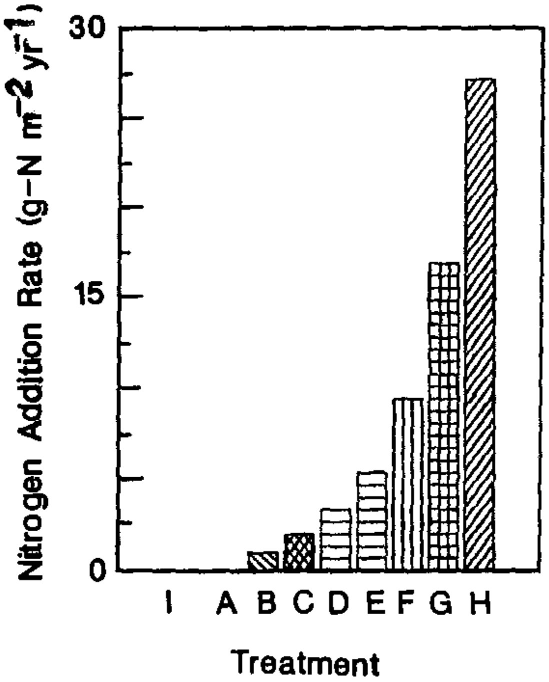


Figure 6. Experimental rates of nitrogen addition for microplot and macroplot nitrogen gradient experiments. Note that rates are expressed as g/m^2/yr of N (added as ammonium nitrate). Letters A through H refer to the treatments illustrated in Figure 5 (except for the Single Nutrient Plots). Treatment I received no nutrients. Treatments A through H received the same mix of P, K, Ca, Mg, S, and trace metals.

al. 1971; Specht and Rayson 1957; Al-Mufti et al 1977; Bakelaar and Odum 1978; Tilman 1982), nutrient cycling (Gorham, Vitousek and Reiners 1979), plant species composition (Tilman 1982), herbivory (Fretwell 1977; Oksanen et al. 1981) and plant physiognomy (Beadle 1954; Cody and Mooney 1978). We have established experimental productivity gradients so that we may determine if there is a causal relation between productivity (nitrogen supply rate) and such ecosystem features. We have used the basic design detailed above to establish three different types of experiments:

(A) **Undisturbed Microplot Nitrogen Gradients** are performed on the existing **natural vegetation** in each of the four fields, but inside mammalian **herbivore exclosures**;

(B) **Disturbed Microplot Nitrogen Gradients** are performed on newly **disturbed** (thoroughly disced) ground in each field (except Field D) inside mammalian **herbivore exclosures**;

(C) **Microplot Nitrogen Gradients with Herbivores** are performed on the existing **natural vegetation** in each field (except field D) in an area that is **open to herbivores.**

These three different experimental types, because of the replication of treatments within each field and the replication of experiments among the fields, allow us to assess the direct and indirect effects of several processes. The Undisturbed Microplot Nitrogen Gradient experiments show the effects of changes in nitrogen supply rates on productivity, species diversity, vegetation height, vegetation composition, and litter dynamics for existing vegetation. The Microplot Nitrogen Gradients with Herbivores will demonstrate how mammalian herbivory depends on primary productivity and standing crop. They can be compared with the microplots without herbivores. This comparison will demonstrate if the herbivores are having a significant impact on species diversity, species dominance patterns, primary productivity, and litter dynamics. The difference between the fenced and the unfenced plots is a measure of the total effect of mammalian herbivores. The Disturbed Microplot Nitrogen Gradient experiments, in comparison with those on indisturbed ground, test for convergence and thus for the presence of multiple stable equilibria in these ecosystems. If ecosystems have multiple stable equilibria

(Lewontin 1969; Strobeck 1973; May 1977, 1979), all future states of an ecosystem will depend on its past history. This is because multiple stable equilibria imply that, even in exactly identical physical environments with exactly the same repertoire of species, the long-term outcome of their interactions will depend on initial species densities. Although Connell and Sousa (1983) suggested that multiple stable equilibria may be rare in nature, theory predicts that they could be common (May 1977, 1979). There are not yet any field experiments with sufficient replication and a sufficiently long period of observation to determine if or when ecosystems have multiple stable equilibria. Our comparisons of the long-term outcomes of the microplot nitrogen gradient experiments performed on disturbed versus those on adjacent undisturbed ground should determine the frequency of multiple stable equilibria in old fields. We will compare these results with those from qualitatively similar experiments performed at the Niwot Ridge LTER site.

The microplots, in conjunction with a variety of short-term experiments, are providing information on the mechanisms of interspecific interaction. Such information is critical in testing hypotheses suggested by our old field chronosequence survey. One of the goals of our work is to determine how small scale processes can be integrated into landscape level patterns. For instance, our old field survey suggests that long-term changes in nitrogen availability may be a cause of the successional pattern (Fig. 3). If this hypothesis is correct, then the pattern of vegetational composition along experimental nitrogen gradients should be consistent with the patterns observed along the natural nitrogen gradients both within and among the 22 fields of our survey. Although 4 years is too short a time within which to expect vegetation to reach a new state determined by our experimental rates of nitrogen addition, there are already broad similarities between the patterns in Fig. 3 and those observed in our Undisturbed Nitrogen Gradient Microplots (Tilman, #1 in review). If the long-term pattern of change in the microplots proves to be consistent with the pattern of field-to-field variation in the old field chronosequence and if the 2300 quadrats in the old fields show changes consistent with the original pattern in the old fields, then it could be validly concluded that the mechanisms encompassed by the microplots were an important control of landscape patterns.

Microplot Results to Date

These experiments have already yielded a wealth of information. Indeed, we have prepared four manuscripts, containing 100+ pages of text and 22 figures, based on our results to date (Tilman, #1 in review; Tilman, #2 in review; Inouye and Tilman, in review; Inouye and Huntly, in review). We can provide but a brief summary of these here.

In none of the fields, for none of the microplot nitrogen gradient experiments, did total plant biomass, plant height, species richness, litter production or light penetration respond to the combined addition of P, K, Ca, Mg, S and trace metals. In contrast, plant biomass and height increased significantly, and light penetration decreased significantly with added nitrogen in all three experimental types in all four fields (Fig. 7). This supports the view that nitrogen is the major limiting soil resource in old fields and native vegetation at Cedar Creek.

Species Richness

Although species richness was unaffected by or increased slightly with nitrogen addition during the first field season, species richness decreased significantly with the rate of nitrogen addition in subsequent years. On average over all the experiments in all the fields, more than 50% of the species had been displaced from high nitrogen treatments by 1985 (Fig. 7 M-P). The decreased diversity observed along these gradients is consistent with predictions of resource competition theory. Theory (Tilman 1982: 113) predicts that species richness should decline most rapidly with enrichment when all resources but one are added in excess. This is because all species should become limited by the same resource (the resource not added -- here, probably light), and the one species that is the superior competitor for that resource should displace all others. A superior competitor for a resource is a species that is able attain a more rapid net growth rate at low levels of that resource (Tilman 1980). The strong inverse correlation

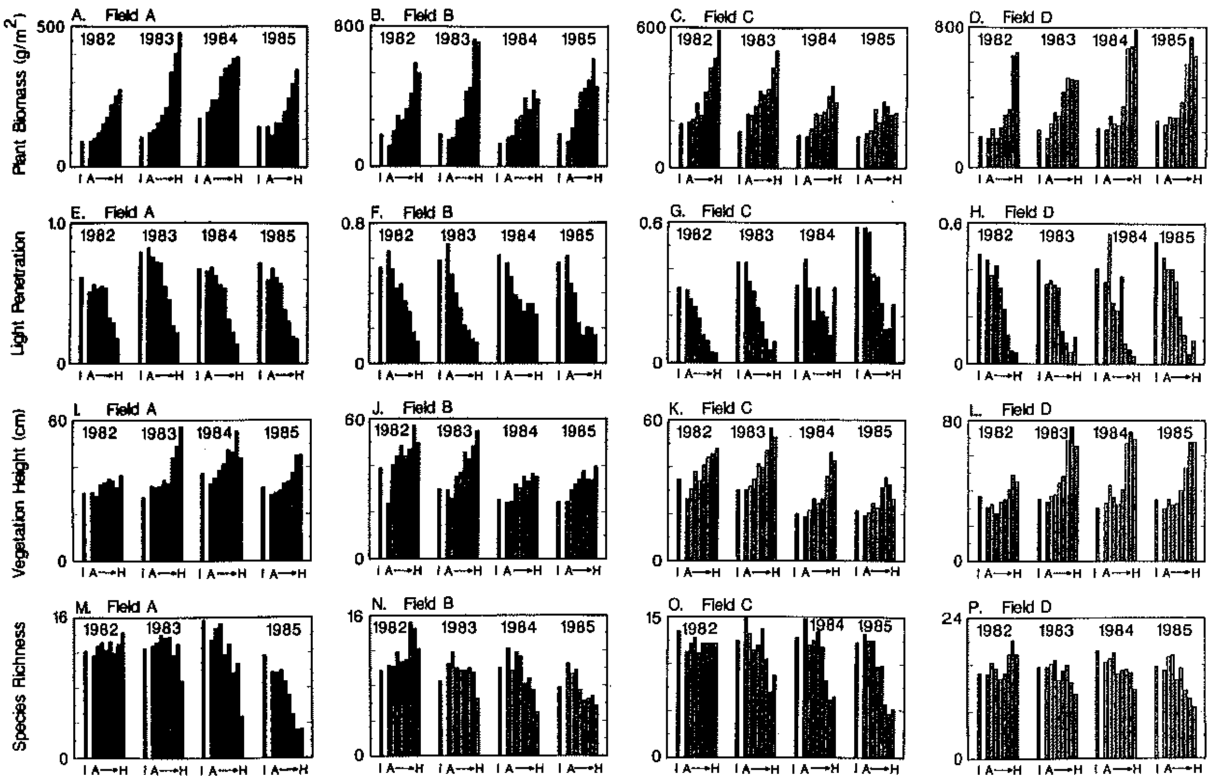


Figure 7. **Undisturbed Nitrogen-Gradient Microplot Experiments.** Each bar in each histogram of this figure shows the average value of a variable over all 6 replicates for a particular field and year. Treatment I, the control, received no nutrients. It is shown separate from, and to the left of, treatments A through H. Treatments A through H form the nitrogen gradient, with the rate of nitrogen addition increasing progressively from treatment A (no nitrogen) to treatment H (highest rate of nitrogen addition each year). Treatments A through H received the same mixture of P, K, Ca, Mg, S and trace metals. Parts A-D of this figure show total above-ground living plant biomass in all treatments in 1982, 1983, 1984 and 1985 in fields A, B, C and D, respectively. The proportion of light penetrating to the soil surface is similarly shown in parts E-H. Average vegetation height, shown in parts I-L, was calculated as a weighted average of heights of the major species. Species richness, shown in parts M-P, is the average number of species found in $0.3m^2$ samples collected in the six replicates of each treatment.

between species richness and light penetration (Fig. 7) supports this view. Our experimental results to date are consistent with the work of Beadle 1966, Dix and Smeins 1967, Grime 1973, Huston 1980, Bond 1983, Elberse et al. 1983, Milton 1947, Willis and Yemm 1961, Kirchner 1977, Bakelaar and Odum 1978, Silvertown 1980, and Tilman 1982. They also agree with the significant decrease in species richness that we observed in our more nitrogen rich old field quadrats (Inouye et al. 1986).

Herbivory

There were some significant differences between the nitrogen gradient experiments with herbivores and those without. Various grasshopper species (Melanopus femurrubrum and M. bivittatus), a vole (Microtus pennsylvanicus), and the plains pocket gopher (Geomys bursarius) (Fig. 8) demonstrated strong preferences for the plots receiving higher rates of nitrogen addition. Several other herbivorous insects responded similarly (Strauss, in review). The strong preference of gophers for the high nitrogen treatments was associated with a much greater rate of microsite disturbance within these plots caused by gopher mounds (Fig. 8). This increased gopher activity caused within-plot spatial variation in light penetration to increase with productivity. This increased spatial heterogeneity apparently allows several annual and short-lived perennial plants to persist in high nitrogen treatments from which they were displaced in the absence of gophers (Tilman 1983). Thus, there is an indirect, feedback effect of gophers on successional dynamics because gophers prefer more productive sites but their activity creates early successional conditions. Up to the present time, however, despite significant effects of the nitrogen gradients on herbivores, the presence of herbivores has not led to qualitative changes in the responses of most dominant plant species to the nitrogen gradients. This may mean that herbivores do not greatly influence successional dynamics and local spatial structure at Cedar Creek, or that more than four years are required for them to have an effect. Our next four years of work should provide the answer.

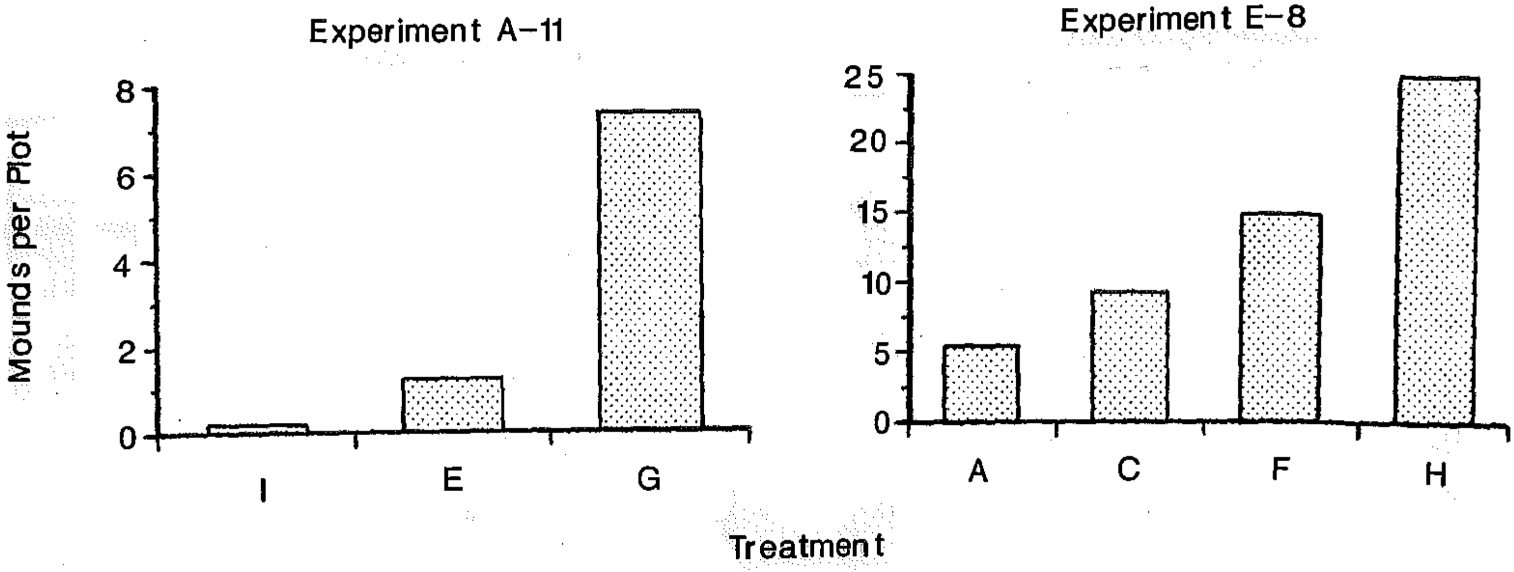


Figure 8. Production of new gopher mounds (see Fig. 4D) increases highly significantly with nitrogen addition rate. Treatments I to E to G represent a gradient of increasing N supply, as do treatments A, C, F and H. In all fields in which gophers are present, there is increased gopher feeding activity and disturbance, as estimated by gopher mounds, in more productive micro or macro plots.

Transient Dynamics

Annual plants comprised a noticeable portion of the pre-treatment plant biomass (as estimated from the 1982 samples of the unfertilized controls) in the Undisturbed Microplot Nitrogen Gradient experiments in Fields A and B, but were rare in Fields C and D. In Fields A and B, the relative abundance of annual plants, as a group, increased significantly along the nitrogen gradients in 1982, but decreased significantly along the gradients by 1984. The relative abundance of all vascular perennial plants decreased significantly along the gradients in 1982 in but increased along in 1984 and 1985. Thus, nitrogen fertilization led to a period of transient dominance by annual plants, which were then displaced by various perennial species.

Similar patterns of transient dominance can be seen in the population dynamics of individual species. In general, the species that increased most in response to nitrogen addition the first year decreased along the gradient in the second, third and fourth years. For instance, in Field A the relative abundances of Berteroa incana and Ambrosia artemisiifolia increased greatly along the gradient in 1982, but decreased in 1983 or 1984 (Fig. 9). The relative abundances of Agropyron repens, Achillea millefolium and

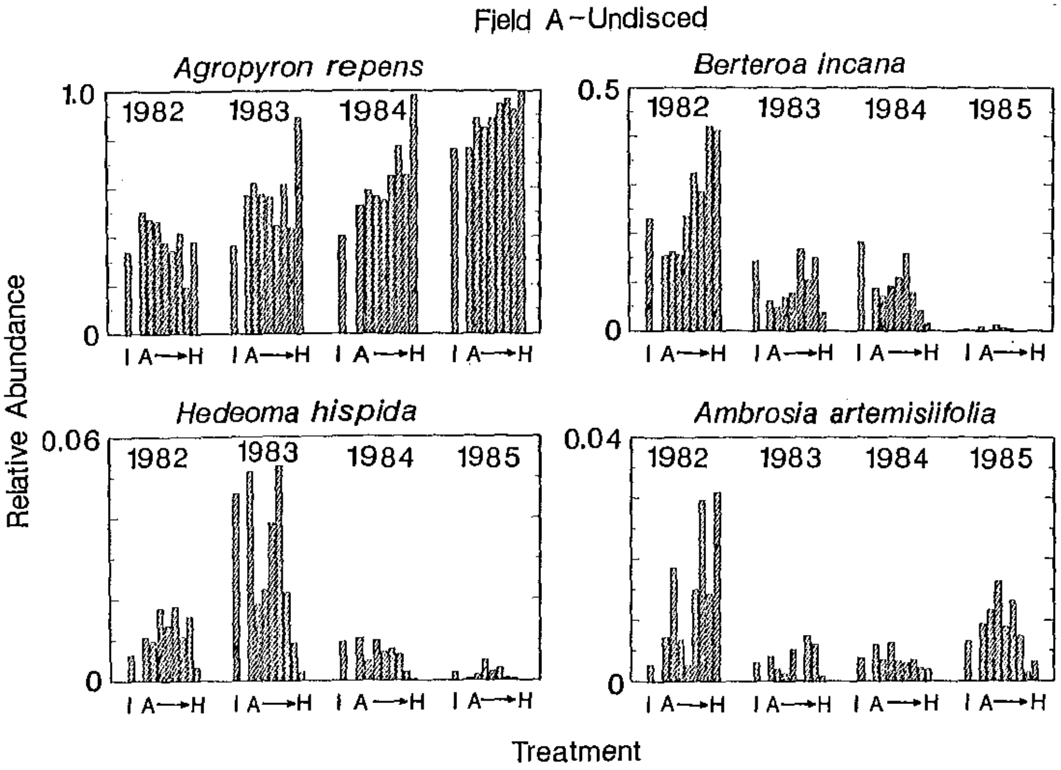


Figure 9. Relative abundances of some major species in the Field A Undisturbed Nitrogen-Gradient Microplots. Note the transient increases by Berteroa, Ambrosia and Hedeoma before their displacement by Agropyron. See Figure 7 for a detailed explanation of these graphs.

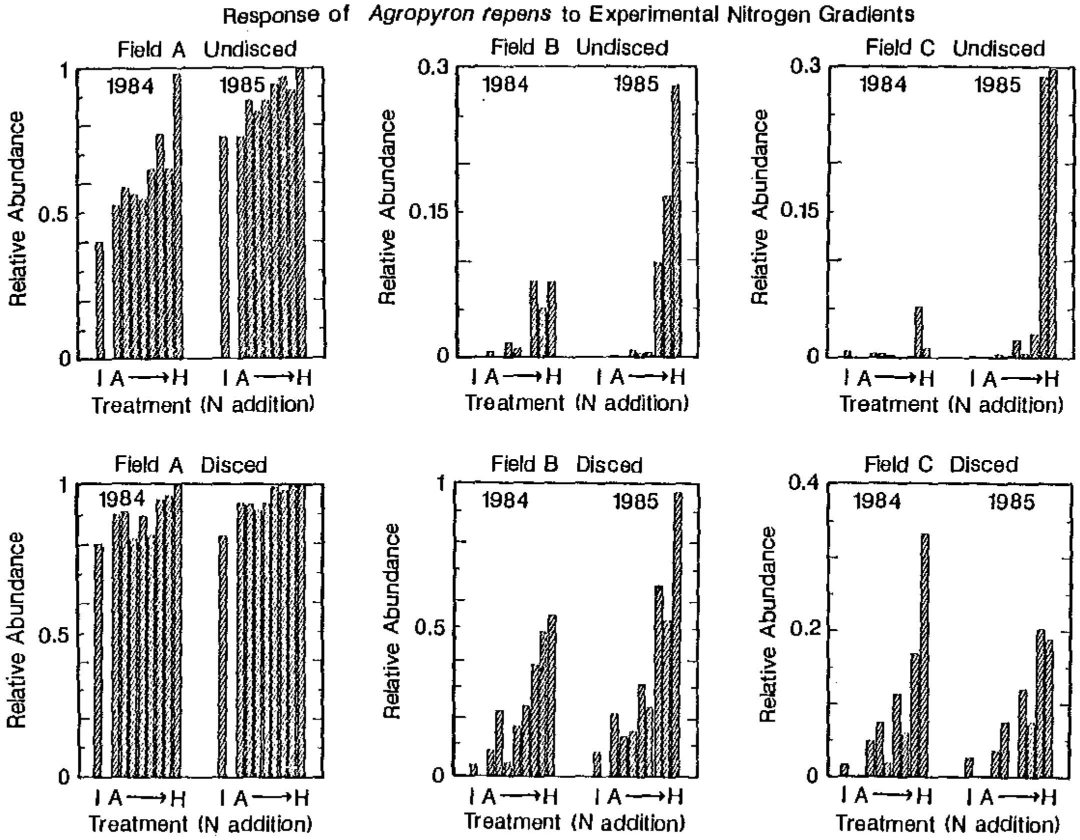


Figure 10. Response of Agropyron repens to experimental nitrogen gradients in both disced and undisturbed plots. For brevity, only the 1984 and 1985 responses are shown. See Figure 7 for a detailed explanation of these graphs.

Erigeron canadensis did not change along the gradient in 1982, but increased along the gradient in 1983. Thus the species that grew the most rapidly initially, following an increase in the supply rate of nitrogen, were displaced by other species that did not respond initially, but which did increase under the new conditions of higher plant biomass and lower light penetration. In Field B, Rumex acetosella was the only major species to increase significantly in relative abundance along the gradient in 1982. In 1983 and 1984, its relative abundance decreased significantly along the gradient with its absolute abundance in the highest nitrogen plots dropping by a factor of 30 from 1982 to 1983. Similar patterns occurred in Fields C and D.

These results demonstrate that the immediate response to addition of nitrogen is often the exact opposite of the response observed several years later; i.e., that nitrogen addition leads to a period of transient dominance by species that are later displaced. Theory (Tilman 1985) suggests that at least some of the species dominant during the fourth year of these experiments may also be transients. It is imperative that experiments such as these be allowed to proceed for a period long enough to distinguish long-term effects from transient responses.

Our results to date provide an important warning. Most ecological theory is equilibrium theory. It attempts to predict the long-term effect of a given variable or process. However, many ecological field experiments last only one to three years. The results we have obtained in the first four years of our experiments at Cedar Creek demonstrate the existence of transient responses to our experimental manipulations. Our results suggest that these transient responses can be the exact opposite of the long-term responses. If this is so, the current emphasis on short-term experimentation could lead ecologists to draw improper conclusions because their experiments are too short to detect the long-term, total effects of the manipulations.

Convergence, Divergence and Multiple Stable Equilibria

Although the four fields differed in their initial soil chemistry and initial vegetational composition, the treatments imposed similar nitrogen gradients in all four fields. If nitrogen supply rates are more important than past history in determining vegetation response, then each species should have a qualitatively similar distribution and occur in the same order along the experimental nitrogen gradients in these four fields (Tilman 1982).

Comparisons within the Undisturbed Nitrogen Gradient Microplots: By 1985, *Agropyron repens* had similar distributions along the experimental gradients in Fields A, B and C (Fig. 10). It increased significantly along the gradients in all 3 fields in 1985, despite its initial rarity in Fields B and C. It invaded and dramatically increased in abundance in many high nitrogen plots from which it was absent in 1982. *Poa pratensis* had similar, highly significant Gaussian distributions along the gradients in Field C and D in 1985 (Fig. 11). *Schizachyrium scoparium* declined in abundance along the nitrogen gradients by 1985 in all fields in which it occurred (Fig. 11). Indeed, of all the major producer species in common among two or more of these experiments, all except one had qualitatively similar distributions along the experimental nitrogen gradients in the undisturbed plots by 1985. Although their qualitative responses seem to be converging, their absolute abundances are not converging, as indicated by the progressively decreasing values of the proportional similarity index we have observed in the high nitrogen treatments in Field B and C (Inouye and Tilman, in review). To demonstrate that there are no multiple stable equilibria will require that both qualitative patterns and absolute abundances converge (Strobeck 1973; May 1977). It is likely to be many more years before the vegetation stabilizes and allows us to validly test these hypotheses.

Disced versus Undisced Plots: Because of discing, the Disturbed Microplot Nitrogen Gradients and the Undisturbed Microplot Nitrogen Gradients in each field differed greatly in the initial abundances and life history stages of major plant species, litter cover and depth, and soil profiles. If multiple stable equilibria occur in successional fields, these plots should reveal them. We have analyzed the data collected during the first four years in two different manners (Inouye and Tilman, in review). First, we used a

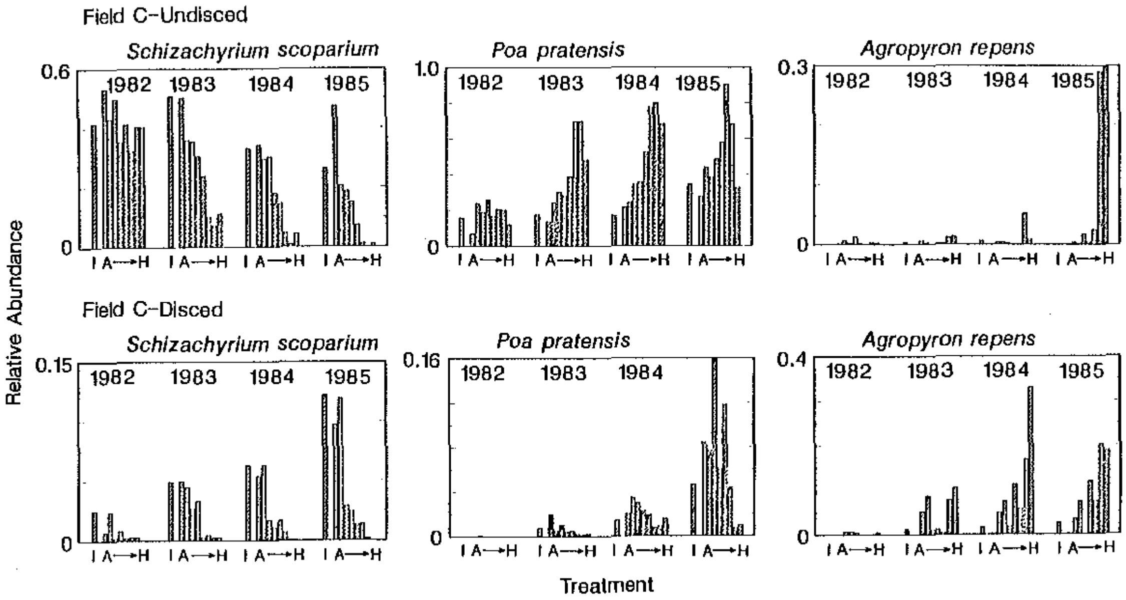


Figure 11. Convergence in the response of three dominant plants to the experimental nitrogen gradients in disced versus undisturbed areas of Field C.

proportional similarity index (Pielou 1984) to compare treatments between disced and undisced plots in the same field (Fig 12). Within each treatment, similarity increased strongly through time in Field A. Similarity was low, but increased through time in Fields B and C (Fig. 12). Second, we compared the responses of major species to the gradients in the disturbed and the undisturbed fields (e.g., Fig. 11). In general, this suggested that convergence was occurring but there were some cases of divergence. Whether or not these plots converge is of great ecological importance, for it is a measure of the role of history versus biotic interaction in structuring ecosystems. Thus, we plan to sample all these plots once each year for as long as we have funding.

We will also perform a series of **invasion experiments** to determine if species not yet present in particular plots or fields can successfully increase in abundance. This is an especially important question for the high nitrogen plots, since many of these have become virtual monocultures. They may be monocultures because the dominant species are the superior competitors of all the species at Cedar Creek, or they may be invasible by other species that are not yet present in the field. We will perform two different types of invasion experiments. Both will be located in the Unfenced Nitrogen Gradient Microplots, because we have 16 replicates of each treatment for these plots and thus can afford to use several replicates in this experiment. One experiment will consist of reciprocal transplants of 20 cm diameter cores of turf among low, medium and high nitrogen plots in Fields A and D. This will determine if native tallgrass prairie species and/or Agropyron repens can invade and displace each other. We will also perform seed addition experiments to determine if seeds and vegetative plants of a given species differ in their ability to invade. If they do, this would suggest that there could be multiple stable equilibria in this vegetation, since established plants would have a lasting advantage. These invasion experiments, in combination with the ongoing observations in the microplots, should determine the extent and prevalence of convergence, divergence and multiple stable equilibria in Cedar Creek successional

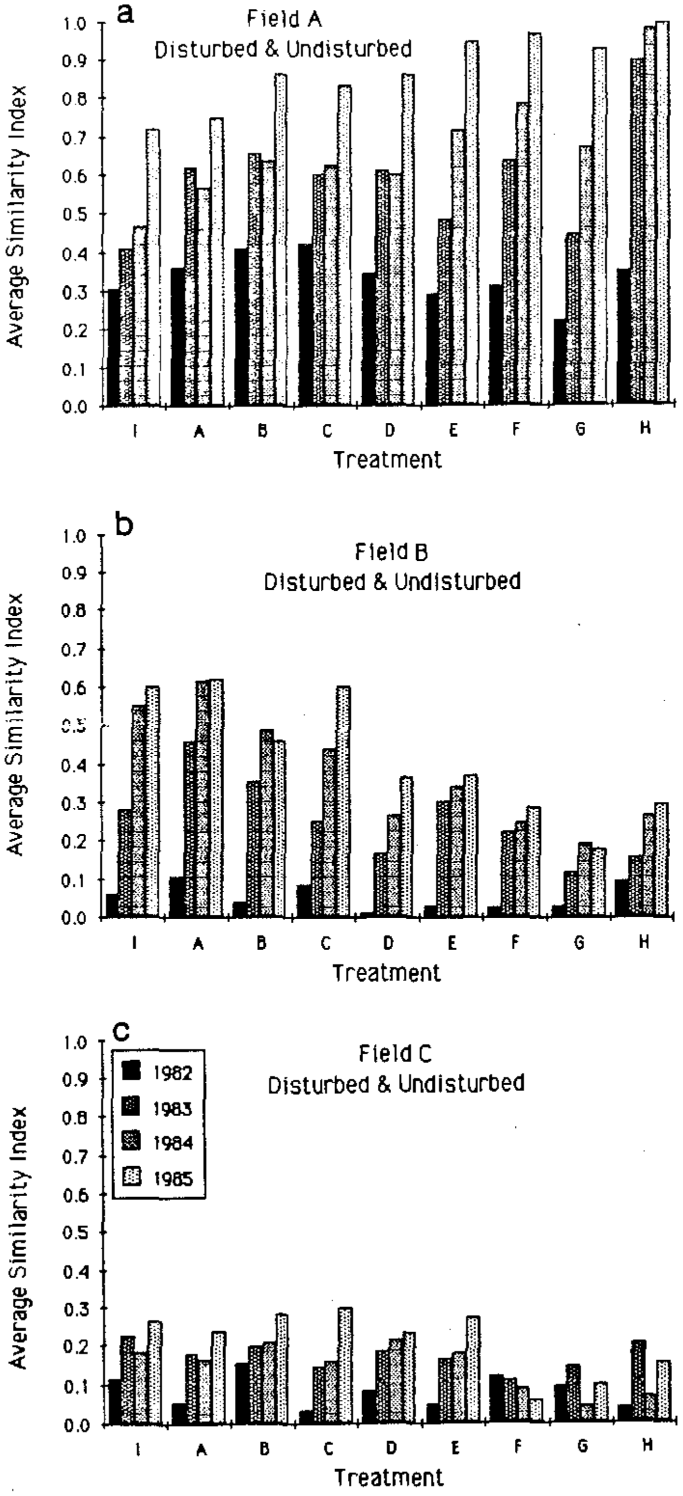


Figure 12. Average similarity of disced versus undisced plots within each field. Each bar is the mean proportional similarity (Pielou 1984) of the 36 pairwise comparisons among disced versus undisced plots in each treatment. Note the sharp increase in similarity through time.

vegetation.

Landscape Patterns versus Microplot Experimental Results

All of the plant species dominant in the microplots are also dominants at some time during secondary succession at Cedar Creek. The old field chronosequence data (Figs. 2 and 3) have shown a strong correspondence between soil nitrogen levels and the abundances of these species. For most species, abundance depends on soil nitrogen within each field in the same way that it depends on nitrogen when all fields are considered together. This suggests that the same processes that cause point-to-point variation in vegetation within the landscape of a single field cause field-to-field variation in vegetation across fields of different successional ages. It also suggests that soil nitrogen may be a main cause of these spatial and temporal patterns. If this is so, then plant species should become separated along the microplot nitrogen gradients in the same way that they are separated along the temporal nitrogen gradient of succession and the spatial nitrogen gradients within each field. We have used the data available from the fourth year of the microplot experiments to test this hypothesis (Tilman, in review). Clearly, this must be considered a preliminary test since plant abundances are still changing rapidly by the fourth year.

If this hypothesis is correct, the response of a species to experimental nitrogen addition should depend on the total nitrogen level within the field. If the nitrogen level in a field is beyond the peak of the old field distributional curve of a species, as it is in all fields for Rumex acetosella, Hedeoma hispida, Lespedeza capitata, Agrostis scabra, Ambrosia artemisiifolia, and Berteroa incana (Fig. 7), then nitrogen addition should cause these species to decline in abundance. Although the absolute and relative abundances of many of these species increased significantly with the rate of nitrogen addition in 1982 or 1983, none of them did so in 1984 or 1985. By 1984 and 1985, the absolute and relative abundances of 5 of these 6 species **declined significantly** along the experimental nitrogen gradients (Tilman, in review).

Species with their peak abundance in the old field survey at a soil nitrogen level greater than in an experimental field (such as Schizachyrium scoparium, Artemisia ludoviciana, and Sorghastrum nutans) should have a Gaussian (quadratic) distribution along the experimental gradients. This was so for Artemisia ludoviciana and Sorghastrum nutans in Fields B, C and D in 1984 and 1985. However, Schizachyrium scoparium declined along the experimental nitrogen gradient, without any sign of increasing at low rate of N addition, as would be predicted by its response as shown in Figure 3.

Lastly, for species that increased in percent cover throughout the entire nitrogen range in the old field survey (Agropyron repens, Rubus sp., and Poa pratensis), an increasing or Gaussian distribution is expected along the experimental gradients. These species showed just such responses to the experimental nitrogen gradients.

In total, 12 of the 15 most abundant plant species responded qualitatively similarly in 1985 to the experimental gradients and the spatial and temporal gradients of the old field survey. By 1985 we observed marked similarities in the responses of major plant species to nitrogen addition in all our experiments, whether or not herbivores were present and whether or not they were disturbed. These preliminary results thus support the hypothesis that increases in soil nitrogen through time may be a major cause of the pattern of secondary succession observed at Cedar Creek and that spatial heterogeneity in nitrogen may be an important determinant of spatial variation in vegetation within a landscape. They also suggest that herbivores may be much less important than nitrogen mineralization rates in determining plant community structure at Cedar Creek. However, as discussed later, herbivores, especially gophers, seem to be a major cause of soil spatial heterogeneity. Thus, it seems likely that the total effect of herbivores may become increasingly great through time. This is a possibility that will be addressed during our next four years.

Litter Dynamics

To gain a better understanding of litter dynamics, we performed an experimental study of litter decomposition in the Undisturbed Microplot Nitrogen Gradient experiments.

In these experiments, we harvested little bluestem (Schizachyrium scoparium) in plots that had received three different treatments: no N addition, moderate N addition, and high N addition. We then placed the little bluestem in litter bags in the field, and collected litter bags each month of the growing season during the next 1.5 years. We found little direct effect of nitrogen addition on litter decomposition. However, we did find that litter produced by plants growing on higher N plots had a lower C:N ratio, and this lower ratio corresponded with an increased rate of decomposition (Pastor, Stillwell and Tilman, in preparation).

Our microplots afford us another opportunity to study litter dynamics. Each year we have sampled and will continue to sample both peak living plant standing crop and litter mass in each of the 369 fenced Nitrogen Gradient Microplots. In addition, we perform biweekly sampling of vegetation and litter in selected plots in Field C. These samples allow us to directly observe seasonal and yearly dynamics of litter and the dependence of these dynamics on rates of nitrogen addition and above-ground plant production. For instance, for the Undisturbed Nitrogen Gradient Microplots of Field A, total litter was independent of treatment in 1982 but was highly dependent on treatment by 1984 and 1985. We have also used our data on litter and primary production to calculate the proportion of annual production that decomposes during the next year. For Fields A and D, litter decomposition rate increased significantly with the rate of nitrogen addition. However, the opposite pattern was observed in Fields B and C. Our seasonal sampling of litter and above-ground plant biomass revealed that litter accumulates at a fairly constant rate from early May through mid-August, and then rapidly declines. This means that living plant standing crop and litter both reach peak levels at the same time. The rapid decline in both litter and living standing crop after mid-August means that most litter decomposition occurs in September and October. Our data on seasonal production in these plots suggests that early season production of litter is a major factor inhibiting late season production by cool-season grasses. The most likely mechanism to explain this is that early season litter causes bacterial immobilization of available soil nitrogen later in the season, and thus inhibits late season growth. This may explain the unexpected rapidity with which *Poa pratensis* displaced *Schizachyrium scoparium* from high nitrogen plots. It may also explain the tendency for fire to lead to a replacement of *Poa* by *Schizachyrium*. Because of the critical role of litter in the nitrogen cycle, we will continue to monitor litter dynamics in these plots. We plan to expand our studies of litter decomposition and its effects on nitrogen availability and plant growth (see next section).

Litter Feedback Effects on Vegetation

An additional reason we plan to expand our studies on litter comes from some intriguing dynamic interactions we have observed in the high nitrogen plots in Field B and C. Before we began our experiments, these plots tended to be dominated by *Schizachyrium scoparium* (little bluestem) or *Poa pratensis* (bluegrass). *Agropyron repens* (quack grass) was rare. However, following nitrogen addition, *Agropyron* increased greatly in the plots which initially contained some *Agropyron*. In plots in which *Agropyron* was initially absent, *Poa pratensis* became dominant, provided it had been present initially. Replicates that initially lacked both *Poa* and *Agropyron* became dominated by *Schizachyrium*. Thus, there was a pattern of marked divergence in these high nitrogen treatments. This divergence amounted to a magnification of pre-existing plot-to-plot variation in the abundances of these three species.

The litter characteristics of these three species led to an even greater divergence. *Schizachyrium* and *Agropyron* both have stiff, strong, lignified stems. *Poa*, in contrast, has a relatively thin and weak stem. The dense stands of *Poa* which were produced on some plots in response to our two highest rates of nitrogen addition lodged in the late autumn of 1984. This created a dense, thick litter layer through which the shoots of the plants that had lived in the plots in 1984 did not penetrate in 1985. The main plants present in the lodged plots in 1985 were a few species of annuals (*Chenopodium album* and *Polygonum convolvulus*) that were able to invade and grow despite the thick, dense litter layer.

Despite their rarity, these annuals, because of their rapid growth, completely covered these plots by the end of the 1985. Thus, we have a case of apparent "retrograde succession" caused by a rapid increase in the productivity of a species that lodges easily.

We do not know what will happen in these plots in the long-term. Clearly, their future composition is going to depend on the rate of Poa litter decomposition and on the ability to invade of species that are not so easily lodged. If Agropyron can successfully invade these plots and can displace Poa (as it has done in other replicates of these treatments), this event may prove to be a 4 to 6 year transient on the way to a single stable equilibrium point determined by the treatment. However, it may be that Agropyron will be unable to invade. Some Poa had re-established by the end of 1985 but there had been no invasion by Agropyron. If Poa increases again, and again lodges within a few years, high productivity could lead to a pattern of cyclic succession. The next 5 to 10 years will show us which course nature takes. To understand the cause of this course, we plan to initiate a series of litter addition and removal experiments within subsections of the microplots, and determine the effects of these on plant growth and nitrogen mineralization rates.

Dynamics of Below and Above Ground Production

The objective of this work is to examine root and foliage dynamics at the community level as they relate to old-field succession. The study is being conducted in the unfenced nitrogen gradient microplots in Fields A, B, C, and D. The main questions being addressed are:

(1) Do whole-community root:shoot ratios shift along successional and nutrient gradients?

(2) What is the relationship between observed root:shoot ratios and the actual patterns of below and above ground production?

To address these questions, we are taking matched, bi-weekly samples of both below and above ground plant biomass throughout the growing season. Because high rates of nitrogen supply could lead to water depletion, we have installed neutron probe tubes in the plots. This allows us to detect interactions among nitrogen, water, and field age. For above-ground biomass, we manually separate living plant material from litter. For below ground biomass, we wash samples and then manually separate roots from soil organic matter. Although the sandy soils of Cedar Creek make this work much easier than it would be on most other soils, the separation of roots is time-consuming. Our preliminary results show that root:shoot ratios increase during secondary succession at Cedar Creek from about 5.2 : 1 in young fields to about 11 : 1 in our 50 yr old field. We have also seen that fertilization leads to increased root:shoot ratios in early succession but to decreased ratios in late successional fields. Once we have completed our analysis of root samples (which are kept frozen from the time they are obtained until analyzed), we will use the sequential difference method to estimate the seasonal total rates of both above and below ground production in our plots.

3. MACROPLOT NITROGEN GRADIENT EXPERIMENTS

In addition to the microplot experiments, we have established a series of 20m x 50m "macroplots" in the four fields. These macroplots receive three different treatments: no nutrient addition, addition of N and all other nutrients at an intermediate rate (treatment E of the microplots; Fig. 6) and addition of N and other nutrients at a high rate (treatment G; Fig. 6). In Fields A, B and D there are 3 replicates of each of these 3 treatments, giving a total of 9 plots per field. Because of limited space, there are only 2 replicates per treatment in Field C. Except for small portions to be discussed later, these plots are open to all herbivores. Each plot is large enough to include the home ranges of several individual small mammals and for selective habitat patch foraging by deer. As such, they are providing us with information on **total** responses of these old field ecosystems to changes in their productivity, because the observed effects include both the direct effects of changes in productivity on plants and various indirect effects mediated through herbivores. Much of our work on nutrient inputs, outputs, and cycling is performed in the macroplots, as is much of our work on direct and indirect effects of herbivores. The herbivore work includes both population responses of herbivores to changes in primary production and vegetational changes in small areas from which various herbivore species or functional groups are excluded.

Lysimeters

Within each macroplot we installed two soil core tube lysimeters that are equipped, at their bottom (1 m depth), with a porous cup attached to an evacuated collecting chamber. These were made by driving a 15 cm diameter piece of PVC pipe around existing vegetation to a depth of 1 m, removing the pipe with its soil/vegetation core intact, and gluing a porous cup to its bottom. The lysimeter was then placed back in the hole. We collect soil leachate from these 66 lysimeters throughout the growing season. Our analyses of the leachates have allowed us to determine nitrogen leaching loss rates in Fields A, B, C and D. To date, we have not found a significant increase in nitrogen loss rates following nitrogen addition, suggesting that the soil microbial community is efficient at retaining nitrogen. Precipitation collectors in each field have shown that the annual rate of atmospheric nitrogen loading corresponds closely with those reported by nearby NADP stations. Interestingly, the estimated annual rate of increase in soil nitrogen during succession (6.8 ppm of N/yr for the upper 10 cm of soil) is very close to the rate of atmospheric nitrogen loading. This suggests that the soil nitrogen increases we observe during succession at Cedar Creek may be caused by atmospheric inputs coupled with low leaching losses. However, for this process to lead to a leveling off of soil nitrogen in late successional soils, loss rates must increase on richer soils. Although we do yet have evidence that this is caused by leaching, we will continue to monitor nitrogen leaching loss.

Nitrogen Mineralization and Nitrification

We determined net nitrogen mineralization and nitrification during the 1984 growing season by the in situ buried bag incubation method (Eno 1960). This method correlates highly with estimates of N and P cycling in croplands, grasslands, forests and savanna (Westermann and Crothers 1980; Nadelhoffer et al. 1983; Pastor et al. 1984; Vitousek and Matson 1985; Schimel et al. 1985). Three samples were taken of the upper 10 cm of soil in each treatment in each macroplot in each field, placed in a polyethylene bag, and incubated monthly beneath the thatch in an adjacent portion of each field. Paired samples estimated initial levels of NH_4-N and NO_3-N. Inorganic N was extracted from both incubated and initial samples with 1N KCl within 24 hrs after sampling. Net N mineralization is the increase in NH_4-N and NO_3-N while net nitrification is the increase in NO_3-N in the incubations relative to their paired initials (Schimel et al. 1985).

Net nitrogen mineralization in control plots increased with field age, from 4.4 g/m^2/yr in the youngest field (A) to 6.5 g/m^2/yr in the oak savanna (D). Average annual N mineralization (N_{min}) was significantly correlated with the average total N (TN) content of the soil:

$$N_{min} = 17.69 + 0.029TN \qquad (r = 0.915,\ P < 0.05).$$

Greater than 90% of the monthly N mineralization was nitrified, except in July, when 65% was nitrified. The proportion of total N mineralized in control fields (relative N mineralization) decreased with field age, from 6.2% in field A to 4.8% in field D. These results are comparable to those for Colorado shortgrass prairies (Schimel et al. 1985), but are lower than for Wisconsin forests (Nadelhoffer et al. 1983; Pastor et al. 1984).

The increase in soil C/N ratios and the decrease in relative N mineralization we observed suggests that there may be a decline in organic matter quality during succession. Schimel et al. (1985) found similar trends in a toposequence of shortgrass prairie soils and hypothesized that this indicates an increase in recalcitrant, older forms of humus. A model of soil C and N dynamics in prairie soils (Parton et al. 1983) indicates that increases in both older recalcitrant humus and inputs of lignified material could decrease relative N mineralization rates. In our future research, we plan to determine if the litter of later successional species is more highly lignified, and if lignin content of our soils increases with field age. We have many reasons to believe that this might be so, since later successional species have more structural material, which tends to be more lignified than photosynthetic tissues. We will also perform litter addition and nitrogen mineralization experiments in Fields A, B, C and D to determine how nitrogen mineralization rates are influenced by the litter of several different early successional species versus several different late successional species.

Carbon and Nitrogen Interactions in Soils

One of our goals is to develop a mechanistic understanding of plant and soil dynamics. Our experimental work on plant growth suggests that the most critical aspect of soils for plants is the rate of nitrogen mineralization. We have already collected data on in situ rates of nitrogen mineralization across the Cedar Creek successional gradient (Pastor, Stillwell and Tilman, in review). Our next objective is to determine how soil nitrogen and carbon interact to determine mineralization rates. In doing our work, we plan to start with two existing models, Parton's "Century Model" (Parton et al. 1983) and Molina's "NC-Soil" model (Molina et al. 1983). NC-SOIL models short-term aspects of nitrogen and carbon transformations in the soil-plant system. Data from our studies of above and below ground production, litter production, litter quality, and litter decomposition will serve as inputs for the models. Parton's Century Model is qualitatively similar, except that it incorporates additional processes that are likely to influence long-term soil dynamics.

In applying, modifying and extending these models, we will address such questions as: How do successional changes in the above- and below-ground pools of nitrogen and carbon affect mineralization and production? Where are the most active pools, where are the bottlenecks, and does this change during succession? What changes occur in nitrification and denitrification? Ultimately, we want to go beyond such descriptive models to a model that explicitly includes the mechanistic interactions of soil microorganisms with soil organic compounds and nutrients. This logical extension of consumer-resource theory (Tilman 1982) to the decomposer community would provide an opportunity to integrate evolutionary and population concepts with an ecosystem perspective of soils.

We will link our soil model with a model of plant competition and dynamics (Tilman 1980, 1982, 1985, 1986a). The end result will be a mechanistic, ecosystem model of the dynamics of soil change, primary production, species turnover, species diversity and successional dynamics. Critical tests of this model will be provided by a variety of our experiments, especially the nitrogen gradient microplots, the long-term monoculture and competition experiments, and the old field chronosequence observations.

Herbivore Population Densities

We have established permanent trapping stations in each macroplot to determine seasonal and year-to-year population dynamics of small mammals. We also regularly determine densities of herbivorous insect species, especially grasshoppers. In doing our work, we have found an intriguing indirect interaction between gophers and grasshoppers. Grasshoppers preferentially oviposit in gopher mounds. This means that local population densities of grasshoppers may be positively correlated with gopher densities. However, both grasshoppers and gophers feed on the same plant species, and thus potentially compete. Such direct competition, if it exists, should make grasshopper and gopher densities be negatively correlated, and would seem to select against grasshopper preference for gopher mound oviposition. Seastedt (1985), though, reports that above-ground and below-ground feeding herbivores may function as mutualists because plants, in response to above-ground herbivory, allocate more growth below-ground, and vice versa. We plan to pursue these interrelations at Cedar Creek.

Herbivores: Direct and Indirect Effects

Within each 20m x 50m **macroplot** in Fields A, B and C, we established 7 **herbivore exclosure plots.** Each plot is 2m x 4m. The purpose of this work is to determine the influence of soil nitrogen availability on populations of plants and herbivores, and to determine the feedback effects of herbivores on plants at varying levels of nitrogen supply. The treatments consist of separate removal of each of four different groups of herbivores (using mechanical barriers or selective toxins). The four herbivore groups experimentally removed from the 2m x 4m plots were (1) Microtus pennsylvanicus, an above-ground vertebrate; (2) Geomys bursarius, a fossorial vertebrate; (3) above-ground invertebrates, primarily chewing insects; and (4) below-ground invertebrates. The fifth treatment consisted of removal of all four herbivore groups. The final two treatments were two different controls. Because the same seven treatments were replicated in each of the macroplots in Fields A, B, and C, they allow us to determine how both the total effect and the indirect effect of each herbivore group depends on field age and nitrogen supply rate.

Nitrogen addition directly affected both plant and herbivore populations. Nitrogen limited primary productivity and affected plant species richness and absolute and relative abundance of the common species. Vole and grasshopper populations increased in the fields after nitrogen addition, and appeared to be nitrogen limited. Most herbivores were behaviorally responsive to differences among plots receiving different levels of nitrogen, and were most active on high nitrogen plots. Despite these herbivore effects, dominant plant species changed with nitrogen addition in qualitatively the same manner as in the Undisturbed Nitrogen Gradient Microplots, for which herbivores were excluded.

Both gophers and voles were also behaviorally responsive to the presence/absence of other herbivore groups. Gopher mound production was significantly higher in above-ground and below-ground invertebrate removals in Field A. Vole captures were negatively correlated with mounds produced the previous year. The effects of herbivores on plants varied with nitrogen addition, reflecting both differences in herbivore behavior and changes in competitive relationships among plants. Most significant herbivore effects were herbivore X nitrogen interactions. Effects of herbivores on plants, although statistically significant, were generally minor, at least for the more abundant plant species. Several rarer plant species that were common enough to be analyzed showed large effects of herbivores. Nevertheless, despite three years of herbivore removal, they had an insignificant effect on total community productivity.

The results to date suggest that the patterns of dominance and succession determined by nitrogen addition alone have not been significantly altered by the presence or absence of herbivores. If this pattern holds during the next 5 years of the Cedar Creek LTER project, it would have profound implications for the field of ecology. It would suggest that the pattern of succession is not highly dependent on herbivore population densities. Moreover, by comparing the responses we observe on the nitrogen poor, unproductive soils of Cedar Creek with those observed in other more productive research areas, such as the Konza Prairie LTER site, the Coweeta LTER site, the Andrews LTER site, the successional grassland communities of southern England (Brown 1985), and the Serengeti savanna (McNaughton 1979, 1984), we should be able to determine if there is a tendency, as has been suggested by Fretwell (1977) and Oksanen et al. (1981) for herbivores to have maximal impact in moderately productive ecosystems.

Disturbance Rates

Several times each year we directly enumerate all new gopher mounds and other disturbances in each macroplot. We do this because our work to date suggests that the light and nutrients provided by these mounds are major limiting resources for some plant species.

F. OTHER HERBIVORE STUDIES

Of the hundreds of species of herbivores at Cedar Creek, the plains pocket gopher, whitetail deer, and several species of grasshoppers are the most abundant. Although we have done work on other herbivores, we have focused our initial efforts on these three.

1. Gophers Habitat Use and Effects on Soils and Roots

Most gopher (Geomys bursarius) movement is below-ground. We established a 50m x 100m grid within which we used radiotelemetry to continuously monitor the movement patterns of all resident gophers. We have compared the observed pattern of habitat use with numerous, detailed measures of below-ground plant biomass and soil chemistry in the gopher tracking grid. This has allowed us to learn a great deal about the habitat use patterns and social interactions of gophers, as well as the impact of gophers on soils and below-ground standing crop (Zinnel and Tester, in preparation).

Individual gophers frequently abandoned one territory to take over an adjacent, previously abandoned territory. Newly abandoned territories have significantly lower root biomass than newly selected territories. This suggests that individual gophers exploit resources in one locality, and then move to another. The tendency for the same areas to be used year after year as gopher den sites has a profound impact on soil development. Gophers cache food, urinate, and defecate within the 6 m^2 area that comprises their den site, but forage over ca. 400 m^2. The long-term effect of this behavior is to create a deep, highly organic, nitrogen rich soil at the den site. This soil supports rapid root regrowth. The long-term effect of gopher foraging is to concentrate the limiting soil resource, nitrogen, into patches in which the gopher does most of its feeding. Other sampling of soils of Cedar Creek (Tilman, Inouye and Huntly, in preparation) has shown localized "hot spots" of nitrogen rich soils that may correspond with current or former gopher den sites. Our old field survey suggested that much of the species diversity of old fields could be explained by spatial heterogeneity in soil nitrogen (Inouye et al. 1986). Although our herbivore removal experiments have not shown major short-term effects of herbivores on vegetational composition and dynamics, herbivores may have long-term effects on soil heterogeneity and thus on plant diversity. We plan to thoroughly sample the soils of the gopher habitat use field to determine to what extent its spatial heterogeneity can be explained by gopher activity.

2. Gopher Feeding Experiments

Because little quantitative information is available on the diet and feeding behavior of Geomys bursarius (see, though Myers and Vaughan 1964; Ward et al. 1963; Luce et al. 1980), we established experiments to: 1) determine if gophers prefer certain plant species; 2) determine the relative importance of plant nitrogen and water content on food choices; and 3) investigate effects of plant patch density on feeding activity (Behrend and Tester, in review).

Gophers preferred plant species characteristic of early successional stages to those characteristic of later stages, but showed no preference for plant species with higher tissue nitrogen levels. In addition, gophers did not discriminate among plants of the same species that had been grown at different nitrogen levels. However, gophers fed significantly longer and more frequently in patches with high plant density. These findings are consistent with observations made using the radiotelemetry system and with the highly significant increases in gopher mounds in unfenced high nitrogen plots (Tilman 1983; Inouye and Huntly, in review).

3. Deer Exclosure Experiments

Although Cedar Creek contained forest or oak savanna prior to farming and although all our old fields are bordered by native savanna or forest, woody plants are very slow to establish in old fields. There are several alternative hypotheses which could explain this. First, woody plants may be poor competitors on nitrogen poor soils but superior competitors on the more nitrogen-rich woodland soils on which greater height would be advantageous (Tilman 1986a). Our nitrogen addition experiments will eventually provide a test of this hypothesis. An alternative hypothesis is that deer browsing may prevent the reestablishment of woody plants in old fields. Cedar Creek is a major winter yarding area for deer. Many woody plants experience heavy browsing damage. To determine if deer browsing could be cause for delayed re-invasion of woody plants, in 1982 we established a series of deer exclosures. On the margins of Fields A and B we established 6 permanent 10m x 30m plots. The long axis of each plot was perpendicular to the field/forest ecotone, with 5m of the 30m length of each plot extending into the forest. For each field, 3 of the plots, chosen at random, were fenced to a height of 2 m to exclude deer and 3 were left unfenced. Each year since then we have monitored growth of and browsing pressure on all individual woody plants. Average growth for all trees less than 120 cm tall was consistently greater inside the exclosures. If this trend continues, it would suggest that deer are a major cause of slow tree re-establishment in old fields.

One unexpected result from our deer exclosure plots has been the importance of gophers as a source of mortality for woody vegetation. We have been able to positively identify numerous saplings that were killed by gophers. While the mortality rate per year is low, these trees spend a long time in size classes that are susceptible to gopher predation. Thus, gophers may also be important in preventing the re-establishment of trees. Our various gopher exclosure experiments will ultimately provide us with a test of this hypothesis.

4. Grasshoppers: Transient Population Dynamics?

Our survey of grasshopper densities in the 22 old fields showed that overall grasshopper density declines during succession, but that there is a successional sequence of grasshopper species that is associated with the pattern of vegetational change. However, during the first four years of our microplot and macroplot experiments, the pattern of grasshopper response to nitrogen addition rates differed markedly from the correlational pattern we observed in the old field survey. To date, nitrogen addition has led to increased densities of early successional, rapidly reproducing grasshopper species. We do not yet know if this is a transient effect, or if there will be a significant difference between our experimental and observational results. There are many reasons to expect the grasshopper responses to be transient. During each of the four years of nutrient addition experiments, there have been marked changes in plant species composition. Because one year's population densities of grasshoppers are determined by the last year's reproduction, grasshoppers should respond even slower to experimental changes in productivity than plants. In addition, grasshopper species may be only weakly competing with each other. Their initial response may mainly reflect growth rate differences. Thus, it may take many years for the grasshopper composition of our nitrogen addition plots to reflect the experimentally-induced changes in productivity. If this proves to be so, it may be necessary to re-evaluate the validity of most current studies of insect herbivore community structure, because most studies look only at the one or two year responses to manipulations, and thus may be studies of transient effects.

5. Microtus Response to Sodium and Nitrogen

Belovsky (1978) reported that moose on Isle Royale foraged so as to optimize their intake of two essential nutrients -- protein and sodium. Some serendipitous observations in our single-nutrient addition experiments suggest that Microtus may bias its foraging to increase its sodium intake. One of the treatments in those experiments is the addition of sodium sulfate. We found that the Microtus that invaded the fenced plots over the winter of 1984-1985 had denuded the vegetation of this treatment in Field A. Microtus scat counts were 3.2 times higher in the sodium sulfate plots than controls. This was the only treatment to have significantly greater scat counts than controls, using ANOVA with contrasts. We plan to continue such observations, and are considering an experiment to test for nitrogen/sodium interactions.

G. OTHER STUDIES OF DISTURBANCES

1. Oak Savanna Burn Experiments

In 1966, a 145 ha area in the southeastern corner of Cedar Creek was divided into 12 compartments for a study of the effects of various burning frequencies on vegetation composition. The treatments consisted of (1) annual burning, (2) burning for 2 out of every 3 years, (3) burning every third year, (4) burning every 6 to 7 years and (5) no burning. Each treatment was replicated at least twice. The LTER project has now taken over responsibility for this experiment. The results of the first systematic survey of these burn compartments were published in White (1983). In 1984 we established 24 permanent quadrats in each compartment and sampled soils, plants and herbivores in each quadrat. The data have been entered into a data base and we are proceeding with our analyses. We will resample each of our permanent quadrats in the Oak Savanna Burn Experiments every 5 years.

2. Fire and Secondary Succession

In 1984 we established an experiment in Field B to determine the effects of different fire frequencies on soil development, vegetation dynamics and herbivore densities in a successional field. This experiment was designed to complement the Oak Savanna Burn Experiment as well as the burning experiments being conducted at the Konza LTER. There are four different burn treatments that correspond with those at Konza:

(1) controls that are never burned

(2) plots burned every fourth year

(3) plots burned every other year

(4) plots burned every year.

Each plot is 8m x 8m. There are six replicates of each treatment, with the experiments laid out in the field in a completely randomized experimental design. We sampled soils and vegetation of all 24 plots when they were established in 1983. In 1984 we began the burning regime. We will resample these plots in 1987, when we will have completed one cycle of burning, and in 1991 at the end of 8 years (two complete cycles).

3. Windstorm Forest Disturbance

In 1983, an unusually violent windstorm created a major disturbance in forested areas at Cedar Creek. It toppled and uprooted numerous trees in a swath about 200 m wide and many kilometers long. To study the long-term effects of this major disturbance, we established 11 permanent 10m x 50m plots. In each plot we recorded various characteristics both of the trees that had been damaged or killed and of the trees, saplings and seedlings that were not damaged. In 1985, Michael Palmer, a graduate student at Duke University, resampled these plots. The plots will be resampled again in 1988 and in 1991. By that time we should have a fairly good picture of response of forest vegetation to wind disturbance.

H. OTHER STUDIES OF SOIL/PLANT INTERACTIONS

1. Seasonal Productivity Patterns and Temperature-Dependent Plant Growth

Although it would be impossible for us to sample all our experiments frequently enough to determine the seasonal effects of our various treatments, we realize that peak standing crop is not a good measure of primary productivity and that a single sample per year can mask many potentially important variations that occur within the growing season. Thus, we are sampling some control and fertilized microplots in Field C at biweekly intervals throughout the entire snow-free period. As in all our sampling, we have sorted all plants to species and dried and weighed each species individually. These data have proven critical in interpreting litter dynamics in our plots and in demonstrating seasonal separation of the major producer species.

This sampling is being done in conjunction with an experimental, growth chamber study of temperature, nitrogen and light dependent growth of a warm-season and two cool-season grasses (Schizachyrium scoparium, Poa pratensis, and Agropyron repens). These growth chamber data may be useful in understanding both the observed seasonal separation of these three species and the tendency for nitrogen addition to favor cool season grasses over warm season grasses in the field.

2. Long-Term Grass Monoculture and Competition Experiments

Our first work on soil-dependent plant growth was a greenhouse study of nitrogen-limited seedlings. These experiments, performed on nine plants common during secondary succession at Cedar Creek, showed a highly significant correlation between the nitrogen-limited growth rate of each of species and its order of dominance during secondary succession (Tilman 1986b). Specifically, species that are dominant during early secondary succession have significantly greater rates of biomass gain at low rates of nitrogen supply than do species that are dominant during late succession. This supports the hypothesis that the species dominant on early succession, nitrogen-poor soils of Cedar Creek are superior nitrogen competitors (Tilman 1982). However, the experiments do not suggest why late successional species can displace early successional species as soil nitrogen levels increase.

One hypothesis that could explain the ability of later successional species to displace early successional species from the more nitrogen rich soils of late succession is that light becomes a more important limiting resource during late succession (Tilman 1982, 1985). To test this, we are growing plants in the field in pots containing 8 liters of soil. The soils are various mixtures of subsurface sand with a rich organic top soil. The other experimental variable was light, which is reduced below incident levels using shade cloth. We use 7 different soil mixtures and 7 different light levels in a complete factorial experiment which will be harvested (above and below ground) after two growing seasons. These data should determine if the observed successional patterns of these species and the observed responses of these species to our experimental microplot and macroplot nitrogen gradient experiments are consistent with resource competition theory (Tilman 1982, 1985).

Although 8 liter pots are unusually large for such experiments, they may be too small to include two critical aspects of plant competition: (1) shading and (2) soil modification through litter production. Thus, in the spring of 1986 we will begin field experiments designed to determine the relations between soil nitrogen mineralization rates, soil nitrogen availability, light attenuation, and the dynamics of production and competition for five major grass species (Agrostis scabra, Schizachyrium scoparium, Poa pratensis, Andropogon gerardii, and Agropyron repens). These experiments will be conducted on 10 different soil mixtures, all of which were prepared in the autumn of 1985. The 35m x 35m area was prepared by removing the upper 1 m of surface soil, leaving behind a very nitrogen poor (90 ppm of N) subsurface sand. This sand was then mixed in 10 different proportions with a rich (1400 ppm of N) sandy soil to give nitrogen levels that span the range observed in the Cedar Creek old field chronosequence. In the spring of 1986, each of the 10 soil types will be divided into 64 0.7m x 0.7m plots. Each plot will receive seed of one grass species or of various combinations of these five species. These are our long-term monoculture and competition experiments. During each field season we will monitor the rates of nitrogen mineralization and the amounts of extractable ammonia and nitrate in these plots. These will provide an excellent data base against which to test our nitrogen mineralization models and to determine the effects of nitrogen mineralization on the above and below ground production of each of the species.

The single-species plots will determine if the different qualities of litter produced by each of these species have a long-term feedback effect on the nitrogen cycle. Although it will take several years for a litter layer to develop and influence nitrogen mineralization rates, these five species differ greatly in C:N ratios and lignin content. Only experimental monocultures can determine the long-term feedback effects of individual species on soil dynamics. Thus, these new experiments are a critical part of our attempt to understand the linkages between plant and soil dynamics.

These experiments will also provide a detailed test of the ways in which soil nitrogen mineralization rates and light interception influence interspecific plant competition. Up until now, almost all work on terrestrial plant competition (see review in Harper 1977) has been qualitative and phenomenological. It has described the outcome of the interaction, but could not predict the outcome based on a priori information. We believe that it should be possible to predict the outcome of interspecific plant competition using information on the resource dependence of plant growth (see Tilman 1982). The monoculture experiments will provide the information that theory says is needed to predict the outcome of competition. Thus, these experiments will provide the first test of the validity of resource competition theory for terrestrial plants. If this theory can predict the outcome of interspecific competition, it would have immediate application to many agricultural and forestry problems. We believe that these experiments are a logical and critical step in our attempt to synthesize the mechanisms of interspecific interactions into an ecosystem perspective that includes decomposer dynamics and plant/decomposer/nutrient feedback effects.

3. N^{15} Uptake — Spatial and Seasonal Dynamics in Natural Vegetation

This research is testing the hypothesis that the dominant primary producer species are differentiated in their timing and location of nitrogen uptake, and that such niche differences facilitate the coexistence of these plant species. These experiments, performed in Field C, involved replicated plots into which N^{15} was injected at two different depths (2 cm and 12 cm) at each of three different times of the year. N^{15}

uptake is being monitored using foliar samples for the seven most abundant species in the plots (Schizachyrium scoparium, Poa pratensis, Ambrosia coronopifolia, Solidago nemoralis, Artemisia ludoviciana, Anemone cylindrica,and Panicum oligosanthes). Isotope ratio analysis of the first samples has shown significant between-treatment differences and clear niche separation by depth for several species. An exciting direction for future work in this area is to look for niche shifts in pairs of selected species. Thus, assuming that our analyses of these data, once completed, shows this to be a valuable technique, we plan to apply it to interspecific interactions in our long-term monoculture and competition experiments.

4. Nitrification and Soil pH

In conjunction with Dr. Edwin Schmidt, Department of Microbiology, University of Minnesota, we have established a full factorial soil pH x soil nitrogen experiment. This experiment is designed to determine the effects of soil pH and nitrogen supply on the population dynamics of both nitrifying bacteria and vascular plants. Our sampling will begin in 1986. This work adds another major physical factor, soil pH, to those studied at Cedar Creek, and could potentially help tie together the dynamics of major decomposer and producer species.

I. Syntheses: Theoretical and Intersite

Our research program is motivated by a series of broad, general ecological hypotheses. Although it is absolutely necessary to perform detailed experimental and observational tests of these hypotheses in a particular ecosystem, as we are doing at Cedar Creek, we firmly believe that our research is providing insights and a theoretical framework that apply to all ecosystems. It is our goal to understand the general mechanisms of interaction among species and between species and their physical environment, and to synthesize these into a theory of ecosystem structure and function. Our work represents a constant process of feedback between theory, experimentation and observation. Our initial hypothesis that foodweb (consumer-resource) interactions could provide the necessary framework for such a synthesis has been reinforced many times during the first four years of our LTER research, as has our belief in the value of integrating evolutionary, population, and ecosystem perspectives.

Several of our published papers reflect the synthetic approach we are taking. In one paper (Tilman 1986a) we have suggested that the same processes that select for different plant life histories, morphologies and physiognomies along current productivity gradients were also responsible for the pattern of evolution of land plants from single-celled algae 350 million years ago. We further suggested that this link between ecosystem productivity and the evolution of plant life histories and morphologies is the major factor leading to convergent evolution in the biomes of the world. We have recently developed an explicit size-dependent model of plant competition to explore these ideas in more depth. The results of this further theoretical work as well as a synthesis of the first four years of research at Cedar Creek are being prepared for publication as a book that has been accepted for publication by Princeton University Press. We have also developed a new theory of succession, "the resource ratio hypothesis of succession" (Tilman 1985). This theory, which includes plant life history differences, plant competitive abilities, and soil nutrient and light availabilities, predicts that there should be a continuum between primary successions, secondary successions on poor soils, and secondary successions on rich soils, but that the relative importance of plant life histories, competitive abilities and habitat modification change along this continuum. A third major synthetic paper presents and analyzes a multi-trophic-level model of foodweb interactions, and discusses its generality and applicability (Tilman 1986c).

Because it is our long-term goal to explain those general patterns that occur across the world's ecosystems, we will continue to seek and test both empirical and theoretical syntheses. The LTER network provides us with a unique opportunity to make such syntheses, for it spans a wide range of ecosystem types. We have already begun a number of studies at Cedar Creek that can be directly compared with research being performed at other LTER sites. Specifically:

(1) A major theme of the Niwot Ridge LTER project is that disturbance tends to increase the rate at which ecosystems change toward a state that reflects current environmental conditions. Our microplot experiments provide an opportunity to test this hypothesis and to compare old field ecosystems with tundra. We imposed identical nitrogen gradients in the disturbed and the undisturbed nitrogen gradient microplots. Our results to date strongly suggest that the disturbed and undisturbed plots are converging and that the disturbed plots are responding somewhat more rapidly (Figs. 10 and 12). Dave Tilman plans to visit Pat Weber at Niwot Ridge this summer to establish the framework for comparisons between Cedar Creek and Niwot Ridge.

(2) A central focus of the Konza LTER project is the role of disturbance by fire in structuring the prairie ecosystem. Fire was also historically important at Cedar Creek. Thus, we have established a series of permanent sampling quadrats within a 145 ha block of oak savanna that was divided into 12 plots that have been subjected to various burn frequencies since 1966. We have also begun an experiment on the effect of fire disturbance frequencies on the pattern of old field succession. The data collected in these two experiments will allow us to make extensive comparisons of the effects of fire on Cedar Creek versus Konza vegetation, soils, and herbivores.

(3) Fossorial mammalian herbivores are of great importance both at Cedar Creek and at the Niwot Ridge LTER site. At both sites, these organisms are a major source of soil disturbance and thus have a potentially major impact on a variety of local and landscape patterns. John Tester (Cedar Creek) and Jim Halfpenny (Niwot Ridge) are working on a comparison and cross-site synthesis of gopher impacts.

(4) We are also interested in cross-site comparisons of processes controlling the seasonal and year-to-year dynamics of above-ground and below-ground productivity. Tilman's recent theoretical work has led to some predictions of patterns of allocation to above versus below ground processes that could be ideally tested using data from the other terrestrial LTER sites.

(5) Another area of cross-site comparative work concerns the impact of herbivores on primary producers. Analyses that we (Huntly, Inouye, Tilman, Tester) are just now completing suggest that herbivores have maximal impact in moderately productive habitats. We are interested in seeing if this pattern holds, in general, across a wide range of ecosystems. We already have some evidence that it may apply to aquatic foodchains (Sterner 1986) as well as terrestrial foodchains. We (Huntly, Inouye and Tilman) plan to organize an intersite symposium on this question, as we believe that almost all LTER sites have data that are relevant to this question.

(6) Briand and Cohen (1984) have suggested that all foodchains have a similar structure, with an approximately constant proportion of the total ecosystem species richness occurring on each trophic level. The actual proportions that they reported from a survey of 62 foodchains agree amazingly well with predictions of consumer-resource theory (Tilman 1986c). However, this agreement may be caused more by the taxonomic biases of the investigators than by actual patterns. We plan to determine if the data being collected at the other LTER sites on primary producer, herbivore, predator, and decomposer species can provide additional tests of these ideas.

(7) The broad range of ecosystems included in the LTER network provide a major opportunity to test the generality of the consumer-resource theory that we are developing. To this end, we propose establishing one set of Unfenced Nitrogen Gradient Microplot experiments at the Niwot Ridge LTER site and one at the Jornada Desert LTER site. The serpentine soils of northern California, such as at Jasper Ridge, would be an ideal site for a third set of plots. We have chosen these sites because they are dominated by herbaceous vegetation, but they differ dramatically in their soils and climate from Cedar Creek. Although these experiments would require a considerable dedication of time by Tilman, they are of critical importance in determining the generality of the Cedar Creek results.

There are many other areas in which we are collecting data that are of potential intersite interest, including data on the controls of nitrogen mineralization rates, litter decomposition rates, seasonal patterns of primary productivity, grasshopper dynamics, precipitation chemistry, and nitrogen leaching loss rates. Although the long-term experiments and observations are the main focus for the Cedar Creek LTER project, we designed these experiments to answer a series of broad ecological questions. We are eager to form contacts with other sites so that we may determine the generality of our experimental and theoretical results. As the LTER network has developed, an increasingly great portion of our efforts have gone toward syntheses and cross-site comparisons. With the cross-site experimental work that is currently in operation and that we are planning, we feel justified in asserting that more than 15% of our annual budget is being spent on such syntheses and cross-site comparisons (see Section C of the budget justification).

J. SUMMARY

During the first four years of the Cedar Creek LTER project, we have established a wide array of well-replicated, long-term experiments and a series of long-term observational plots in successional fields and native oak savanna. Twelve of our major field projects, and the frequency with which various physical and biotic components will be and have been measured, are summarized in Table 2. The central goal of our work is to understand the various direct and indirect processes that structure successional ecosystems and that lead to the patterns of succession that we observe at Cedar Creek and in other habitats. Our work is an attempt to place the mechanisms of interspecific interaction into the framework of the entire ecosystem. As suggested by Figure 2 and Table 1, we consider all the various elements of our project to be interrelated. We are focusing our work on disturbance, soil processes, plant/soil interactions, herbivore/plant interactions, and herbivore/soil interactions. We believe that the qualitative similarities of succession worldwide (MacMahon 1981) suggests that there are a few general processes that underlie successional dynamics worldwide. As our experimental work clarifies the role of various processes in controlling succession at Cedar Creek, we will continually apply our results to other areas to try to determine how

TABLE 2. PROPOSED SAMPLING FREQUENCY FOR THE PERMANENT CEDAR CREEK LTER EXPERIMENTS.

The following codes are used to indicate the frequency with which a particular item or process has been and will be measured within a particular experimental or observational plot. See text for a full description.

A = Sampled every other week of the growing season
B = Sampled 2 to 4 times per growing season
C = Sampled once each year
D = Sampled every other year
E = Sampled every 3 or 4 years
F = Sampled every 5 to 7 years
N = Not sampled

	ITEM BEING MEASURED OR OBSERVED					
Experiment	Vegetation	Root Mass	Litter	Soil Chem	Herbivores	Disturbance
Single Nutrient	C	N	C	C	C	C
Undisturbed N Gradient Microplots	C	N	C	C	B	B
Disturbed N Gradient Microplots	C	N	C	C	B	B
Nitrogen Gradients with Herbivores	D/A[1]	A[1]	A[1]	A[1]	B	B
Macroplot N Gradients	D	N	D	D	B	B
Macroplot Herbivore Exclosures	D	N	D	D	B	A
Old Field Chronosequence	F	F	F	F	F	F
Oak Savanna Burns	F	F	F	F	F	F
Fire and Secondary Succession	E	E	E	E	E	E
Deer Exclosures	C	N	N	E	B	C
pH, N & Nitrification	D	D	D	B	D	D
Long-Term Monoculture & Competition	B	B	B	B	B	N

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[1] Sampled every other week in two field seasons only.

general they are.

Most of the research that we propose for the next funding period represents a continuation and extension of our present work. Although we will perform other short-term studies on particular processes, the focus of our efforts is our long-term plots. We firmly believe that the field of ecology needs **long-term experimentation** in order to understand the processes that cause the patterns we see in nature. Only experimentation can separate spurious correlation from causation. Only experimentation can demonstrate the total effect of one element of an ecosystem on another element. Long-term experiments are needed because of the long life spans of many organisms, and because indirect effects, which are propagated through other species and processes, necessarily take longer than direct effects. The strongest argument for the need for long-term experiments, though, comes directly from our experimental results to date. For both plants and herbivores, we have seen highly significant **transient responses** (e.g., Fig. 9) to our experimental manipulations. These transient responses, probably caused by differences in maximal growth rates, in initial starting conditions, and in time scales for direct versus indirect effects, may well prove to be the opposite of the long-term effect of the manipulations. Whatever their cause, the presence of such transient responses provide an important warning: the response of an ecosystem to an experimental manipulation depends on the time scale on which it is measured. Up to the present time, most ecological theory has been concerned with the long-term effect of various processes. However, this theory has most often been "tested" using short-term experiments. Such experiments, despite their apparent statistical rigor, may not have tested the hypotheses proposed. The Cedar Creek experiments can provide a uniquely thorough, long-term record of the ways in which various direct and indirect effects influence the structure and dynamics of successional communities.

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IV. PERSONNEL

A. The LTER Working Group

Cedar Creek is used the year around primarily by research scientists and graduate students involved in research. Because it is only a 40-minute drive from the University of Minnesota, researchers have the dual advantages of a natural area and nearby urban facilities. Most scientists working at Cedar Creek have been from the University of Minnesota. However, Cedar Creek has funds that are available each year specifically to encourage outside researchers to start a project at Cedar Creek. Such funds have helped Dr. James Reichman (Kansas State University), and Dr. Mark Davis (Macalester College) start projects at Cedar Creek.

Cedar Creek has a full-time, year-around staff that includes a resident manager (David Bosanko), a secretary (Bev Medvecky), a chief electronics engineer (Larry Kuechle), an associate scientist (Richard Reichle), and a teaching assistant (Kathleen Zinnel). In addition, during the spring, summer and autumn, up to 40 more individuals work at Cedar Creek on a variety of ecological research projects. The LTER project is the largest of these. The researchers most heavily involved in the LTER project are :

Faculty and Post-Doctoral

Dr. David Tilman, Professor, Department of Ecology and Behavioral Biology, U of M
Dr. John Tester, Professor, Department of Ecology and Behavioral Biology, U of M
Dr. David Grigal, Professor, Department of Soil Science, U of M
Dr. Richard Inouye, Post-Doctoral Researcher and LTER Site Manager
Dr. Nancy Huntly, Post-Doctoral Researcher on the LTER project
Dr. John Pastor, Research Associate (20% time on LTER)

Graduate Students

David Wedin, NSF Pre-Doctoral Fellow (Advisor: D. Tilman)
Robert McKane, Ph. D. student (Advisor: D. Grigal)
Mike Norland, Ph. D. student (Advisor: D. Grigal)
Jeff Brokaw, Ph. D. student (Advisor: P. Regal)
Robert Sterner, NSF Pre-Doctoral Fellow (Advisor: D. Tilman)
Rebecca Goldburg, Ph. D. student (Advisor: P. Morrow)
Sharon Strauss, Ph. D. student (Advisor: D. Strong, Florida State U.)
Mark McKone, Ph. D. student (Advisor: E. Cushing; Ph. D. completed 9/85)
Taber Allison, Ph. D. student (Advisor: P. Jordan)
Kathleen Zinnel, Ph. D. student (Advisor: J. Tester)
Mary Cowan, M.S. student (Advisor: D. Tilman)
Andrew Behrend, M.S. student (Advisor: J. Tester; M.S. completed 9/85)

Because most graduate students at the University of Minnesota are supported by University fellowships or by Teaching Assistantships, the LTER project can attract student researchers by offering just supply and equipment funds. In addition to the individuals listed above, there are several other scientists whose research has been partially supported by LTER funds or whose projects have built on or been coordinated with the LTER project:

Dr. James Reichman, Department of Biology, Kansas State University
Dr. Edwin Schmidt, Departments of Microbiology and Soil Science, U of M
Dr. Patrice Morrow, Department of Ecology and Behavioral Biology, U of M
Dr. Mark Davis, Department of Biology, Macalester College, St. Paul, MN
Dr. David Tonkyn, Post-Doctoral Researcher, Ecology and Behavioral Biology

To this group must be added the cadre of undergraduates who have worked as field assistants each year. The LTER project hires 10 - 12 field assistants each summer (five of these with funds provided by the Field Biology Program). These individuals, most of them undergraduate biology majors or incoming ecology graduate students, are coordinated by two crew leaders hired by the LTER project, and are overseen by our Site Manager, Dr. Richard Inouye.

The current group of researchers has a range of skills and research interests that complement each other and span the full breadth of questions that we are pursuing (see attached Vitae for details). The main focus for this project, and its continuity, are provided by the long-term experimental and observational plots that we have established and by the tenured University of Minnesota faculty researchers, especially the Principal Investigator, David Tilman. In any research group of this size, it is natural for its composition to evolve through time as various scientists complete their projects and as others are attracted to the group, perhaps because of new questions or problems that arise. However, we believe that the long-term experimental and observational plots we have established, our thorough documentation of our experimental design and data, our data management, and the commitment of senior researchers will assure the long-term continuity and viability of this project.

B. Project Organization and Data Management

The Cedar Creek LTER project is a coordinated, multi-investigator effort designed to address the questions posed in this (and the preceeding) proposal. The project is coordinated by David Tilman, the PI. When we started the project, we decided that we could accomplish our research goals most effectively by establishing a rigorous series of field experiments that we would monitor on a regular basis for the duration of the project. We believe that such experiments are absolutely essential if we are to help make ecology a potentially predictive, mechanistic science. In addition, these experiments are providing a pool of common, shared information that individual investigators can use in building and testing various synthetic hypotheses. For these reasons, we have allocated a large portion of our resources to establishing, sampling and managing the data that come from our experimental plots. These data will provide the tests of our major hypotheses and are the framework upon which all our synthetic and theoretical efforts are built. However, we have also felt that our project needed more breadth than could be provided by our 10 major field experiments. To attain this breadth, we have hired post-doctoral researchers and have encouraged faculty and graduate students to perform additional work in the experimental plots or in the same fields in which the experiments are located. This has the dual advantages of allowing these investigators to know much more about the biology of the organisms they are woking on and providing the project with knowledge of other processes at work in these fields. This approach, we believe, has allowed our project to have an unusually strong experimental approach at the same time that it has significant breadth.

The large number of samples we collect caused us to have sample analysis and data management problems during our first two years. For instance, during the first field season we collected more than 3000 soil samples to establish pre-treatment soil chemistry for all our experimental plots. In order to analyze these for total nitrogen, pH, P, K, Ca, K and Mg, we had to establish a highly automated soil chemistry laboratory. We have now done that. Our analytical instruments (balances, a one-channel Autoanalyzer, and a two-channel Autoanalyzer) are all interfaced with microcomputers that served as data loggers and data analyzers. These allow us to accurately analyze several hundred soil chemistry samples per day, and to have the data immediately added to our data base. Our project employees a full-time individual at the level of "Junior Scientist" to run our chemistry laboratory as well as several part-time student laboratory technicians.

We solved our second major problem using similar technology. Because we sort all our field samples to species, we have to weigh more than 10,000 plant samples each summer.

The first year we weighed the samples, manually recorded the data on data sheets, entered the data into a computer data base, verified the data, and then manipulated the data to have proper units. We have greatly simplified those steps and increased our accuracy by interfacing electronic balances with microcomputers. Now, in the time required for a balance to weigh a sample, we enter the sample code into the microcomputer, and the microcomputer records the weight. We have written software that transforms these data files into the form needed by our data management software. Thus, at the end of every week of the field season, we have available to us the final data base detailing the data that have just been collected.

Data management, itself, was our third major problem. We initially tried using mainframe computer data management software and statistical packages. However, we found this to be cumbersome, expensive (more than $15,000 per year in computer charges), and lacking the interactive graphics capabilities crucial for understanding large data sets. We have now switched to IBM-XT microcomputers and use Knowledgeman and Statgraphics software. The relational data base management system and the interactive graphics capabilities of these packages, combined with the ability of hard disks to store large data sets, has been an ideal comibination. In addition to the technological side of data management, we have spent much time throughly documenting all our data sets, and assuring that the various data sets are compatible. We have also found that data management is a full-time job. Our data manager is a full-time employee with a M.S. in statistics.

The data collected in our field experiments, the services of our chemistry laboratory, and the services of our data manager are available to all members of the LTER working group. These data and services, and the focus provided by our coordinated field experiments and observations, are the major elements binding together the different researchers in the Cedar Creek LTER project.

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A. BUDGET JUSTIFICATION (First and Subsequent Years)

Although the following budget justification specifically lists the relevant amounts only for the first year of this four year project, each of the remaining three years is essentially identical to the first year, except that most salaries have been adjusted for inflation (assumed to be 5% per year). Thus, years 2, 3 and 4 are all budgeted with the same number and types of personnel as given here for year 1. Any substantive deviation from the justification listed for the first year is specifically listed on the Proposal Budget form (NSF Form 1030) for that year.

A. 1. Senior Personnel

Although many faculty are actively engaged in the LTER project, most are supported on 12-month contracts, and thus do not need summer salary. For that reason, when this project began we decided to limit summer support for senior personnel to the PI. This policy has allowed us to have more funds available to direcly support the post-doctoral researchers, research associates, graduate students and technicians who are more direclty involved in the day-to-day operation of the project. We feel that this policy has been a major reason that we have been able to establish and sample our wide range of experimental and long-term observational projects.

B. 1. Post-Doctoral Associates

a. Soils (Dr. John Pastor; 20% time as a "Research Associate")	$ 5,990.
b. Soil/Ecosystem Ecology (full-time; being advertized now)	18,488.
c. Plant-Herbivore Interactions (Dr. Nancy Huntly)	18,488.
d. Plant-Soil Interactions (full time; being advertized now)	18,488.

Post-doctoral research associates are a major source of breadth for the Cedar Creek project. Clearly, post-doctoral associates are not long-term appointments. However, such appointments allow the flexibility that is required in a long-term, evolving research program. Post-doctoral associates can be hired to answer specific research questions as they arise and encouraged to establish long-term experiments. We believe that many of these individuals will continue their committment to their research after they leave Cedar Creek. By hiring a sequence of post-doctoral associates with a broad range of skills and interests, we hope to build a core of researchers dedicated to the Cedar Creek program that is much more diverse than could ever be accomplished with the slow rate of turnover of university faculty.

There are three individuals who are currently appointed at the post-doctoral level: Dr. John Pastor, Dr. Nancy Huntly, and Dr. Richard Inouye. (Because Dr. Inouye is our Site Manager, he is officially in the "Other Professional" category below). Our new budget calls for us to hire two more post-doctoral researchers. Because of the importance of these positions, we have already started to advertise them, and hope to them on-board for the 1986 field season. We will only consider those individuals who have proven their scientific productivity. From among this group we will chose those individuals whose expertise can broaden our project and help address the new questions that have been raised by our research.

B. 2. Other Professionals

a. Site/Data Manager (Dr. Richard Inouye)	$23,615.

Dr. Inouye is responsible for the day-to-day supervision of our summer field crew. The Site/Data Manager also oversees data collection and data management for the project.

b. Soil Chemist (Cliff Maddox, Junior Scientist)	$21,396.

Cliff Maddox works full-time running our analytical soil chemistry laboratory. He performs thousands of analyses of soil samples each year for such items as total soil nitrogen, extractable nitrate and ammonia, pH, sand/silt/clay, as well as analyzing atmospheric wet and dry fall and lysimeter samples.

B. 3. Graduate Students

One half-time graduate student, 12 months per year (Most Ecology graduate students are supported by fellowships.)	$10,797.

B. 4. Undergraduate Students

a. Two "Crew Leaders" for the summer field crew ($2,575 each for 10 weeks of summer field work)	$5,150.
b. Five "Crew Members" for the summer field crew ($2,472 each for 10 weeks of summer field work)	$12,360.

The Cedar Creek project has a very ambitious sampling schedule. The only way that we are able to accomplish our research is by hiring undergraduate students who assist with sample collection, sorting, weighing and data entry. Our actual summer field crew is approximately twice the size budgeted, with the other individuals hired using funds provided by the University of Minnesota Field Biology Program.

B. 5. Secretarial-Clerical

This individual assists with many aspects of the research project, especially with data entry, data base management, microcomputer-assisted statistical data analysis, and microcomputer-assisted drafting.

C. Fringe Benetits

The currently fringe benefit rates are 25.5% for faculty, 22% for civil service (including post-doctoral researchers), and 1.8% for graduate students. No fringe benefits are charged for undergraduate students.

D. Permanent Equipment

Although we have not yet identified the items we are likely to need, based on our past experience we will need about $12,000. for permanent equipment.

E. Travel

1. Domestic	$5,600.

Attend Scientific Meetings (3 scientists at $350 each)
Visit other LTER sites for intersite research (total of $3,400 for airfare, car rental, living expenses while performing research at other LTER sites and possibly one additional site)
Outside advisory committee (3 member's travel totaling $1,150)

2.Foreign $2,900.

To visit and sample the Park Grass Experiments at the Rothamsted Experimental Station, Harpendon, England. These experiments, which are probably the most long-term ecological experiments in existence, were established over 130 years ago, and are still in operation today (Tilman 1982). However, because of changes in the focus of the research staff at the Rothamsted Experimental Station, there are no longer any personnel at Rothamsted with the skills and desire to sample them. They have not been sampled since 1975 (Thurston, Williams and Johnston 1976). I believe that it is essential that these, the most long-term ecological experiments in existence, continue to be sampled. I feel especially strongly about this because the experiments are quite similar to the Cedar Creek macroplot nutrient addition experiments, and, indeed, helped inspire the Cedar Creek work. Although the Park Grass Experiments lack replicates of any treatments, they provide a unique, detailed, long-term view of the dynamics of unmanipulated and manipulated vegetation that is a perfect complement to the highly replicated Cedar Creek experiments. The University of Minnesota has granted me a Single Quarter Leave for next spring (a 3 month leave of absence with pay) so that I may sample the Rothamsted plots. However, I also require funds for airfare and living expenses. (I am trying to obtain the needed funds from several other sources, and will not use LTER funds if other sources become available.)

These funds will also allow me to present an invited paper on the Cedar Creek LTER Project at the International Botanical Congress in West Berlin, Germany, 24 July to 1 August, 1987.

G. 1. Materials and Supplies

This category includes all the expendable supplies needed to perform this research. The amount given is based on our experiences of the past four years, and includes expenses for fertilizers and reagent-grade chemicals used in our field work; chemicals for laboratory analyses; expendable laboratory supplies such as glassware and deionization columns; electric lawn-edging shears, blades, and bags for plant samples, fencing and iron posts used in field experiments; xeroxing; photographic services, including annual photographs of each experimental plot; aerial photography of all our experimental fields; miscellaneous office supplies; miscellaneous field supplies; equipment repair.

B. BUDGET ALLOCATION TO INTERSITE SYNTHESES

Because our research is motivated by a series of broad, general ecological hypotheses, most of our data can be used for intersite comparisons that could lead to new syntheses and theory. However, in indicating how our resources are allocated to intrasite versus intersite activities, we will include as intersite expenditures only those items that are directly related to intersite activities that are already planned or underway. The main expense for intersite research is salary. D. Tilman will spend most of his summer effort and much of his academic year effort pursuing intersite syntheses. However, in order for Tilman to do so, it is necessary that the Site Manager take over more of the day-to-day administrative duties that Tilman would otherwise perform during the summer and academic year. Thus, in the table below we indicate that 70% of Tilman's summer salary and 50% of the Site and Data Manager's annual salary are dedicated to intersite activity. Based on the interests of N. Huntly, J. Pastor and R. Inouye, we estimate that about 10% of their time will be spent in intersite research. Although about 60% of the annual effort of our field crew and site and data manager is dedicated to collection of data used for intersite comparisons (i.e., disturbed versus undisturbed microplots; herbivore plots; burn experiments), these data are also essential to our on-site efforts. Thus, only 30% is attributed to intersite activities. Airfare, car rental and living expenses while visiting other sites are another major expense.

Expenses Allocated to Intersite Research and Syntheses[1]

Item	1987	1988	1989	1990
D. Tilman (70%)	16,808	17,647	18,526	19,454
Site/Data Manager (50%)	20,455	21,478	22,551	23,679
Post-Doctoral Researchers (10% of salary of 3 individuals)	9,608	10,088	10,593	11,122
Field Crew (30% of salary of 7 individuals)	7,459	7,832	8,223	8,635
Travel and Living Expenses at Other Sites	3,400	3,400	3,400	3,400
Research Supplies	1,100	1,100	1,100	1,100
Total	58,830	61,555	64,393	67,390
Percent of Total Annual Budget	17%	17%	17%	17%

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[1] All dollar amounts shown already include both fringe benefits, if applicable, and overhead.

VI. CURRENT AND PENDING SUPPORT

DAVID TILMAN

Current Support: NSF. Succession, productivity and dynamics in temperate mixed ecosystems in Minnesota (with J. R. Tester). $1,495,000. January 15, 1982 to January 14, 1987. 30% effort. Located at Cedar Creek Natural History Area.

Pending Support: NSF. Succession, productivity and dynamics in temperate mixed ecosystems in Minnesota. $1,475,000. January 15, 1987 to January 14, 1991. 30% effort. Located at Cedar Creek Natural History Area.

Proposals Planned: None.

Other Agencies: This proposal will not be submitted to any other agency.

JOHN R. TESTER

Current Support: NSF. Succession, productivity and dynamics in temperate mixed ecosystems in Minnesota (with D. Tilman). $1,495,000. January 15, 1982 to Janaury 14, 1987. 25% effort. Located at Cedar Creek Natural History Area.

Fur Institute of Canada. Determination of certain biological parameters in foxes caught with live trapping systems (with U. S. Seal). $199,970. June 1, 1985 to May 31, 1987. 5% effort. Located at Cedar Creek and Jamestown, ND.

U. S. Department of the Interior. Fertility control in wild horse populations (with D. B. Siniff). $710,920. October 1, 1985 to September 30, 1988. 10% effort. Located in Nevada.

Proposals Pending: NSF. Improvement of research facilities at Cedar Creek Natural History Area. $99,580. July 1, 1986 to June 30, 1988. 5% effort. Located at Cedar Creek.

Proposals Planned: None

NANCY HUNTLY

Current Support: None
Proposals Pending: None
Proposals Planned: None

RICHARD INOUYE

Current Support: None
Proposals Pending: None
Proposals Planned: None

VII. APPENDICES

A. PUBLICATIONS OF THE CEDAR CREEK LTER PROJECT

Published Papers

Inouye, R.S., N.J. Huntly, D. Tilman, J.R. Tester, M. Stillwell and K.C. Zinnel. 1986. Old field succession on a Minnesota sandplain. Ecology. (In press.)

McKone, M.J. 1985. The reproductive biology of several bromegrasses (*Bromus* L.): Variation in breeding system, pattern of fruit maturation, and seedset. American Journal of Botany 72:1334-1339.

McKone, M.J. and D.D. Biesboer. 1986. Nitrogen fixation in association with the roots of goldenrods (*Solidago* L.). Soil Biology and Biochemistry. (In press.)

McKone, M.J. and D. Tonkyn. 1986. Intrapopulation gender variation in common ragweed (*Ambrosia artemisiifolia*), a monoecious annual herb. Oecologia, in press.

Reichman, O.J. and S. Smith. 1985. Impact of pocket gophers on overlying vegetation. Journal of Mammalogy 66:720-725.

Sterner, R.W. 1986. Herbivores' direct and indirect effects on algal populations. Science 231:605-607.

Tester, J.R. 1986. Seasonal changes in activity rhythms of some free-ranging animals. Canadian Field Naturalist. (In press.)

Tilman, D. 1983. Plant succession and gopher disturbance along an experimental gradient. Oecologia 60:285-292.

Tilman, D. 1984. Plant dominance along an experimental nutrient gradient. Ecology 65:1445-1453.

Tilman, D. 1985. The resource ratio hypothesis of plant succession. American Naturalist 125:827-852.

Tilman, D. 1986. Evolution and differentiation in terrestrial plant communities: the importance of the soil resource:light gradient. Pages 359-380 in T. Case and J. Diamond, eds., *Community Ecology*. Harper and Row, New York.

Tilman, D. 1986. Theory of consumer-resource interactions. American Zoologist. (In press.)

Tilman, D. 1986. Nitrogen-limited growth in plants from different successional stages. Ecology. (In press.)

Tilman, D. 1986. Resources, competition and the dynamics of plant communities. In M. Crawley, ed., *Plant Ecology*. Blackwell. (In press.)

Tilman, D., R. Kiesling, R. Sterner, S. Kilham, and F. Johnson. 1986. Green, bluegreen and diatom algae: taxonomic differences in competition ability for P, Si, and N. Archive fur Hydrobiologie. (In press.)

Zinnel, K.C. and M.F. Marozas. 1986. Computer data entry techniques used in scientific applications. Pages 61-72 in W.K. Michner, ed., *Research Data Management in the Ecological Sciences*. Belle W. Baruch Library in Marine Science, No. 16, University of South Carolina Press.

Manuscripts in Review in Major Refereed Journals

Behrend, A.F. and J.R. Tester. Aspects of feeding ecology of the plains pocket gopher (Geomys bursarius) at Cedar Creek Natural History Area, Minnesota.

Huntly, N.J. Influence of co-occurring consumers on resources: independent, collective and interactive effects of mammalian herbivores on vegetation.

Huntly, N.J. and R.S. Inouye. Occurrence of small mammals along a grassland chronosequence: successional patterns and correlations with vegetation.

Huntly, N.J. and R.S. Inouye. Herbivory in successional old fields in Minnesota: interactions of nitrogen availability, herbivore populations, and vegetation dynamics.

Inouye, R.S. and N.J. Huntly. Fine-scale microhabitat selection by small mammals in response to fertilization and disturbance in old fields in Minnesota.

Inouye, R.S. and D. Tilman. Convergence and divergence along experimental nutrient gradients.

Inouye, R.S., N.J. Huntly, D. Tilman, and J.R. Tester. Gophers, soils, and vegetation in old-field succession on a Minnesota sandplain.

Pastor, J., M.A. Stillwell, and D. Tilman. Nitrogen mineralization and nitrification in Minnesota old fields.

Strauss, S. Direct and indirect effects of host plant fertilization on an insect herbivore community.

Tilman, D. Do old-field plant communities have multiple stable equilibria?

Tilman, D. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients.

Manuscripts in Preparation

(Listed below are only those manuscripts for which all necessary data have been collected and data analysis and writing are currently underway.)

Brokaw, J. The effects of nocturnal foraging and diel migration on rates of parasitism suffered by caterpillars of Satyrium edwardsii.

Brokaw, J. The wood ant, Formica obscurpes, as a keystone species determining the species composition of insect herbivores on burr oaks.

Huntly, N.J. Variation in seed number and size in relation to nitrogen availability of the maternal habitat.

Huntly, N.J. and D. Tilman. Correlations of tissue nitrogen with successional occurrence and competitive ability along a nitrogen availability gradient.

Huntly, N.J., D. Tilman, M.L. Cowan, and R.S. Inouye. Nitrogen and light limitation of growth and allocation in Agrostis scabra.

Inouye, R.S., N.J. Huntly, and D. Tilman. Effects of nitrogen availability on grasshopper assemblages in Minnesota old-fields.

Inouye, R.S. and T. Allison. Effects of deer removal on invasion of old fields by woody vegetation.

Inouye, R.S. and N.J. Huntly. Old field grasshoppers and vegetation.

McKane, R., D. Grigal, and M. Russelle. Niche separation and overlap in an old-field plant community as measured by competition for 15N.

McKane, R. and D. Grigal. Carbon and nitrogen dynamics during old-field succession.

Norland, M., B. McKane, and D. Grigal. Changes in above- and below-ground production within and among species along successional and nutrient gradients.

Norland, M. and D. Grigal. Nitrogen nutrition, soil water content, and above-ground production of an old-field successional sequence.

Pastor, J., M.A. Stillwell, and D. Tilman. Litter dynamics in Minnesota old fields.

Tester, J.R. et al. Effects of fire frequency on native oak-savannah vegetation in east-central Minnesota.

Tilman, D., R.S. Inouye, and N.J. Huntly. Soil heterogeneity, plant abundance patterns and species diversity during old field succession.

Tilman, D., N.J. Huntly, R.S. Inouye, and M.L. Cowan. Do plant species differentially reduce limiting resources?

Zinnel, K.C. and J.R. Tester. Effects of pocket gophers (Geomys bursarius) on root biomass.

Book in Preparation

Tilman, D. The Dynamics of Plant Competition. (To be published by Princeton University Press.)

Theses

Behrend, A. 1985. The feeding ecology of the plains pocket gopher (Geomys bursarius) in Minnesota. M.S. Thesis, University of Minnesota.

Haarstad, J.A. 1985. Ecological relationships among eight species of coexisting burying beetles in east-central Minnesota (Coleoptera: Silphidae, Nicrophorus). Ph.D. Thesis, University of Minnesota.

Malody, K.J.A. 1985. The effects of fertilizers on lichens. M.S. Thesis, University of Minnesota.

McKone, M.J. 1985. Gender in hermaphrodites: intraspecific variation in some wind-pollinated plants and the effect of breeding system. Ph.D. Thesis, University of Minnesota.

Presentations at National and International Meetings

Behrend, A.F. and J.R. Tester. 1985. Feeding behavior of plains pocket gophers (Geomys bursarius) in Minnesota. Paper presented at American Society of Mammalogists meeting, University of Maine, Orono.

Brokaw, J. 1984. The effects of ant-tending and nocturnal foraging on the rates of parasitoid attack on caterpillars of Satyrium edwardsii. Bulletin of the Ecological Society of America 65:164.

Goldburg, R. 1984. Ground beetle populations in fertilized and unfertilized old fields in Minnesota. Bulletin of the Ecological Society of America 65:164.

Goldburg, R.J. 1985. Sequential flowering of neighboring plants and the movement of pollen-feeding beetles. Paper presented at the Ecological Society of America meeting, University of Minnesota, Minneapolis.

Huntly, N.J. and R.S. Inouye. 1984. Grasshopper distribution patterns within and among Minnesota old fields. Bulletin of the Ecological Society of America 65:92.

Huntly, N.J. and R.S. Inouye. 1984. Experimental and observational studies of grasshoppers on the Anoka sandplain. Abstracts of the Ninth North AmericanPrairie Conference 9:16.

Inouye, R.S. and N.J. Huntly. 1983. Microhabitat selection by old-field small mammals in response to nitrogen fertilization and disturbance. Paper presented at theAmerican Society of Mammalogists meeting, Gainesville, Florida.

Inouye, R.S. and N.J. Huntly. 1983. Patch choice by insects and mammals: responses to fertilization of old fields. Paper presented at the Ecological Society ofAmerica meeting, Grand Forks, North Dakota.

McKane, R.B. 1984. Root biomass dynamics during old-field succession. Bulletin of the Ecological Society of America 65:107.

Norland, M.R. 1984. Above-ground productivity of old fields along a successional gradient. Bulletin of the Ecological Society of America 65:107.

Stillwell, M.A. 1983. Nitrogen availability and organic matter accumulation during 50 years of old field succession in northern Minnesota. Bulletin of theEcological Society of America 64.

Stillwell, M.A. 1984. Nitrogen inputs, leaching losses, and availability as controls of old field succession in Minnesota. Bulletin of the Ecological Society of America 65:189.

Strauss, S.Y. 1984. The effects of nitrogen fertilization on the insect community associated with Artemisia ludoviciana. Bulletin of the Ecological Society of America 65:163.

Tester, J.R., R.S. Inouye, G.D. Tilman, N.J. Huntly, M.A. Stillwell, and K.C. Zinnel. 1984. Succession in old fields in east-central Minnesota: patterns of vegetation, soils, and gopher activity. Bulletin of the Ecological Society of America 65:107.

Tilman, D. and J.R. Tester. 1982. Micro and macro views of succession, productivity and dynamics in oak savanna. Paper presented at the Ecological Society of America meeting, State College, Pennsylvania.

Tilman, D. 1982. Plant succession: experimental tests of a new theory of succession. Paper presented at the Ecological Society of America meeting, State College, Pennsylvania.

Tilman, D. 1983. Succession along an experimental nutrient gradient: gopher disturbances and other indirect effects. Bulletin of the Ecological Society of America.

Tilman, D. 1983. Mechanistic models of resource competition in plants. Annual Meeting of American Society of Zoologists.

Tilman, D. 1984. Old-field plant dominance along experimental nitrogen:light gradients. Bulletin of the Ecological Society of America 65:65.

Tilman, D. 1984. Trade-offs and community structure. Invited paper for the Calimigos Ranch Conference on Community Ecology, Malibu, California.

Tilman, D. 1985. Experimental studies on resource competition and succession in old fields. Bulletin of the Ecological Society of America 66:283.

Tonkyn, D.W. and P.A. Morrow. 1985. Effects of similarity among plants on diffusion of a specialist herbivore. Paper presented at the Ecological Society of America meeting, University of Minnesota, Minneapolis.

Zinnel, K.C. and J.R. Tester. 1984. Non-intrusive monitoring of plains pocket gophers. Bulletin of the Ecological Society of America 65:166.

Zinnel, K.C. and J.R. Tester. 1984. Winter movements of plains pocket gophers (Geomys bursarius) in Minnesota. American Society of Mammalogists Abstracts 64:19.

B. SITE DESCRIPTION AND FACILITIES

1. Site

Cedar Creek Natural History Area is a 2,185 ha (9 square mile) experimental ecological reserve located 60 km north of the University of Minnesota in Minneapolis. It lies in a floristic tension zone with many species near their southwestern limits while others are at their northern limits. Cedar Creek's southern relict outpost of boreal forest species, its extensive oak savanna, old fields, western prairie-type lakes and marshes, many soil types, and closeness to the University make it a unique research site. Cedar Creek is owned and managed by the University of Minnesota. Although Cedar Creek lies near a large metropolitan area, it is large enough to withstand urban pressures; its important natural areas are buffered by extensive oak forests and abandoned fields.

Cedar Creek contains a variety of natural and culturally disturbed habitats, including a thorough sequence of successional areas with known past history (Inouye et al. 1986). The major vegetation types at Cedar Creek and their approximate sizes are: old fields (850 ha); wetland marsh and carr (710 ha); oak savanna (250 ha); oak-hickory-aspen forest (130 ha); conifer bog (70 ha); and Great Lakes pine forest (40 ha). Woodlots have been free of grazing and cutting for 45 or more years and are semi-natural. Forest composition is strongly dependent on relation to natural firebreaks.

Cedar Creek lies within the Anoka Sand Plain, a large outwash plain covering about 2200 km^2. In some of the area, outwash sands have been reworked by wind, resulting in a dune-shaped topography dominated by the Sartell soil series (Grigal et al 1974). In other areas, deposition was apparently by slower moving waters and this, combined with a flat, low physiographic position, has led to the formation of soils of the Soderville series. On the broad flats located some distance above the water table, soils of the Nymore series, under the influence of savanna vegetation, have formed a Mollisol or prairie soil. The Zimmerman series is represented on much of the remaining mineral upland. Glacial till appears at the surface in some spots and both Inceptisols and other Alfisols can be found there. Cedar Creek also has extensive areas of organic soils, or Histosols, associated with a variety of lowland vegetation types.

2. Facilities

Cedar Creek has nine permanent buildings, including a new, modern, year-around research laboratory, a newly-remodeled dormitory-kitchen, a shop building, a large storage building and work area, a winterized animal holding facility, and four year-around family homes. The facilities, which have been considerably expanded during the past four years because of the needs of the LTER project and of other new research projects, provide all the space and services we need to perform our research. We have a complete, well-equipped analytical chemistry laboratory that is used for soil, water and plant tissue analyses. Major items of equipment in the laboratory are: two Technicon Auto Analyzers; two Apple II-e microcomputers that control the Auto Analyzers and act as data loggers; analytical balances; shaker tables; centrifuges; fume hood; three spectrophotometers; muffle furnace; high-volume still; drying ovens; pH meter; culture boxes; autoclave; block digester. Other major items of equipment include: a walk-in drying oven; three IBM-PC controlled analytical balances for automated weighing and data entry; three IBM-XT microcomputers; a Hewlett-Packard Vectra microcomputer; Hewlett-Packard graphics plotter; one letter quality and four dot-matrix printers; drafting equipment and automated lettering machine; microcomputer-controlled automatic radio tracking grid for small mammals; Lambda PAR collector and meter; wet- and dry-fall atmospheric collectors; a truck; a station wagon; a tractor.