COVER SHEET FOR PROPOSAL TO THE
NATIONAL SCIENCE FOUNDATION

APPENDIX IV

For Consideration by NSF Organization Unit(s) (Indicate the most specific unit known, i.e. program, division, etc.)	For NSF Use Only
Long-Term Ecological Research	**NSF Proposal Number**
Program Announcement/Solicitation No./Closing Date	

Date Received	Number of Copies	Division Assigned	Fund Code	File Location

Employer Identification Number (EIN) or Taxpayer Identification Number (TIN)	Show Previous Award No. If This is: ☒ A Renewal or ☐ An Accomplishment-Based Renewal	Is This Proposal Being Submitted to Another Federal Agency? YES___ NO XX If YES, List Acronym(s)
41-6007513		

Name of Organization to Which Award Should be Made:	Address of Organization, Including Zip Code
Regents of the University of Minnesota	Office of Research and Technology Transfer Administration
Institutional Code (if known)	1100 Washington Avenue South, Suite 201 Minneapolis, MN 55415

Is Submitting Organization:	☐ For-Profit Organization; ☐ Small Business; ☐ Minority Business; ☐ Woman-Owned Business
Branch/Campus/Other Component (Where work is performed, if different)	Institutional Code (if known)

Title of Proposed Project

Succession, Biodiversity and Ecosystem Functioning at the Prairie-Forest Border

Requested Amount	Proposed Duration (1-60 months)	Requested Starting Date
$ 3,780,000	72 months	November 1, 1994

Check Appropriate Box(es) If This Proposal Includes Any of the Items Listed Below:

☐ Vertebrate Animals   ☐ National Environmental Policy Act   ☐ Facilitation for Scientists/Engineers with Disabilities
☐ Human Subjects   ☐ Proprietary and Privileged Information   ☐ Research Opportunity Award
☐ Historical Places   ☐ Disclosure of Lobbying Activities   ☐ International Cooperative Activity:
☐ Research Involving Genetically Engineered Organisms

Country/Countries

PI/PD Department	PI/PD Postal Address
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NOTE: The FULLY SIGNED Certification Page must be submitted immediately following this Cover Sheet.

*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.

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PROJECT SUMMARY

This is a request for renewal of the Cedar Creek Natural History Area Long-Term Ecological Research project. We are using long-term observation and experimentation to examine the controls of successional dynamics and biodiversity in ecosystems at the prairie-forest boundary. We are also studying the effects of biodiversity on the functioning and stability of these ecosystems. Our approach combines studies of numerous species on several trophic levels with studies of the ecosystem processes that they affect and that affect them. Our work is designed to combine and synthesize the often disparate approaches of population, community, and ecosystem ecology. The 12-year record that we have already accumulated at our site demonstrates that ecosystems at the prairie-forest border are highly sensitive to climatic variation, and that their responses to climatic variation depend on biodiversity.

Our studies focus on the various direct, indirect and feedback processes that control the composition, dynamics and biodiversity of these grassland and savanna ecosystems, and on the effects of the composition and biodiversity of these ecosystems on their stability and functioning. Specifically, we will

(1) continue a series of on-going, long-term experimental and observational studies in successional grasslands and native prairie openings,

(2) initiate and expand studies in oak savanna, and

(3) initiate a large experimental study of the consequences of biodiversity for prairie and savanna ecosystems.

All of this work addresses the causes and consequences of successional dynamics and biodiversity patterns in grasslands and savanna near the prairie-forest border.

B. PROJECT DESCRIPTION:

SUCCESSION, BIODIVERSITY, AND ECOSYSTEM FUNCTIONING
AT THE PRAIRIE-FOREST BORDER

Among all the LTER sites, Cedar Creek Natural History Area is unique because of its location on the climatically and edaphically controlled boundary between prairie and forest (Fig. 28). As Curtis (1959) suggested, the oak savanna vegetation that characterizes this "tension zone" between forest and prairie is highly sensitive to climatic variation (Figs. 1, 2, 3, 23; Tilman and El Haddi 1992, Faber-Langendoen and Tester 1993, Tilman and Downing 1994). It is also strongly impacted by edaphic factors, especially soil nitrogen availability (Tilman 1987, 1988, 1993; Inouye et al. 1987c; Hairston and Grigal 1991), by fire frequency (White 1983, Tester 1989, Faber-Langendoen and Tester 1993) and by herbivores and predators (Inouye et al. 1987a, 1987b, Huntly and Inouye 1984, 1987, 1988, Ritchie and Tilman 1992, 1993 and in prep.). Its large tracts of oak savanna, of prairie and successional grasslands, and of oak forest, and its smaller stands of basswood-sugar maple, of white pine, of jack pine, and of red pine provide a diverse mosaic of upland ecosystems that have been shaped by these forces. Moreover, the dominant vegetation of the region, oak savanna, itself has unusually high species richness because its flora and fauna include both prairie and forest species.

It is the diversity and dynamics of these ecosystems that form the focus of our research. Three major questions, and a host of subsidiary issues, guide our research:

(1) What factors, interactions and positive and negative feedback effects control the species composition and species dynamics of our successional grasslands and native savanna ecosystems?

(2) What forces determine how many species can persist on various trophic levels within our ecosystems, i.e., what controls biodiversity?

(3) What are the impacts of species composition and biodiversity on the functioning of these ecosystems?

Succession and biodiversity are tightly linked. We are interested in succession because it is the process of ecosystem assembly. Disturbances often cause the local loss of species. The dynamics of succession, and the factors that drive the successional processes, are thus the processes that allow species to invade into a habitat and persist with other species. The environmental constraints, organismal tradeoffs, and feedback effects that control the rate, pattern, and direction of succession (Huston and Smith 1987) are likely to be the forces that maintain these features, including biodiversity, once successional changes cease (Tilman 1988, 1990). Successional dynamics are thus the dynamics of community assembly, and can provide great insights into the forces that control and maintain diversity.

Cedar Creek is an ideal site to pursue these questions because it contains numerous stands of native savanna and a rich chronosequence of over 100 successional grassland fields of known ages, ranging from newly abandoned to 67 years post-agriculture (Inouye et al 1987c). The past history of over half of these was known when our LTER began (Pierce 1954), and that of the remainder has been determined by interpretation of aerial photographs taken from 1930 to the present. The permanent LTER plots in this chronosequence, and those in our experimental manipulations, are providing a detailed record of the sequence and timing of species invasions and losses during succession.

Much of Cedar Creek has experienced another major disturbance during the past century, fire suppression, and is undergoing successional change in response to this. Depending on landscape location, many areas within Cedar Creek were subject, until European settlement in the late 1800's, to regular fires with frequencies as great as fire every other year. Fire suppression is leading to the gradual conversion of oak savanna into oak woodland (White 1983; Faber-Langendoen and Tester 1993), but the rate and extent of this successional change is not yet understood. However, 220 ha of Cedar Creek, and 35 ha on adjacent Nature Conservancy land (the Allison Savanna), have been subject to regular burns over the past 30 years, and contain excellent savanna vegetation. An additional 110
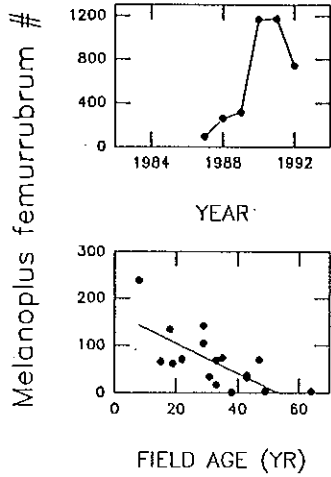
Fig. 20. The upper portion of each pair of graphs shows the average abundance across all successional fields of a grasshopper species versus year. The lower portion of each part shows its average abundance across all years versus successional age of each field. If there is a significant dependence of abundance on age, this is indicated by a solid line. Where no line is shown, it is not significant (p>0.05).
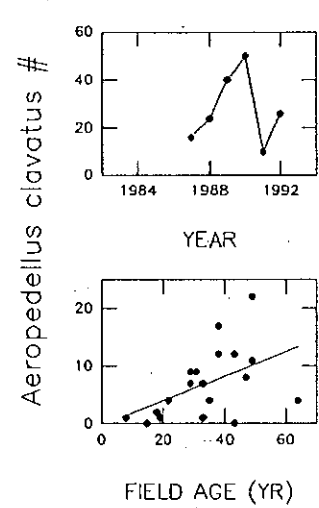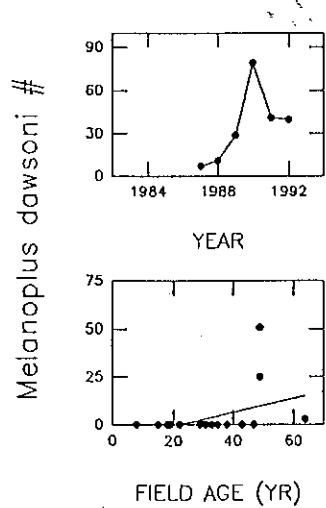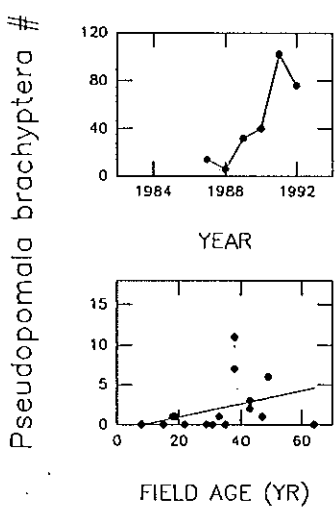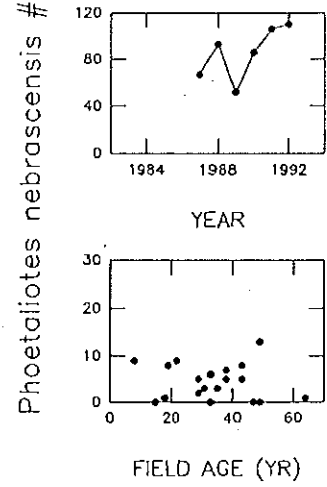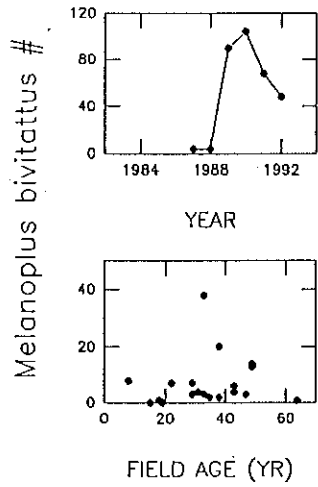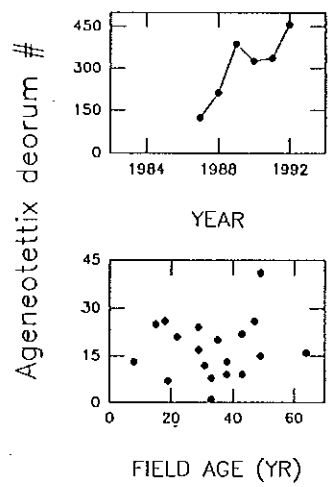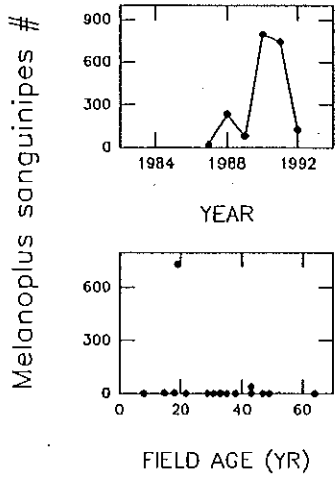
ha of Cedar Creek that had been oak savanna at the time of settlement, and that has not been clearcut or farmed, is now part of an expanded LTER burning program. Although oak savanna once covered about 10% of Minnesota (Nuzzo 1986), most has been converted to agriculture. The remaining stands now cover less than 0.02% (Nuzzo 1986), with those at Cedar Creek and the Allison Savanna being about half of the known regional savanna.

Climatic variation is the other major external disturbance that impacts our ecosystems. During the most recent interglacial period, the vegetation of Cedar Creek has fluctuated between spruce forest, hardwood forest, prairie and savanna, apparently in response to climatic variation and/or the effects of climate on fire frequency (Cushing 1963; Grimm 1984). Thus, the boundary between forest and prairie has migrated frequently, and may provide an early warning of the ecological impacts of future climatic changes.

Climatic conditions during the first 12 years of the Cedar Creek LTER were extremely variable, which has provided us with unique insights into the effects of climatic variability on population, community and ecosystem processes (Tilman and El Haddi 1992, Faber-Langendoen and Tester 1993, Tilman and Downing 1994). These insights were only possible because our long-term data provided a temporal context against which the effects of climatic change could be measured (e.g., Figs. 1, 2, 3). However, this extreme climatic variability has made it difficult to understand succession because its slower and more subtle dynamics were overwhelmed by the dramatic effects of drought. It was not until 1993, 5 years after the drought, that many traits of our plots, including species richness (Fig. 2D), productivity (Fig. 2C) and abundances of some major plant species (Figs 29C, 30A,B) had returned to their pre-drought levels. We now need several relatively normal years if we are to distinguish successional dynamics from the effects of climatic extremes. However, as our data clearly demonstrate, successional dynamics are climate dependent, and thus each successional series will have unique aspects that represent the signature of the climatic conditions it has experienced.

In the past 12 years, we have gathered a richly detailed record of the dynamics of successional grasslands and prairie openings, and of their response to climatic variations and other disturbances. We have performed numerous long-term experiments that have provided insights into the underlying forces that control the composition, successional dynamics, and diversity of these systems. Our work focuses on these factors, and on how the interactions and feedbacks among them determine the species composition, dynamics and biodiversity of these ecosystems. More recently we have begun studying the impacts of biodiversity on the stability and functioning of these ecosystems.

We will continue to seek the underlying mechanisms that cause broad scale patterns in ecosystem composition, diversity, and productivity in our successional grasslands and prairie openings, and will expand our efforts in oak savannas. We are interested in and greatly concerned about the potential impact of global climatic change on biotic diversity, and believe that our long-term experimental and observation studies will help address this issue. Our ongoing studies will further quantify the effects of biodiversity on ecosystem resistance to and resilience from climatic variability. Our new biodiversity experiment, described later, should provide some of the first direct field evidence of the effects of species and functional diversity on numerous aspects of population and ecosystem stability and functioning.

For convenience in describing our proposed work, we divide it into three interrelated and interdependent parts. All five of the major investigators are involved in all three parts, and results obtained in one part are designed to give insights into the other two. The first part describes the continuation and expansion of our work in successional grasslands and in prairie openings. The second describes our continuing and expanded work in oak savanna. The third summarizes our new biodiversity manipulation experiment.

A. Microtus pennsylvanicus
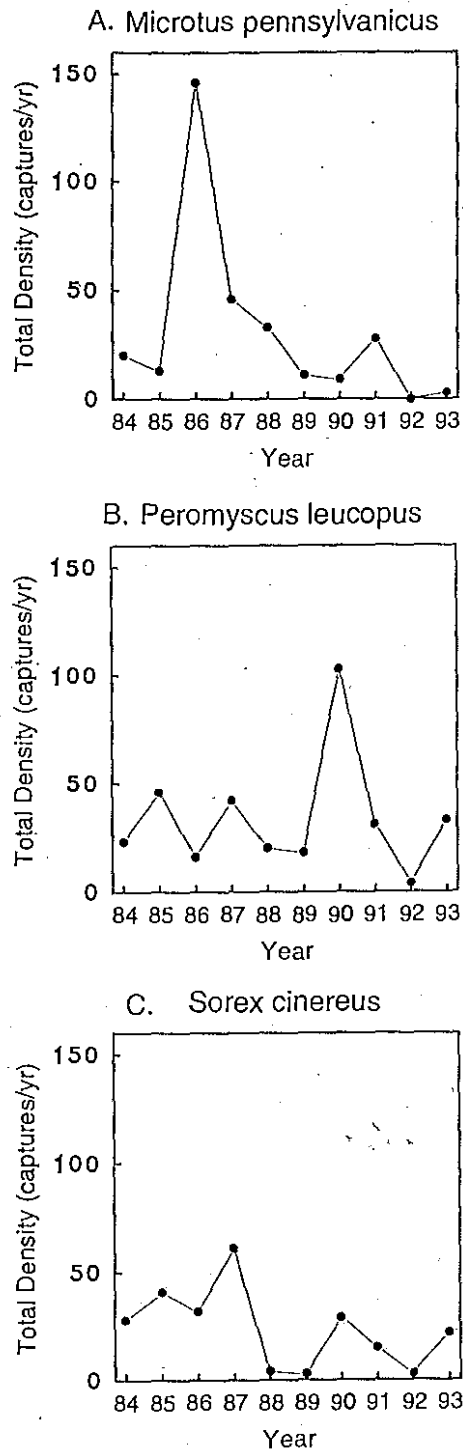
B. Peromyscus leucopus

C. Sorex cinereus

Fig. 21. Annual abundances, averaged across all fields in the chronosequence, of three small mammal species. Total density is the total number of animals captured each year. The same number of trap nights and the same positioning of traps is used each year.

PROPOSED RESEARCH

I. CONTINUING STUDIES OF GRASSLAND SUCCESSION AND BIODIVERSITY

A number of hypotheses may explain successional dynamics or the local persistence of species-rich communities (Hutchinson 1959, 1961; Connell and Slatyer 1977; Armstrong and McGehee 1980; Levins 1979; Tilman 1982, 1985, 1988, 1990; Huston and Smith 1987), but they all share a common element (Tilman and Pacala 1993). All assume that two or more factors constrain the fitness of individual organisms, and that there are interspecific tradeoffs in the abilities of individuals to deal with these constraints. Any of the constraints and tradeoffs that can explain succession can also explain the stable coexistence of numerous species (Tilman 1990). None of these hypotheses of succession or biodiversity has any logical supremacy or seems any more likely based on an invocation of Ockham's Razor. Only detailed observational and experimental studies can determine which hypothesis explains a given successional sequence, and which explains the persistence of numerous species in a habitat. Moreover, only such studies can test the additional hypothesis that the same forces that control succession also maintain diversity once successional replacements cease.

Theories that explain the maintenance of species richness fall into five groups (Tilman and Pacala 1993): (1) spatial heterogeneity in the physical environment; (2) temporal variability and non-equilibrium conditions; (3) multi-trophic level interactions and trophic complexity; (4) neighborhood interactions and dispersal in spatial habitats; and (5) competitively identical species.

Spatial heterogeneity can allow the stable coexistence of numerous species (e.g., Hutchinson 1959, 1961) if there are interspecific tradeoffs in the abilities of the species to deal with this aspect of the physical environment. For instance, if plants are limited by two different soil resources, such as N and P, and if their supply rates vary from point-to-point in a landscape, then tradeoffs in their resource competition abilities might allow an unlimited number of species to stably coexist (Tilman 1982). Similarly, if organisms are limited by a single resource, but are also affected by a physical factor such as temperature, then a potentially unlimited number of species could stably coexist along a geographic temperature gradient if species had different temperature optima (Tilman et al. 1981, Tilman and Pacala 1993). Non-equilibrium conditions, such as fluctuations of limiting resources, can also potentially allow an unlimited number of competing species to stably coexist (Levins 1979, Armstrong and McGehee 1980). This requires a tradeoff between the ability to compete for the average availability of the resource versus its ability to compete when concentrations fluctuate (e.g., Sommer 1984, 1985; Grover 1988, 1989). A potentially unlimited number of species may stably coexist when all species compete for a single limiting resource in a physically homogeneous habitat if the organisms compete in their immediate neighborhood and if there are tradeoffs between neighborhood competitive ability and the ability to disperse to other localities (Skellam 1951, Levins and Culver 1971, Horn and MacArthur 1972, Levin 1976, Durrett and Levin 1994, Tilman 1993). Our work, to date, has supported this last hypothesis more than any other (Tilman 1990, 1993, 1994; Gleeson and Tilman 1990). Interactions among trophic levels may also allow an unlimited number of species to stably coexist if there are tradeoffs between competitive ability versus resistance to predators, pathogens or parasites (Levin, Stuart and Chao 1977, Tilman 1982). Thus, the trophic structure of our food webs, and the tradeoffs faced by each species between acquiring its resources versus defending itself from predators and pathogens, may also explain the long-term persistence of our species rich communities. Our long-term manipulations of trophic structure and soil resources are allowing us to test this hypothesis, and should help resolve the debate about the relative importance of top-down versus bottom-up forces in controlling production and diversity (e.g., Carpenter et al. 1985, Carpenter and Kitchell 1988, 1993, Power 1990a,b, Oksanen et al. 1981, Fretwell 1977, Hairston and Hairston 1993).

An alternative to tradeoffs is for species to be competitively identical. Numerous functionally identical species can persist if the rate of evolution of new species balances the rate at which existing species go extinct (Hubbell and
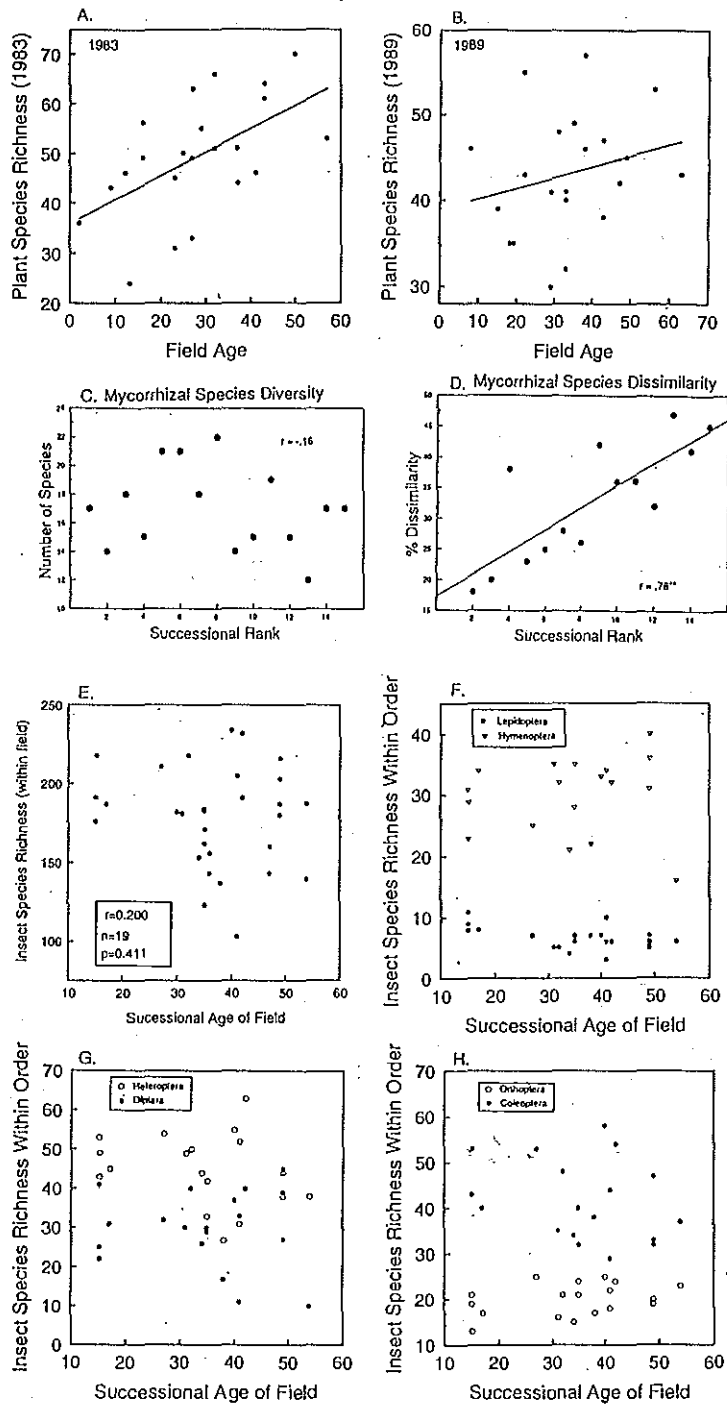
Fig. 22. The dependence of species richness on successional age. A. and B. Plant species richness was a significantly increasing function of field age in both 1983 and 1989, but the relationship was much weaker in 1989, just after the drought. C. There was no rank order correlation between the number of mycorrhizal species in a field and its successional age. D. However, comparing all other fields to the youngest successional field, fields that differed greatly in their successional rank (age) also differed greatly in the similarity in composition of the mycorrhizal community. E., F., G., H. Neither the total number of insect species per field nor the total number of species in the Hymenoptera, Lepidoptera, Heteroptera, Diptera, Orthoptera or Coleoptera was significantly dependent on field age.

Foster 1986). Our studies of competition among various grass species have revealed that two of the seven pairs of species we have studied are extremely similar in their requirements for nitrogen (Fig. 13A) and that these pairs are persisting after 8 years of competition (Fig. 13C,D). Thus, we have some support for this hypothesis, and will continue to develop and test it.

The first four of the diversity theories summarized above can also explain successional dynamics. The heterogeneity hypothesis is logically identical to the resource ratio hypothesis of succession (Tilman 1985). The non-equilibrium coexistence model can be expanded to describe succession as the transient dynamics of interspecific interactions. The spatial coexistence model is a mathematical elaboration of the competition-dispersal (or "r and K") model (MacArthur and Wilson 1967; Werner and Platt 1976). The multi-trophic-level model predicts that succession can be driven by successive invasions of dependent species. Herbivores can live in a habitat only after their host plants are present. The parasites and predators of these herbivores can invade and survive only after their hosts are at sufficient density. Thus, succession may result from the sequential invasion of higher trophic levels, with early successional species being more susceptible to herbivory, and later successional species either being more resistant to herbivory, or having their herbivores better held in check by parasites, pathogens, predators, and disease.

We are addressing these issues and questions through a series of long-term observational and experimental studies. All of these, which are discussed below, will continue with a renewal of our LTER grant. For brevity, we summarize methods. Complete details are in the primary literature, as cited below.

A. Old Field Chronosequence (E014 and E054)

It is essential that successional dynamics be thoroughly described if we are to test among alternative successional hypotheses. Thus, a major effort is the on-going collection of data on a chronosequence of successional fields (Inouye et al. 1987c). In 1983 we chose 22 fields, ranging in age from 1 to 56 years, that had similar soils and slope, had been annually cropped until abandonment, and for which the last year of agriculture was well-documented (Pierce 1954). We established, in each field, 100 permanently marked 0.5 m^2 plots. The 100 plots were laid out in 4 rows of 25 plots, each separated by 25 m. Each plant in a plot was identified to species and its percent cover estimated for all 2200 plots (Inouye et al. 1987c). A 2.5 cm diameter x 15 cm deep soil core was extracted from the center of each plot. A portion was analyzed for total soil N and C, and the remainder archived for future analyses. All 2200 transects are resampled for soils and vegetation every 6 years.

We also established a 5 m x 5 m plot adjacent to the first plot on each transect. These are annually sampled for aboveground vegetation via clipping and sorting, to species, a 10 cm x 300 cm subsection. In three fields (14, 24 and 48 yr post agriculture) 12 additional plots have been sampled annually (Fig. 29). These plots, which are controls for the N addition experiment (E001), provide our most fine-scale information on successional dynamics. These dynamics are generally consistent with those inferred from the chronosequence (compare Fig. 12 and Fig. 29A), but this is blurred by the effects of drought (Fig. 29C).

Each field is sampled four months each growing season for abundances of grasshoppers, the major herbivore (Fig. 20). These are sorted to species and stage, and counted. Each year the number of gopher mounds in these regions is enumerated as a measure of gopher disturbance. Small mammals are trapped and identified to species three times each growing season.

Our goal is to identify patterns of abundance of major consumer species, determine factors responsible for those patterns, and discern the effects of herbivore dynamics on other trophic levels. Densities of small mammals are generally low at Cedar Creek, but there is marked annual variation in their densities that (Fig. 21), over an 11 year period, we cannot attribute to variations in climate, but that seems to depend on plant productivity (Huntly and Inouye 1987, Inouye and Huntly in prep) and, perhaps, plant N content, which we began annually measuring in the chronosequence in 1993. Thus, we will test the effects of both plant quality and quantity on consumer dynamics.

Single Nutrient Additions

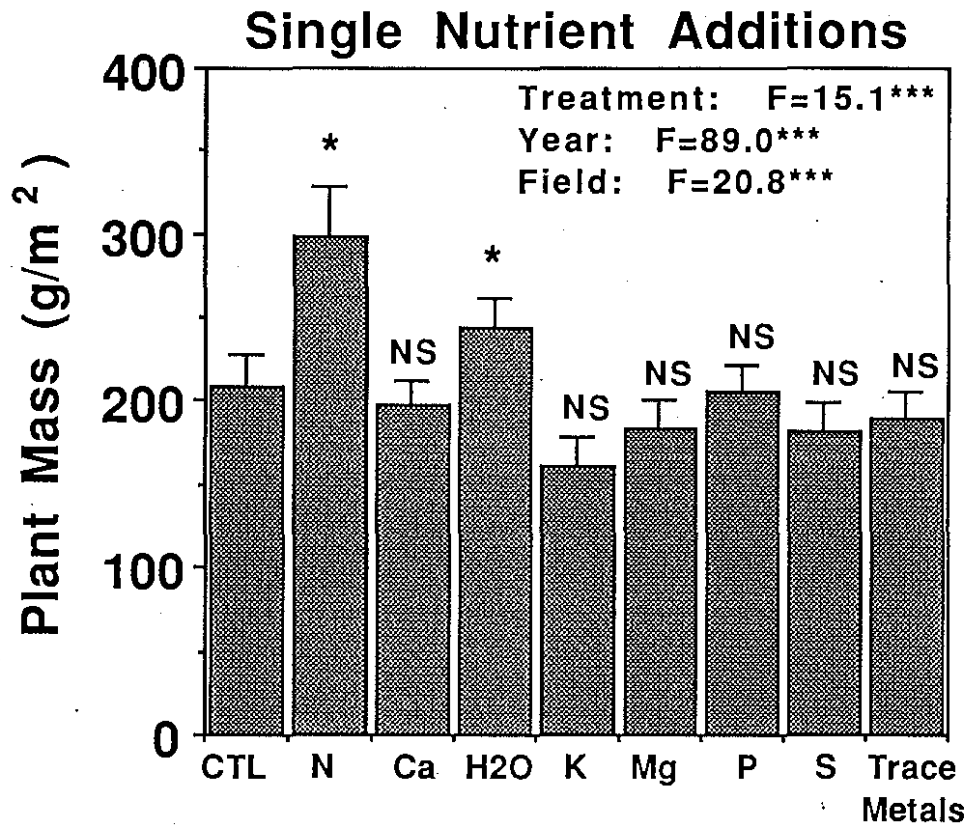Fig. 23. An experiment in which various nutrients were added one at a time to replicate plots in four different fields for eight years in a row (1982–1989). ANOVA of the effects of treatments, years, and fields on aboveground biomass in these 144 plots showed that all were highly significant. The addition of N led to significantly greater biomass than in the unmanipulated control, as did water in 1988.

This well-described chronosequence is also used for periodic studies of other organisms and processes that may change during succession, such as densities and abundances of mycorrhizal fungal species (Johnson et al. 1991), microbial biomass and organic matter dynamics (Zak et al. 1990), litter mass (Inouye et al. 1987c), plant allocation to roots, leaves, stems, and reproduction (Gleeson and Tilman 1990), plant tissue C and N, insect abundances (all taxa; Siemann, Haarstad and Tilman, in prep.), and free-living soil microfungi.

A problem with interpreting a chronosequence is the assumption that the rate and intensity of successional processes depend only on successional age, and not on actual time. The impact of the drought belies this assumption. Our resampling of the chronosequence in 1989, immediately after the drought, provided additional information on the impact of the drought, but gave few insights into plant dynamics because abundances had been greatly modified by the drought. We had planned to compare the rate of change in species abundances in each plot from 1983 to 1989 with the rate inferred from the chronosequence to test the validity of the chronosequence. However, we will now wait until 1995 to have data from a period (1983-1995) not totally overshadowed by the drought. Because soil total N and C are more conservative, their dynamics of change (Fig. 14) may be less dependent on drought. In total, our sampling of these 22 fields is providing a detailed record with which to test alternative successional theories.

B. Effects of Nitrogen on Productivity, Diversity, and Successional Dynamics

One of our central long-term experiments is our N addition gradient study (E001), which is replicated in three successional fields and in a savanna prairie opening. This experiment contains a total of 162 plots (each 4m x 4m) in 3 successional fields and 45 plots (each 2 m x 4 m) in the prairie opening. The treatments imposed in each field, with 6 replicates each in the successional fields, and 5 in the savanna, are a control, addition of all nutrients except N, and addition of all nutrients including N, with N added at one of 7 different rates. All nutrients are added twice each year, with detailed methods given in Tilman (1987). In brief, this experiment is annually sampled for aboveground (to species) and belowground biomass, litter mass, light penetration, and soil chemistry (extractable NH_4 and NO_3), and periodically sampled for insect abundances, mycorrhizal fungal species densities, and microbial biomass. This experiment, perhaps because it is the largest and most long-term of all our field experiments, has provided some of our most significant insights, to date, into the causes of successional dynamics (e.g., Tilman 1987, 1988, 1990), causes of diversity differences along productivity gradients (Tilman 1990, 1993), the impacts of diversity on ecosystem stability (Tilman and Downing 1994), and the impacts of climatic variation on biodiversity (Tilman and El Haddi 1992).

However, every year of additional data gives us fuller insights into these issues. For instance, the decline in diversity during the 1988 drought was only overcome five years later. We do not yet know if species composition and diversity will stabilize at pre-drought levels, or if composition will change and diversity attain a new post-drought level. The latter seems to be happening in the three successional fields. Drought led to marked increases in the abundances of C-4 prairie grasses, which are still more abundant 5 years after the drought than before. A longer time series will also allow us to test the hypothesized relationship between habitat heterogeneity and biodiversity. The treatments imposed in each field have made these fields much more spatially heterogeneous in their N supply rate. Theory predicts that this increased heterogeneity should lead to increased species diversity (Hutchinson 1959) because different species will be superior competitors for each rate of N addition, and the broad range of rates imposed across the habitat should thus allow new species to flourish. To date, however, this has not happened (Fig. 31). Rather, the greater heterogeneity created by our N additions has led to decreased total plant species richness per field. This occurred because the species initially favored by N addition were already present in each field. As they increased in abundance in higher N plots, they drove rarer species to local extinction, thus decreasing total diversity. However, if the theory is correct, the higher N plots should be invasible by a suite of novel species that were initially rare or absent. If these invade, they should increase species richness in the high N plots, and thus in the entire
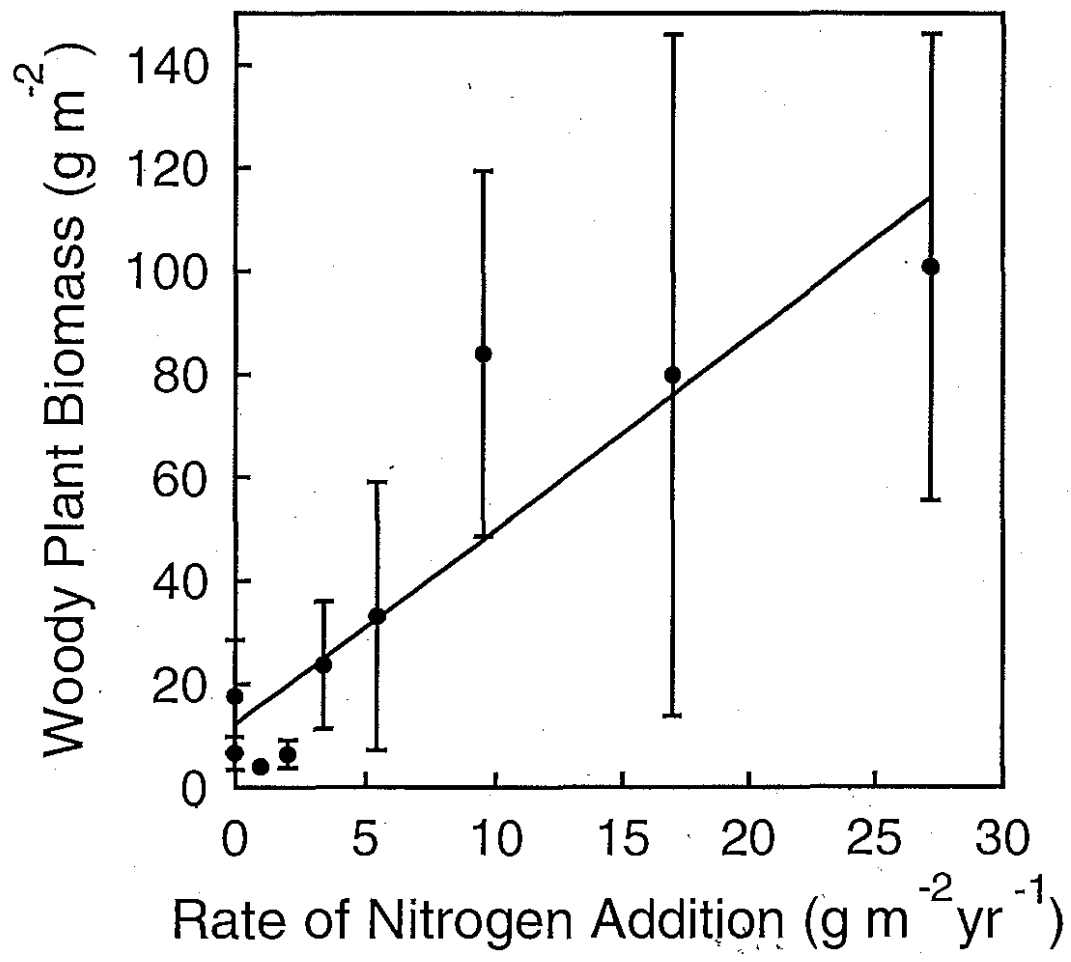
Fig. 24. The dependence of woody plant biomass on the rate of N addition to the long term N addition plots (E001). Each point is the mean across all four experimental fields of woody plant biomass for a given rate of nitrogen addition. Standard errors are shown. These are high because there are no woody plants in the youngest field.

field. Such novel species are invading, and increasing total species richness, but these increases have not yet overcome the loss of species richness caused by N addition and by the 1988 drought. Only a much longer duration for this study will overcome such colonization limitation of local diversity and determine the long-term relationship between species richness, heterogeneity, and productivity.

C. Effects of N on Productivity, Diversity and Succession in Disturbed Plots

This study, experiment E002, was established simultaneously with the one above, in the three successional fields. It is identical in all ways in both design and sampling to the experiment above, except that plots were initially disturbed, in 1982, via thorough disking. It thus is allowing us to determine the dynamics of secondary succession in plots that differed in their initial species composition as well as in their rate of N supply.

Species composition of disturbed and undisturbed plots receiving the same N treatment has converged, through time, in all three fields (Fig. 32; Inouye and Tilman 1988). Also, within a given field, the greater the difference in the rate of N addition to a pair of plots, the less similar their vegetation has become (Fig. 33). Because our initial questions were essentially answered after 10 years, we have used these plots in one of two new experiments. In each experiment, we randomly chose 3 of the 6 replicates of each treatment for the new manipulation, and allowed the other 3 replicates to continue their former treatment. Specifically, in Fields A and C our new treatment, beginning in 1993, was cessation of nutrient addition. This will allow us to determine the extent to which productivity, composition and diversity can recover from a long-term perturbation (N addition), and its dynamics. In Field B, we started a program of annual spring burning in the 3 plots per treatment, yielding a total of 27 burned and 27 unburned plots along the experimental N gradient. These have already shown marked divergence in composition, productivity, and diversity in response to fire, and will allow us to determine the interactive effects of fire and fertility. The remaining 3 plots per treatment serve as controls for the new experiment and allow us to continue our study of convergence.

D. Interactive Effects of Productivity and Disturbance on Composition and Biodiversity

Many plant ecologists consider productivity and disturbance to be the two major forces structuring plant communities (Grime 1977, Grubb 1985, Tilman 1988). This study, experiment E052, contains 104 plots, each 5m x 5m. It was established in 1988 to determine the joint effects of productivity and disturbance on a successional grassland. By imposing three different repeatable intensities of mechanical soil disturbance, as well as no disturbance, and by imposing three different rates of N addition, as well as no N addition, in a replicated full-factorial design, we established 16 combinations of productivity and disturbance. We have studied the effects of these treatments on plant species composition and diversity (Wilson and Tilman 1991a, 1991b, 1993), on composition and diversity of mycorrhizal fungi (Johnson, in preparation), and on the strength of interspecific competition for both aboveground and belowground resources (Wilson and Tilman 1993, Reader et al. 1994).

However, these plots are still undergoing rapid successional changes in response to the treatments and to colonization by species that were initially absent but that are favored by treatment combinations. Our continued annual sampling of these plots for vegetational composition, and periodic sampling for soil chemistry, light penetration profiles, and belowground biomass will allow us to determine the joint and interactive effects of disturbance and productivity on species composition, species diversity, and successional dynamics.

E. Fire Frequency and Species Composition and Diversity of Prairie (E012)

As discussed, fire was a major factor in the historical establishment and maintenance of prairie and savanna. However, fire suppression greatly reduced the fire frequency at Cedar Creek. With the exception of a few fields in the vicinity of the savanna burn compartments, none of the Cedar Creek old fields are burned, and all of the old fields chosen for the successional chronosequence are unburned. To determine the long-term effects of fire on species composition and

All Trees & Saplings: Spring 1992
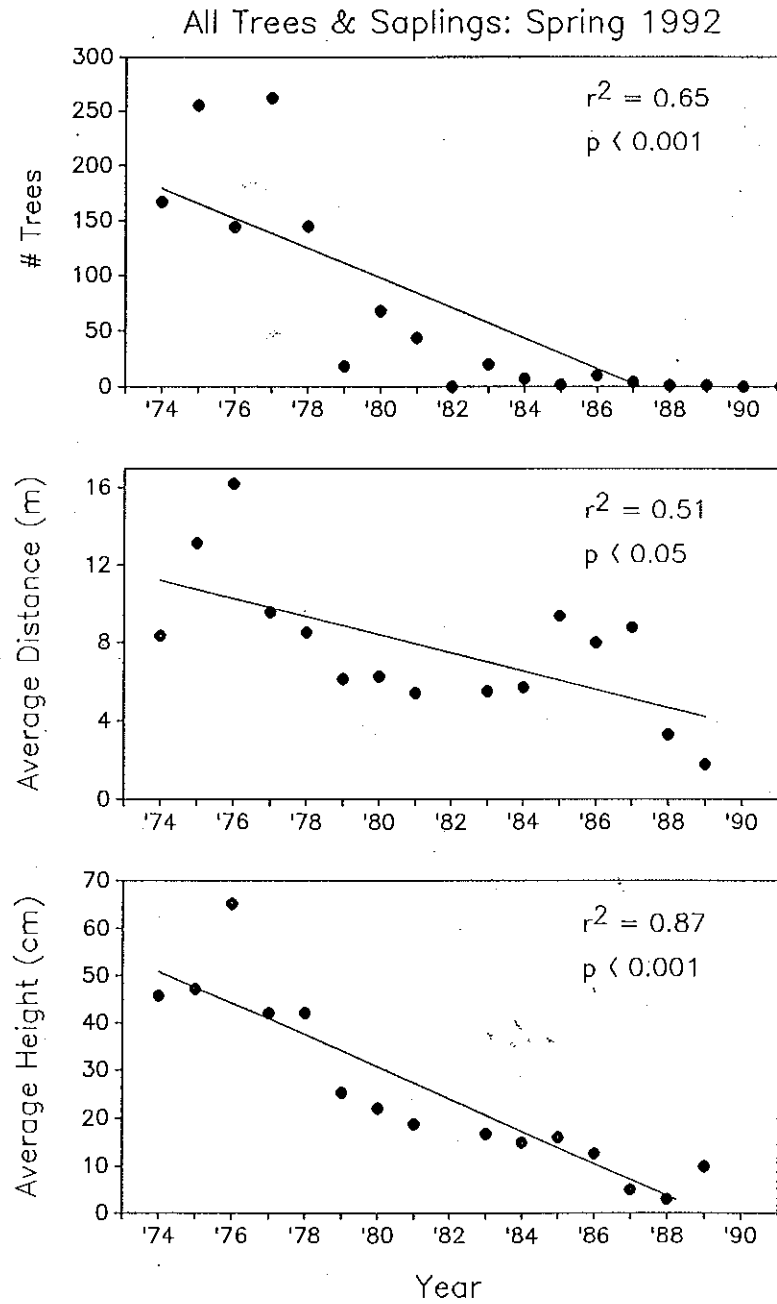
Fig. 25. "Year" refers to the year that a plot was abandoned in the Lawrence Successional strips. Older plots (those abandoned earlier; e.g., '74 is 20 years old) have more trees, further out from the forest edge, and the trees are taller.
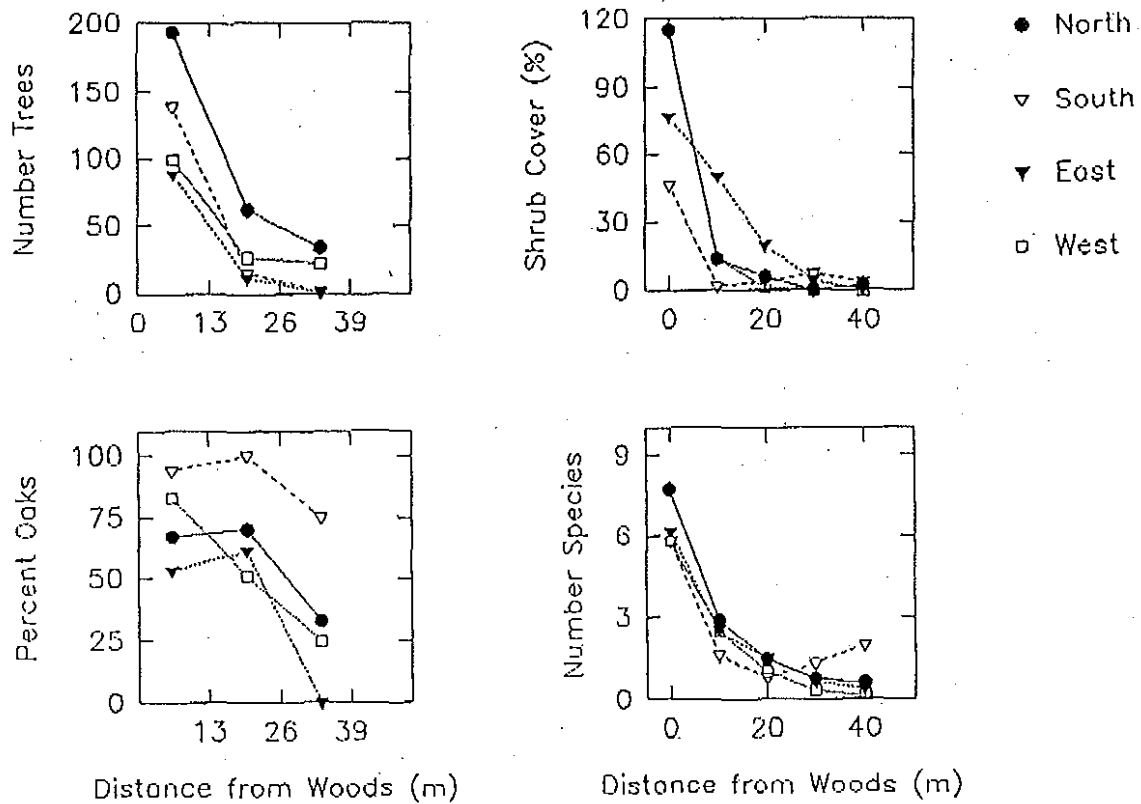
Fig. 26. Areas in an old field that are closer to a forest boundary have more individual seedlings and saplings of tree species, have higher cover of shrubs, a greater proportion of woody plants that are oaks and have a larger number of woody species. Thus, woody plants are more abundant closer to the forest edge and are invading fields from the forest edge. Note the effect of aspect (i.e., North facing margins, etc.).

soils in successional vegetation, in 1983 we established a series of 24 plots, each 8 m x 8 m, in a 25 yr old prairie-like field, with 6 replicates of each of 4 burn treatments: (1) unburned (2) annual burning, (3) burning every second year, and (4) burning every fourth year. All burning, started in 1984, is done before significant production of new leaves, generally in the first week of May.

In 1983 we collected soil cores in each plot for analysis of total soil N and C. Abundances of plant species and litter were determined in 1983 by clipping and sorting to species two 10 cm x 300 cm strips per plot. This sampling was repeated in 1987 and 1991, and will be repeated every 4 years (1995, 1999, 2003). Although there were no significant (ANOVA P>0.05) effects of treatments on species richness or abundances of the 6 most abundant species in 1987, *Schizachyrium scoparium*, an abundant perennial bunchgrass, had significant treatment effects in 1991. Based on observations made in 1993, we believe that many more species will have significant responses to fire frequency by 1995, and that moderate fire frequencies will lead to higher plant species richness than either no burning or annual burning.

F. Hydrologic monitoring and modeling

The profound impact of the drought of 1988 on productivity and diversity emphasized the importance of available soil water in affecting the dynamics of the biota at Cedar Creek (Fig. 3), and led us to expand our monitoring of soil and ground water. This long-term data set will help interpret observed biotic responses to climate. In order to better understand the climate that helped shape the ecosystems of Cedar Creek, and to better understand nutrient fluxes through the soil, we are testing mechanistic hydrologic models.

In addition, starting in 1994 we will expand our monitoring of soil water in 8 successional fields, 12 savannas and 14 forest stands. These sites will be visited ca. biweekly during each growing season with soil water monitored via calibrated time domain reflectometry. We also monitor groundwater depths, which are only several meters below the surface at our highest elevations. Due to this hydrology and the subtle topography and permeable sandy soil, only a few meters of horizontal distance separate upland savanna or old field from adjacent wetlands. The water table or its capillary fringe provides a source of water to deeply-rooted plants on the uplands, especially during droughts. To monitor groundwater, 83 groundwater wells were established in Cedar Creek in 1989. Well depths range from 1 to 7 m, and casings extended 0.5 to 1 m into the water table. Regular monitoring of water table depths (ca. monthly) were begun in June 1989. Well locations and elevations, located by ground surveys from a USGS benchmark, have been added to our GIS coverages. Spatial statistics, including kriging, allowed development of maps of depths to the water table on selected dates (Fig. 34). Modeling of the hydrology of Cedar Creek has been initiated to enable prediction of soil volumetric water content and water potential, changes in groundwater elevations, and of water fluxes. Our modelling efforts are described in Section 2. 4 (page 41).

G. Long-Term Common Garden Experiments

A direct way to determine if individual species have different effects on ecosystem functioning is to grow the species in replicated, long-term plots with initially identical soils. Our intensive "common garden" studies of five dominant grasses showed us the power of this approach (Wedin and Tilman 1990, 1992, 1993; Tilman and Wedin 1991a, 1991b, 1991c). To expand our knowledge of the ecophysiology, nitrogen use efficiency, litter quality, allocation pattern (root, stem, leaf, seed and rhizome), light interception, survival rate, N mineralization rate, and R* for nitrogen (Tilman and Wedin 1991a) of major plant species, we established a new common garden in 1992. More than 50 of the most common Cedar Creek perennials were planted into monoculture plots, most 1.5 m x 2.5 m, but some 1/4 this size. There were 4 replicate randomly-assigned monocultures per species, giving a total of 208 plots. Plots were surrounded with galvanized sheet steel driven into the soil to a depth of 30 cm. The soils for all plots consisted of existing Cedar Creek soil from which the upper 5 cm were removed to decrease the seed bank and to lower total soil N. The remaining N poor soil was fertilized with all nutrients except N (i.e., with P, K, Ca, Mg,

SO$_4$, and trace metals) and thoroughly rototilled, to a depth of 25 cm, before planting. All plots will be maintained as monocultures by hand weeding.

Based on our past work, by 1996 biomass and allocation patterns should have stabilized, and we will determine above and below ground biomass, extractable soil ammonium and nitrate, light penetration, proportion of biomass allocated to root, leaf, stem, seed and rhizome, and an index of growing-season N mineralization using buried ion exchange resin bags in each plot. Because we already know when species reach peak successional abundance, these data will be crucial for calibrating our succession and biodiversity models. Moreover, these plots will be maintained to determine the effects of plant species on soil properties and plant traits responsible for these effects. In addition, we will indefinitely maintain the original Wedin and Tilman (1990) monocultures for further studies of the long-term effects of plant species on soil N and C dynamics. The annual maintenance of all these plots is inexpensive, requiring about 3 person/months per year of field assistance. The return is great because of the species-specific parameters they provide.

H. Recruitment versus Competitive Limitation of Biodiversity

Cornell and Lawton (1992) highlighted two alternative hypotheses to explain the local diversity of a community. On the one hand, interspecific interactions, such as competition, predation and disease, may limit the number of species that can coexist in a locality. In this case, any additional species that enter a habitat as propagules either go locally extinct or must displace some other existing species to survive. Alternatively, local diversity may be limited by recruitment, in which case increased colonization rates could lead to a linear increase in local species richness. To test these ideas, we established replicated plots in native savanna. The relative abundances of all species were determined via estimates of cover in 1991. In 1992 we added seeds of either 0, 5, 10, 15, 20, 25, 30, 25, 40, or 54 species, with 6 replicates of each, to 1 m x 1 m plots. Each plot was paired with a neighboring plot that received no seed.

Results for the first two years show that many species can germinate, survive, and reproduce in areas from which they were locally absent, independent of the number of species added (Fig. 11A). Thus, initial results support the recruitment limitation hypothesis. However, we will continue annual sampling. Because we have added species at a range of rates, and because these rates have led to more than a doubling of species richness, long-term observations should reveal if there continues to be a linear response (supporting the recruitment limitation hypothesis) or a curvilinear, saturating response. The latter would occur if biotic interactions placed an upper bound on species richness, i.e., if invasion by a new species ultimately required extinction of an existing species.

I. Deer Exclosure Experiment

Most trees along forest-field boundaries at Cedar Creek show evidence of repeated browsing, suggesting that wintering white-tailed deer might play an important role in slowing the rate at which old fields become forest or savanna. This experiment, E007, established in fall 1982, was initially designed to test the hypothesis that deer limit the invasion of old fields by trees. Six plots (3 exclosures, 3 controls) are located at the west-facing margins of Fields A. Six additional plots, with the same treatments, are similarly located in Field B. Each plot is 10 m x 30 m, with the long axis perpendicular to the field edge. Each extends 20 m into the field. Trees, tagged and mapped, are measured each spring and browsing on terminal or lateral branches is recorded.

Excluding deer has a significant, but small, effect on tree growth (Inouye et al. 1994). We will continue sampling woody plants, and resample herbaceous vegetation to test for responses to excluding deer. Finally, we will perform laboratory incubations to test for effects of deer on the quantity and quality of soil organic matter resulting from changes in litter inputs. Although this type of indirect effect has been observed in response to removal of other ungulates (Pastor et al. 1987), we do not know if it will occur at Cedar Creek because most browsing occurs during the winter months on low N tissues.

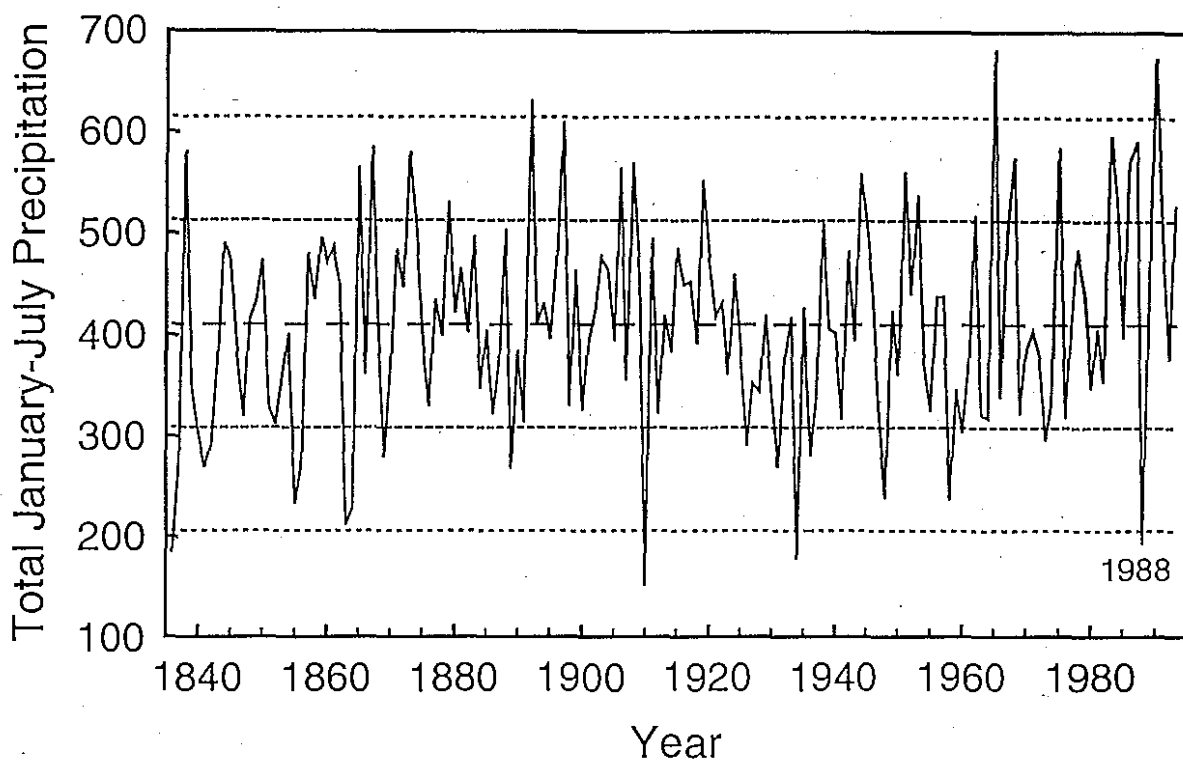Fig. 27. Total growing season precipitation was calculated using
the longest meteorological record for our region, historical Fort
Snelling, approximately 40 miles south of Cedar Creek. Note that
the 1988 drought was one of the four most severe droughts in the
last 160 years. The dashed line at approximately 410 mm is average
precipitation. The dotted lines above and below this are 1 and 2
standard deviations.

J. Gopher/Deer Exclosures

Another major herbivore at Cedar Creek are pocket gophers (*Geomys bursarius*), which have significant and varied direct and indirect effects on vegetation and soils, many of which are consequences of the burrows and mounds they create (Inouye et al. 1987b, Huntly and Inouye 1990). One long-term consequence of soil disturbance by gophers may be increased heterogeneity of soils, and a consequent increase in the heterogeneity and biodiversity of vegetation. This experiment, begun in 1989, was designed to test for effects of gophers and of gophers and deer on soil nitrogen heterogeneity and plant diversity. The three treatments are (1) exclusion of gophers, (2) exclusion of gophers and deer, and (3) controls from which neither were excluded. Gophers are excluded via burial, to a depth of 1.3 m, of an "L" shaped piece of galvanized hardware cloth (1.5 m x .5 m) around the perimeter of each plot. Deer are excluded via aboveground fencing to a height of 2 m. There are 5 replicate 12 x 12 m plots for each treatment, with plots laid out in a completely randomized design along the forest margin of a newly abandoned Cedar Creek field.

Soils were sampled at 1 m intervals over a 10 x 10 m grid centered in each plot in 1989. These 1500 samples were analyzed for total N and C to quantify of the initial pattern of soil heterogeneity. Vegetation is sampled annually, via non-destructive estimates of cover, at the same 100 sample points per plot. We will resample soils, at the same points in each grid, in 1999 to quantify changes in N and C heterogeneity and incubate soils to study soil organic matter quality and microbial activity after 10 years of herbivore presence or absence.

Repeated censuses of marked trees in the deer exclosures and their controls in Fields A, B, and in another successional field has shown that pocket gophers are a significant source of mortality for trees that are invading old fields (Inouye et al. 1994). A second major goal of this experiment is to test for the effects of gophers, and for the combined effects of gophers and deer, on growth and mortality of invading trees. This is why we included the exclosure of both gophers and deer as a treatment. We are annually following establishment, growth and mortality of naturally dispersed oak seedlings, and we have planted additional oak seedlings in each plot to increase the sample size. Thus, this experiment will determine the extent to which gophers and/or deer are responsible for the slow successional re-establishment of woody plants.
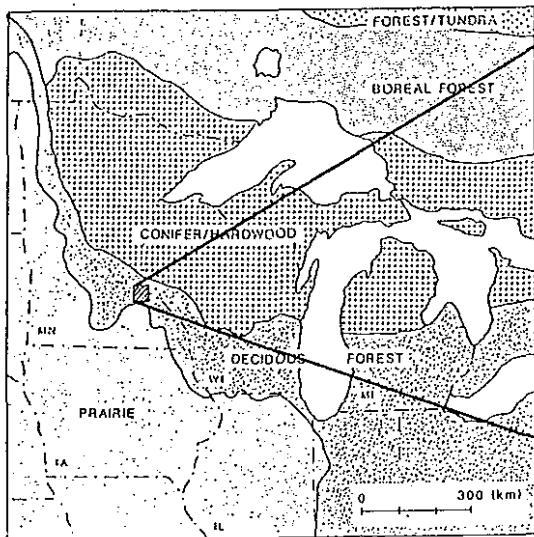
K. Dynamics of Forested Stands

Areas at Cedar Creek that were protected from frequent fires by wetlands and streams were forested at the time of European settlement. We chose 17 such intact stands, 13 upland and 4 wetland, that spanned the range of forest types at Cedar Creek, and began monitoring their dynamics in 1988. We have used quantitative classification techniques to aggregate the 17 stands into six well-defined ecosystem types; oak, pine-oak, mesic hardwoods, northern white-cedar, lowland hardwoods, and savanna. We annually measure litterfall. We have also measured overstory biomass, woody increment over a 10-year period; understory foliage mass; net N mineralization and nitrification rates; and forest floor and surface soil N. We also monitor water table depth and fluctuation. Periodic measurements will continue. We also plan historical reconstruction, via increment cores, airphotos, and other tools, to determine past changes and predict future successional changes in these stands.

L. Tree Invasion into Successional Fields

Tree invasion into successional fields is a critical but poorly understood step in succession from grassland to savanna or forest. Several of our studies, including the deer exclosures, the gopher/deer exclosures, and the nitrogen addition plots are providing insights into the controls of tree invasion. However, we also need a good description of the dynamics of tree invasion.

Thus, we are studying the dynamics of tree invasion into a field from a relatively uniform and straight field-forest margin. The Lawrence Succession Strips, located in a 110 m x 720 m field, are adjacent 20 m wide x 110 m long plots sequentially abandoned from agriculture, one strip per year, beginning in 1974. Since 1989 we have tagged, mapped, and measured tree seedlings and saplings in these strips to test for relationships between successional age and tree

A. The Prairie-Forest Boundary

B. Ecosystems of CCNHA Region

FOREST/TUNDRA

BOREAL FOREST

CONIFER/HARDWOOD

DECIDUOUS FOREST

PRAIRIE

MN

WI

MI

IA

IL

0   300 (km)
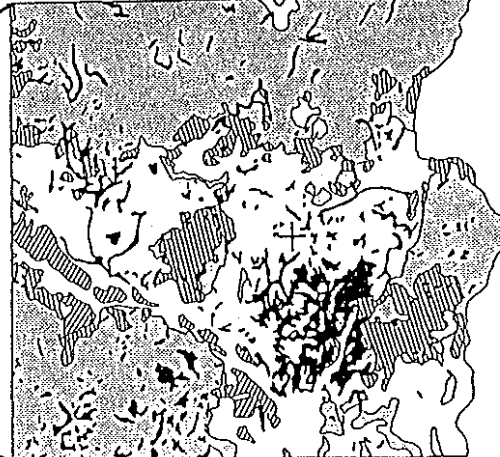
■ Wet Prairies (marsh grasses and reeds)

☐ Oak Openings (scattered bur oaks and prairie)

▨ Prairie

▩ Aspen-Oak (aspen and scattered oaks)

▦ Big Woods (maple, oak, elm, basswood and ash)

Fig. 28. CCNHA is unique within the LTER network because it lies at the border between prairie and forest. The old fields of CCNHA also form a bridge between the highly disturbed agroecosystems of the Kellogg LTER and other LTER sites.
A. The prairie-forest boundary in the lakes states region. The small box, which is shown enlarged in Part B, includes the location of Cedar Creek Natural History Area (CCNHA).
B. Ecosystems of the CCNHA region. Note that CCNHA is a 5400 acre parcel near the center of this map (indicated by the "+"). CCNHA is characterized by "oak openings," a mosaic of prairie, oak savanna and oak forest. The actual boundary between prairie and forest in this region is highly dependent on the parent material on which the soil formed, as well as on local fire breaks. The "big woods" areas around CCNHA occur on glacial till or on deep silty soils, whereas oak openings occur on glacially-deposited outwash sand plains. Thus, the prairie-forest boundary is controlled not only by climate and fire breaks, but also by edaphic factors.

density, size, growth rate, establishment, and mortality. These clearly show the importance of successional age and dispersal distance on tree establishment and growth (Inouye et al. 1994). We will continue this annual sampling, and thus continue to build a detailed description of woody invasion, survival and growth.

In 1993 we established permanent plots for a long-term study of tree invasion into our chronosequence of successional fields. This study samples forest-field margins that represent a range of aspects and field ages, using permanent plots along 25 field margins. Data reveal differences in tree density and species composition associated with aspect (Fig. 26). However, we found few clear relationships between woody plant density and field age (Lawson et al., in prep). We will regularly repeat this sampling to determine rates of woody establishment and mortality. Soils will be analyzed to test the dependence of woody plant establishment and growth on soil N.

M. Predator Exclosure Experiment

Predators, or "top-down" forces, and nutrient inputs, or "bottom-up" forces, interact with climatic variation to govern the dynamics of plants, herbivores, and other consumers in terrestrial ecosystems. The productivity and species richness in each trophic level depend on the relative strengths of these forces (Paine 1966, Harper 1969, Carpenter et al. 1985, Carpenter and Kitchell 1988, 1993, Power 1990a,b, Oksanen et al. 1981, Fretwell 1977, Pacala and Crawley 1992, Hairston and Hairston 1993). However, there is intense debate (Hunter and Price 1992, Power 1992, Matson and Hunter 1992) about whether communities are primarily limited by top-down (Hairston et al. 1960, Carpenter and Kitchell 1988) vs. bottom-up forces (White 1978, Schmitz 1992) and how predator and resource controls interact to limit productivity (Fretwell 1977, Oksanen et al. 1981, Getz 1984, Leibold 1989, Schmitz 1992) and biodiversity (Pacala and Crawley 1992).

Our bird exclosure experiment, begun in 1989, addresses these specific topics, and will be expanded to include another successional grassland and oak savanna. These studies have shown that *exclusion* of birds, which are major grasshopper predators, led to *decreased* grasshopper densities and to *increased* plant species richness. The unexpected effect of birds on grasshopper densities seems to result from increased skink densities associated with bird exclosure. To test for possible skink effects we will expand our experiment to include both bird and skink exclosures, and replicate this in 2 other fields, using ten 9 m x 9 m plots per field. Krylon netting placed over 5 plots will exclude birds. Each 9 x 9 m plot will be split into two 4.5 x 9 m subplots, with one subplot surrounded by 30 cm high aluminum flashing coated with a teflon lubricant to exclude lizards, small mammals, and other non-flying predators (Case 1990).

Grasshoppers will be collected in each subplot by sweep-netting in late August each year. These samples will be identified to species, counted, and weighed to determine grasshopper species composition and density, as well as overall biomass. Plants will be sampled by clipping and sorting to species a 10 cm x 300 cm strip in each subplot in August. Four soil cores from each subplot in August will be analyzed for concentrations of NH^4 and NO^3 to evaluate predator cascading effects on soil nutrients. This expanded study of the effects of top predators will be compared with studies in plots to which nitrogen is added to determine the relative roles and strengths of top-down versus bottom up forces in these successional and savanna communities.

Because densities of predators are crucial for determining the effects of exclosures, these will be monitored in these 3 fields. Birds will be surveyed 6 times per summer, using morning counts of flushed birds and/or songs within five 20 m x 100 m belt transects. Lizards, amphibians, and other invertebrate predators will be sampled with 25 baited pitfall traps at least 20 nights per summer. Predaceous arthropods will be sampled by sweep-netting and pitfall trapping. Large odonates (dragonflies) will be counted during bird surveys.

N. Cross-Site Herbivore Exclosure Experiment

Because herbivores can have dramatic effects on terrestrial plant community structure and ecosystem function (Crawley 1983, Huntly 1991) through direct and indirect interactions among herbivores, plant communities, and nutrient dynamics (McNaughton 1985, Pastor and Naiman 1992, DeAngelis et al. 1989, DeAngelis et al.

Plant Species Dynamics in a 14 Year Old Field

A.

B.

Plant Species Dynamics in a 48 Year Old Field

C.

D.
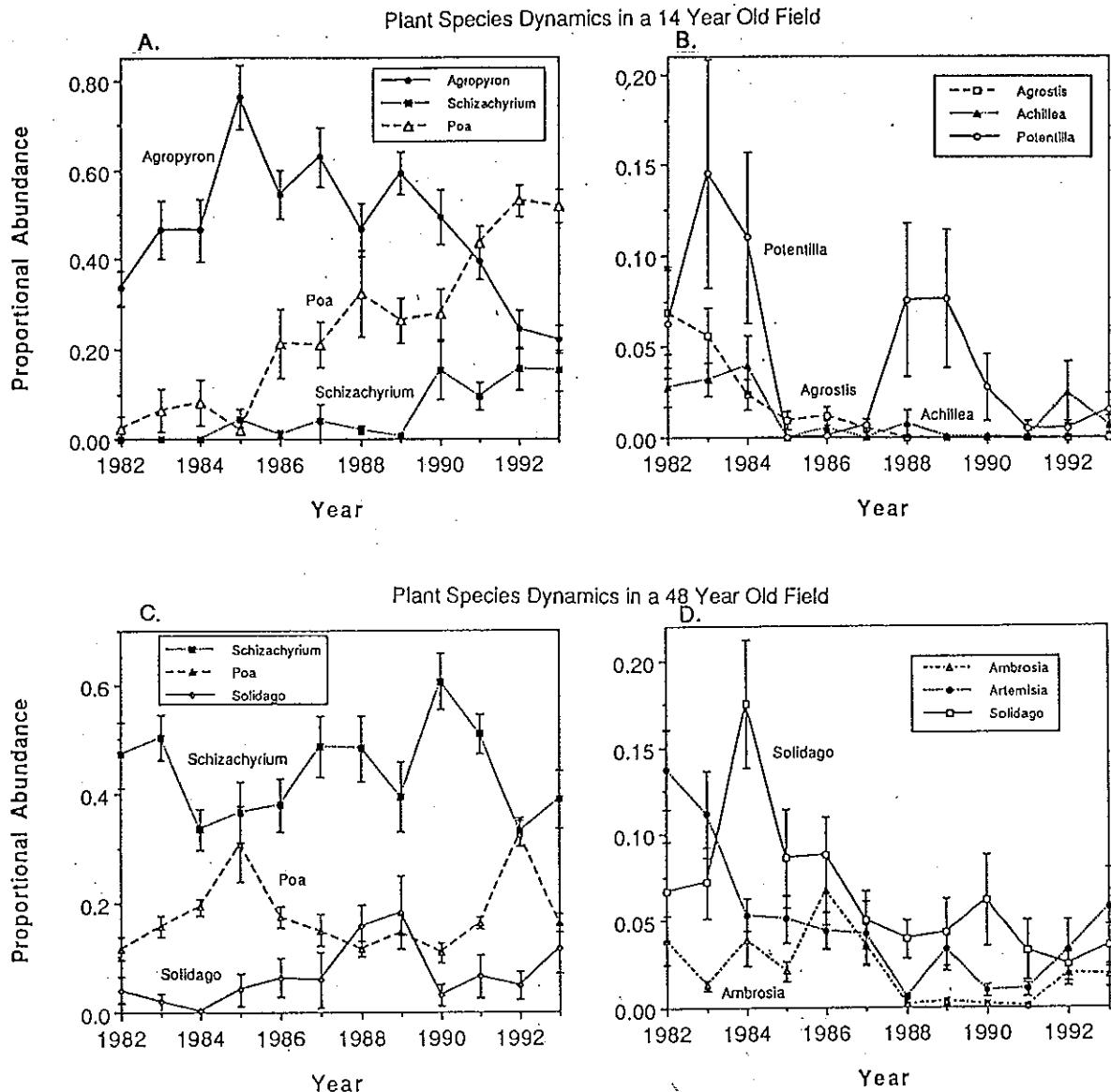
Fig. 29. A, B. Proportional abundances of the most abundant plant species (mean and standard error) for the 6 most abundant species in a 14 year old field. Note that *Agropyron* increased for the first four years but has generally decreased since then. *Poa* increased, as did *Schizachyrium*. These dynamics are quite similar to those inferred from the successional chronosequence (see Fig. 12). C, D. Plant dynamics in a 48 year old field did not show successional trends but did show that the native bunchgrass *Schizachyrium* became more abundant during the drought. *Poa pratensis* decreased during the drought and had not increased to its predrought abundance until the fourth year after the drought. All data from control plots of E001.

1986, 1992), a group of scientists from six LTER sites has proposed a cross-site study of the effects of different-sized herbivores on plant communities and nutrient dynamics across a gradient of productivity and plant growth form in grasslands. This is described in Section 2.6E (page 45).

O. Other Studies

Many other studies have been initiated by graduate students and post-doctoral researchers during our 12 years of LTER. As possible, we maintain these so that the original researchers, or others, may sample them at a future date. We do not have the resources to resample them ourselves. However, our policies requiring permanent labelling of plots, and our procedures for data documentation and archiving, maximize the future utility of these studies.

II. SAVANNA DYNAMICS

As already discussed, we are proposing greatly increased research in oak savanna, especially on the forces that control the balance between the woody and prairie components of savanna, and that maintain its high biodiversity (Ko and Reich 1993). This is one of our two major new initiatives. Savanna is highly sensitive to climatic variation, fire frequency, herbivores, soil, and feedbacks and interactions among these. The 1987-1988 drought led to the loss of up to 1/3 of the mature oaks in our savanna stands. This dramatic shift in woody composition is likely to lead to a long- term successional sequence as the savanna recovers. However, the 40 to 50-year average return period for droughts of this severity (Fig. 27) and the slow recruitment and growth of oaks suggest that savannas may undergo continual cyclic change. Such changes may become even greater if predictions of global climatic models are correct, and may result in unprecedented shifts in the boundary between grasslands and forest.

The original 2,200,000 ha of savanna in Minnesota has been reduced, via cultivation, development and fire suppression, to only an estimated 500 ha (Nuzzo 1986), much of it at Cedar Creek. Prior to European settlement, the prairie-savanna-forest border was a patch mosaic of these three communities, and savanna was an interlaced mosaic of prairie openings and oak patches. Although the broad-scale patchiness was lost with settlement, the savannas of Cedar Creek retain their interlaced mosaic of prairie and oak patches. We are interested in the forces that create and maintain this mosaic patch structure, and with the effects of this diverse habitat on animals and plants. However, the overall community dynamics and underlying mechanisms controlling tree establishment, dominance, survival/mortality and regeneration in the prairie and oak patches of savanna are poorly understood.

Research on oak savannas is rare compared to research on either the grasslands or forests that border it. Part of the difficulty stems from the present rarity of savanna. Our large stands of oak savanna represent a unique research opportunity. Moreover, we should gain greater insights into savanna because we are studying both the successional processes whereby they are assembled and the processes that maintain them.

Proposed Research

Our savanna work will be performed in one or more of 12 large stands that have been maintained as savanna by a prescribed burn program begun in 1965 (White 1983, Tester 1989, Faber-Langendoen and Tester 1993). These savanna stands encompass a range of vegetation types from oak forest/woodland to savanna to prairie, i.e., a full gradient of communities that span the prairie-forest border. The average stand is 14 ha (range: 3 to 27 ha). Stands were randomly assigned to burn treatments and are composed of one pair of each of the six following fire regimes: (1) unburned, (2) burned every tenth year, (3) burned every third year, (4) burned every other year, (5) burned 4 out of every 5 years, and (6) burned for 4 years followed by no burning for four years. The latter treatment will be established in spring 1994 by the division of two stands currently burned at a similar frequency into two sections each, with treatment 6

Plant Dynamics in Savanna Prairie Opening
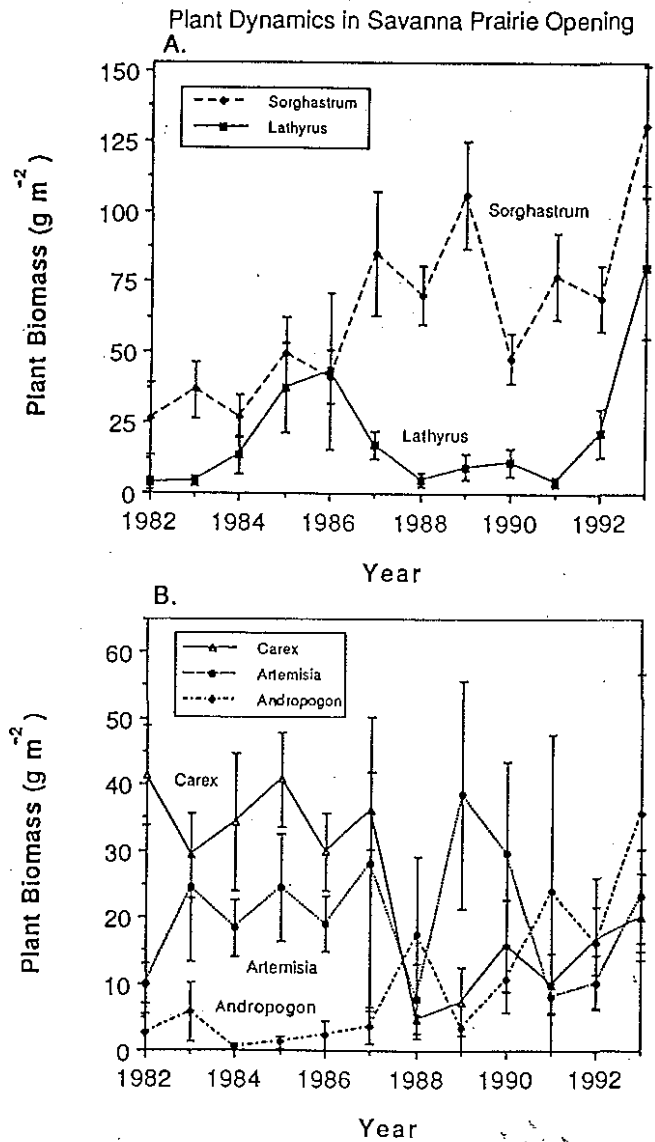
Fig. 30. Above ground biomass of major species in unmanipulated plots of native savannah (controls of E001). A. Note the highly significant increase in *Sorghastrum* during the drought and the concomitant decrease in *Lathyrus*. *Lathyrus*, a legume, did not re-attain its 1986 biomass until 1993. Legumes in general are more abundant during cool, wet years. Big bluestem (*Andropogon gerardi*) increased in abundance during the 1988 drought, partially compensating for the decrease in *Carex*.

randomly assigned to one of the new compartments in each stand. Preliminary studies suggest that early oak establishment is favored by intermediate or frequent burning, but that survival to the young tree class is minimal (Tester 1989, Faber-Langendoen and Tester 1993, Tipper and Reich, unpublished data). The new fire regime will assess the hypothesis that regular burning (as in every other year) will prevent young oaks from growing above the browse and competition line and developing thick enough bark to withstand fire, but that greater intervals between fires may enable more stems to make this transition.

Because burning is weather dependent, in some years it is impossible to perform planned burns. When this occurs, future burn schedules are adjusted to maintain the desired burn frequency. All savanna burning at Cedar Creek is in the spring. These 12 savanna stands provide an ideal setting for a comparative study of the effects of experimentally-imposed fire frequency on the dynamics, biodiversity, composition and stability of savanna, and for more detailed studies of the processes controlling the establishment, survival, and reproduction of both bur and pin oak, and of the processes that create and maintain the interlaced patch mosaic of oaks and prairie in savanna.

In 1984 we established a series of permanent plots in 12 savanna compartments which we sampled for herbaceous and woody species abundances, soil chemistry, small mammal densities, gopher mounds, and other soil disturbances using the same protocols employed in our survey of our 22 field successional chronosequence (Tester 1989). These were resampled in 1989 (Faber-Langendoen and Tester 1993). This work will be expanded with annual sampling of many of these characteristics, and with additional sampling plots within each stand of savanna. Specifically, we will establish four replicated mapped 40 m x 40 m plots within each of 12 savanna stands, or a total of 48 sampling plots.

Our research in the 12 stands will involve:

  A) long-term studies of woody and herbaceous species dynamics and diversity, and oak demography in the 48 plots,

  B) long-term studies of small mammal dynamics in relation to vegetation, soils, and disturbances,

  C) long-term studies of spatial patterns of resource availability in all plots, and of their relationship to vegetation, biotic factors and disturbances,

  D) a long-term experimental study of N supply and savanna productivity,

  E) manipulative studies of growth, allocation, physiology, and survival of oaks and some other species in relation to temporal and spatial variation in light, herbivory, water and nutrients (as influenced by microsite, fire frequency and competition), and

  F) assessment of oak/prairie patch dynamics over broader temporal and spatial scales in relation to fire history and climate via dendrochronological, remotely sensed and direct observations, analyzed via geographic information systems.

These studies are detailed below.

Woody and Herbaceous Community Dynamics: Fecundity, dispersal, and predation influence spatial patterns of seed "availability" within savanna and woodland patches. Direct measurements of acorn production, rain and dispersal will be made annually. To characterize the shape and quantity of the acorn dispersal pattern, 10 seed traps will be positioned at various distances from a mapped oak patch within each of the 48 plots. Acorns will be examined to determine rates of predation by insect larvae, fungi, etc., and to determine the proportion of acorns formed with filled-out seed. To examine predation and dispersal rates by mammals and birds, unprotected acorns will be placed (1) beneath vs. outside of tree canopies, (2) in/out of ant mounds, and (3) in gopher mounds vs. grass patches within two of the plots in each burn compartment. To determine how acorn germination and initial seedling establishment are affected by abiotic factors, protected acorns (hardware cloth cages) will be placed out in the same microhabitat types described above. This will be repeated each year, and these cohorts (i.e., one each year) will be monitored for growth and survival, and proportional transition into subsequent seedling/sapling classes. In addition, censuses will be made annually within four 5 m x 5 m subsections of each plot, in which number and location of newly emerged seedlings of all woody species are monitored, as well as microhabitat
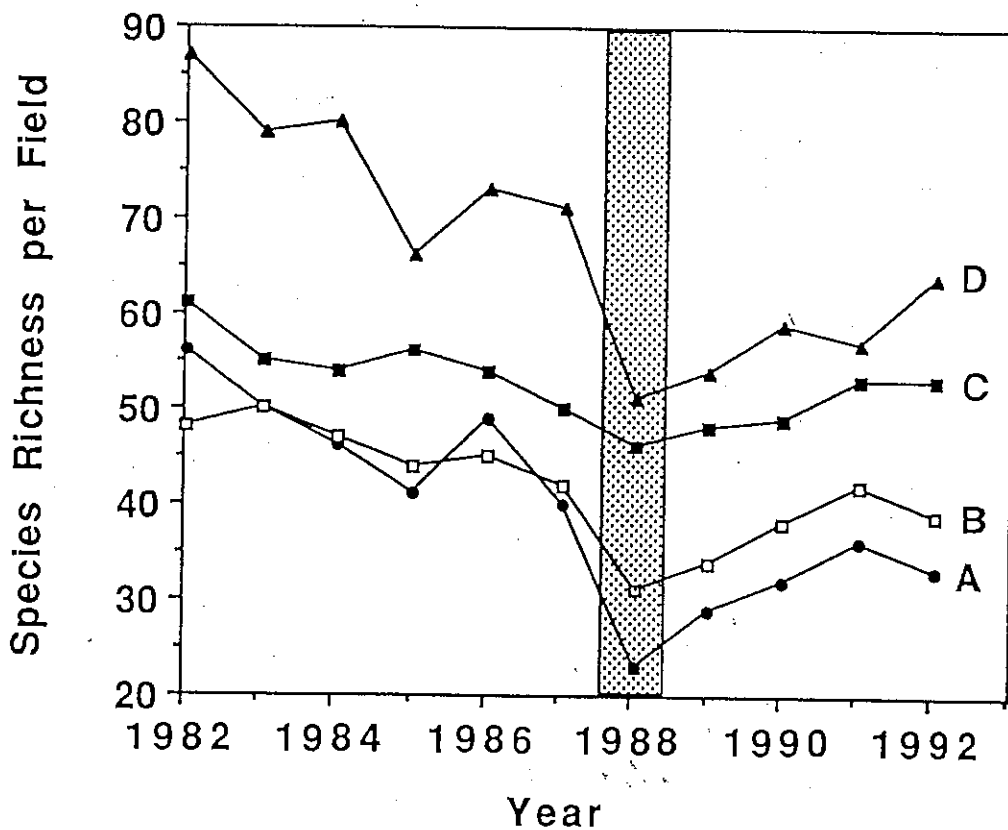
Fig. 31. Total species richness per field is the total number of species observed, in a given year and field, in all replicates of all treatments of the nitrogen gradient experiment (E001). Letters A, B, C, and D refer to Fields A, B, C, and D. The shaded area indicates the time of occurrence of the 1988 drought, which was the most severe drought of the past 50 yr (Tilman and El Haddi 1992). Note that the total number of species per field decreased from 1982 to 1987 in all fields even though N addition greatly increased point to point heterogeneity in these fields. Thus, increased heterogeneity did not lead to increased species diversity by 1993.

conditions (on/off ant mound, gopher mound, grass patch, etc), light availability, and overstory and understory composition.

All woody seedlings (<150 cm ht or <1 cm dbh), saplings (>150 cm ht, and >1 and <10 cm dbh), and trees (>10 cm dbh) will be permanently tagged and mapped in each 40 m x 40 m plot. However, if total numbers within a category greatly exceed 150, 100 and 50, respectively, smaller, replicated subplots will be used to reduce sample sizes to the approximate target maximum. Within each site we will map important microhabitat features, such as ant mounds, gopher mounds, grass patches, open areas outside of tree canopies, and open areas beneath tree canopies. Survival, growth (dbh and height), and dieback or browse damage will be noted annually for all tagged oaks in a census to be made in late summer (August). By quantifying life history tables for both major oak species in contrasting patch types with plots of differing fire history, we will identify the critical processes and stages controlling regeneration and therefore the maintenance of community structure.

Herbaceous biodiversity is greater in savanna than in surrounding prairie patches (Ko and Reich 1993). To examine this and provide annual data on changes in abundances of herbaceous species, two permanent herbaceous sampling subplots (each 5 m x 5 m) will be established in prairie openings in each 40 m x 40 m plot. These will be annually sampled by clipping and sorting to species a 10 cm x 300 cm strip of vegetation. These 96 samples will provide a detailed record of biodiversity, composition, and productivity of savanna herbs in response to climate, fire, and other variables. These samples will be gathered, sorted, weighed, etc., using the same techniques and personnel as for the herbaceous samples gathered in successional fields.

Small Mammal Community Dynamics: Microtus pennsylvanicus and *Peromyscus leucopus* are the two most common small mammals in the oak savanna. Small mammal densities will be determined by trapping all 48 of the 40 m x 40 m plots for three consecutive nights twice each year (June and August). Sherman live traps (9/plot) will be placed at equal spacing in each plot. Animals will be identified, measured, and released. Annual counts of fresh gopher mounds within each of the 48 plots will be used as an index of gopher activity.

Spatial Patterns of Resource Availability: Within each of the 48 permanent plots in the savanna stands, we will establish a grid of 9 evenly spaced, permanently marked sampling sites for soils and light. In the first year of this expanded study, 1995, we will collect a 5 cm x 50 cm soil core from each of these sites and divide it by depth (litter, 0-5 cm, 5-15 cm, 15-30 cm, 30-50 cm). These will be air dried, a subsample analyzed for total N, total C and H, and the rest archived. Soils will be similarly resampled and analyzed every 4 years to determine the dynamics of change in soil stores of N and C. Indices of N availability (separated into nitrification and ammonification), plus nitrate and ammonium pools, will be estimated in the surface 20 cm of mineral soil and plant litter using the *in situ* tube method (Zak and Grigal 1991, Walters and Reich, in prep.) every fourth year at these 9 sites, as will other soil nutrients. The 9 samples per plot will estimate both plot averages and within-plot heterogeneity, and be related to plot vegetational composition and biodiversity.

These same 9 sampling points within each of the 48 permanent plots are the localities at which soil water will be periodically measured using calibrated time domain reflectrometry. This instrument will first be calibrated with gravimetric and soil moisture release curves. Soil water status will be measured monthly throughout the growing season, and at increasing frequency during droughts. During the same time periods, an index of integrated light availability (via measurements of canopy openness) will be made for all 480 subplots using a LiCor LAI 2000, which assesses canopy openness.

Nitrogen Supply and Savanna Biodiversity and Productivity: In 1983 we initiated an experimental study of the effects of N supply on the composition and biodiversity of native oak savanna. Our study uses 9 plots, each 20 m x 50 m, located in a savanna stand burned 2 of every 3 years. Three plots, randomly chosen, received no nutrient additions. Three received a complete mineral

Field A, Experiments 1 & 2

Field B, Experiments 1 & 2

Field C, Experiments 1 & 2

Fig. 32. Graphs of Percent Similarity (PS) versus time for convergence within fields. Each set of eight graphs presents data comparing E1 and E2 in one field. Small circular points represent individual comparisons of two plots of the same treatment, one plot on the undisturbed grid (Experiment 1) and one plot on the disturbed grid (Experiment 2). Each graph contains such 36 points for each year (6 disturbed plots x 6 disturbed plots). Stars indicate average PS for each year. Linear regression lines are drawn where there was a significant linear relationship between average PS and year. Curvilinear lines are drawn where both year and year^2 terms were significant in a multiple regression. For regression analyses, trans-formations were done on average PS (arcsine-square root) and year (year-1981). Nitrogen treatments are denoted by letters in the upper left corner of each graph.

fertilizer that included N, with N supplied at a rate of 9 g m^{-2} yr^{-1}. The other three received the complete mineralizer fertilizer with N supplied at 27 g m^{-2} yr^{-1}. Periodic sampling of the herbaceous and woody vegetation has shown that N has a highly significant effect on composition and diversity of herbaceous species, and on growth of bur and pin oaks. All oak saplings and adults have been tagged and numbered (Faber-Langendoen and Frelich, in preparation), and a subset increment cored (sample size to be augmented in 1994-95), to determine effects of treatments on productivity. All saplings and adult trees will be resampled every 2 years, and herbaceous vegetation will be annually sampled to species (10 cm x 300 cm clip strip) in two subplots per plot.

Manipulative Studies of the Mechanisms of Oak Growth, Physiology and Survival: These studies will examine the effects of resource limitation on oak seedling growth and survival by growing seedlings in trenched and untrenched plots from which mammalian herbivores have been excluded via fencing. We will establish two pairs of trenched and untrenched fenced 5 m x 5 m plots in each of the 12 savanna stands. Trenching increases belowground resource availability (e.g. nitrogen and water; Shirley 1945, Vitousek et al. 1982) by reducing root competition with neighboring trees. Twenty bur and twenty northern pin oak seedlings will be planted in summer of 1995 into each plot. Total design for this experiment includes 12 burn compartments x 2 replicates per stand x 2 trenched or untrenched treatments x 20 individuals of each species (960 seedlings per species). Resource availability, dimensional growth, photosynthesis, water stress, allocation to leaves and roots, and survivorship will be annually measured, as in recent studies (Walters et al. 1993, Walters and Reich 1994, Kruger and Reich 1993a,b; 1994). A subset of the surviving seedlings will be harvested at periodic intervals (probably yearly) to determine biomass allocation and growth.

Broad Scale Spatial and Temporal Dynamics of Tree and Prairie Patches: Each of the 12 savanna stands will be professionally aerially photographed every 5 years using 9" x 9" high resolution false-infrared film during late July. Such photographs, taken in 1983, 1988 and 1993, provide a detailed record of the location and size of individual trees and prairie patches, and allow quantification of patch structure and dynamics at several scales. In each of the 12 stands, 50 trees will be cored and standard dendrochronological analyses made to establish the date of stand origin and past changes in growth in relation to climate, landscape position and fire regime. Along with aerial photographs (analyzed via GIS), this will quantify patch changes over time.

In two stands of intermediate fire frequency, 2.25 ha will be mapped to enable detailed long-term spatial analyses. All trees > 10 cm dbh will be mapped and a grid of 400 points at approximately 7.5 m spacing will be used to map and identify to species, woody and herbaceous vegetation, the presence or absence of ant mounds, gopher burrows, or other physical disturbances, and select abiotic attributes such as N mineralization rates, % canopy openness, and litter depth and quality. These measures will be repeated every five years. The above data will extend our ability to characterize and interpret spatial heterogeneity as observed in annual sampling on all 12 stands, and will provide the most detailed fine scale resolution as part of the overall patch dynamics analyses, within which they will be analyzed.

Summary: These experiments and observations will allow us to identify controls on dispersal, germination, establishment, growth and survival of oaks in relation to temporal and spatial heterogeneity. We will determine whether patch structure is important vis-a-vis oak and total plant community dynamics within and among savannas with different fire regimes, and address questions such as: What is the patch structure within and among Cedar Creek savannas? Are plant communities different in tree/non-tree patches and/or in other kinds of patches (animal burrows, ant hills, etc.)? How does this influence successional patterns and overall species richness? Does the patch structure change in significant ways at different spatial scales (e.g., 2 ha vs 200 ha), and if so,

Field A, Experiment 1

Field B, Experiment 1

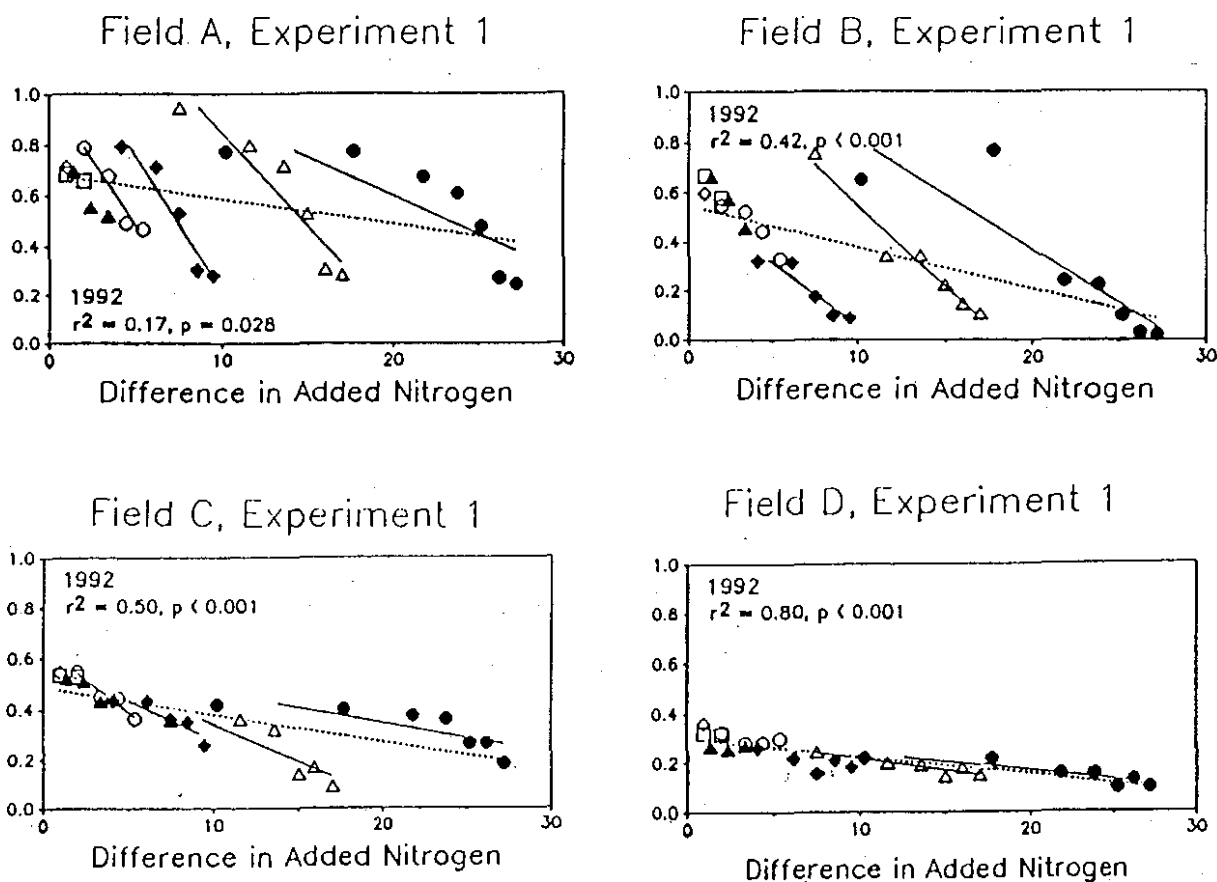Field C, Experiment 1

Field D, Experiment 1

Fig. 33. Graphs of average PS (percent similarity) versus Delta-N for Experiment 1 in even years. Each graph presents data for one year. Regression lines (dotted lines) are drawn in those graphs for which there was a significant linear relationship between average PS and Delta-N for all values of average PS (N=28). Averages for subsets of plots, based on comparisons that included different maximum amounts of N, are plotted with different symbols. For example, average values of PS for comparisons of plots that received 27 $gm/m^2/yr$ N with treatments that received less than 27 $gm/m^2/yr$ are plotted with solid circles; average values of PS for comparisons of plots that received 17.5 $gm/m^2/yr$ N with treatments that received less than 17.5 $gm/m^2/yr$ N are indicated with open triangles. Solid lines are drawn for those subsets for which there were significant linear relationships between average PS and Delta-N. Sample sizes for these subsets ranged from 7 (27 $gm/m^2/yr$) to 4 (5.4 $gm/m^2/yr$). Regressions were not performed for subsets where the maximum amount of N was less than 5.4 $gm/m^2/yr$. (Inouye and Tilman, in review).

what are the implications for the factors controlling processes at these scales? We will also characterize the relationship of herbaceous vegetation and biodiversity to diversity of habitats and resources within the savanna mosaic, and address questions such as: How does herbaceous vegetation and biodiversity vary within and among oak savannas of differing fire frequency, community composition and structure? Is diversity related to total resources in the environment, the patchiness of the environment, or both? How and why does diversity change in response to drought and other aspects of climate change? Does species diversity influence the stability of net primary production of savannas? These studies will extend and complement our strong and ongoing work in the successional grasslands, and when integrated with results for grasslands and forests, provide a synthetic and holistic data base for understanding the past and predicting the future long-term dynamics of communities at the prairie-forest border.

III. BIODIVERSITY EXPERIMENT: EFFECTS OF PLANT DIVERSITY ON POPULATION, COMMUNITY AND ECOSYSTEM DYNAMICS AND STABILITY

This is the second major new project that we propose. Our work has provided the most thorough evidence to date on the effects of biodiversity on ecosystem resistance to and recovery from a major perturbation (Fig. 1; Tilman and Downing 1994). The curvilinear relationship suggests that each additional species lost from an ecosystem has progressively greater impact on ecosystem functioning. Interest in the relationship between biodiversity and ecosystem functioning has grown as society weighs the impacts of habitat destruction and species extinction on global sustainability and habitability (e.g., Schulze and Mooney 1993).

Our results, and other work dealing with diversity/stability (e.g., McNaughton 1968, 1977, 1988, 1993; Pimm 1984, 1991, 1993; Vitousek and Hooper 1993; Lawton and Brown 1993) are largely based on observational data. Determining the overall effect of species richness on ecosystem resistance and resilience motivates a major new thrust of this LTER renewal: an experiment in which plant biodiversity is the experimentally manipulated variable. As in our other work, we are interested in the effects of this variable on population, community and ecosystem processes and dynamics. Only the direct manipulation of biodiversity within a well-replicated long-term experiment will provide the information that science and society needs on the effects of biodiversity on ecosystem stability and functioning.

The experiment consists of 210 large plots (440 m²) randomly assigned to one of 7 general treatments: (1) bare soil, (2) monoculture, (3) 2 plant species, (4) 4 plant species, (5) 8 plant species, (6) 16 plant species, and (7) 32 plant species. Treatment combinations will be designed to represent specific combinations of five plant functional groups.

Objectives

Our objective is to control plant species diversity in a well-replicated, long-term field experiment to determine the effects of plant species richness and plant functional-group richness on (1) stability of primary productivity in response to natural and experimentally induced climatic variation and in response to herbivores, pathogens, seed predators, and disease; (2) the species composition, abundances, stability and diversity of herbivorous insects, seed predators, predaceous insects, and parasitoids; (3) the densities, dynamics, stability and habitat choice of small mammals; (4) the dynamics of soil C, N, and other nutrients, including rates of accretion, leaching losses, rates of mineralization, rates of fixation, and turnover of pools; and (5) the dynamics, species composition and biodiversity of soil micro- and macro-organisms, including soil mycorrhizal fungi, nitrifying bacteria, other bacteria, other fungi, soil micro arthropods, earthworms, and soil arthropods.

Although the major focus of our experiment is the direct effects of biodiversity, the experiment will allow us to explore other questions. Succession, one of our major themes, will be further examined as the floristic composition of our treatment plots shifts through time. Our expanded initiative
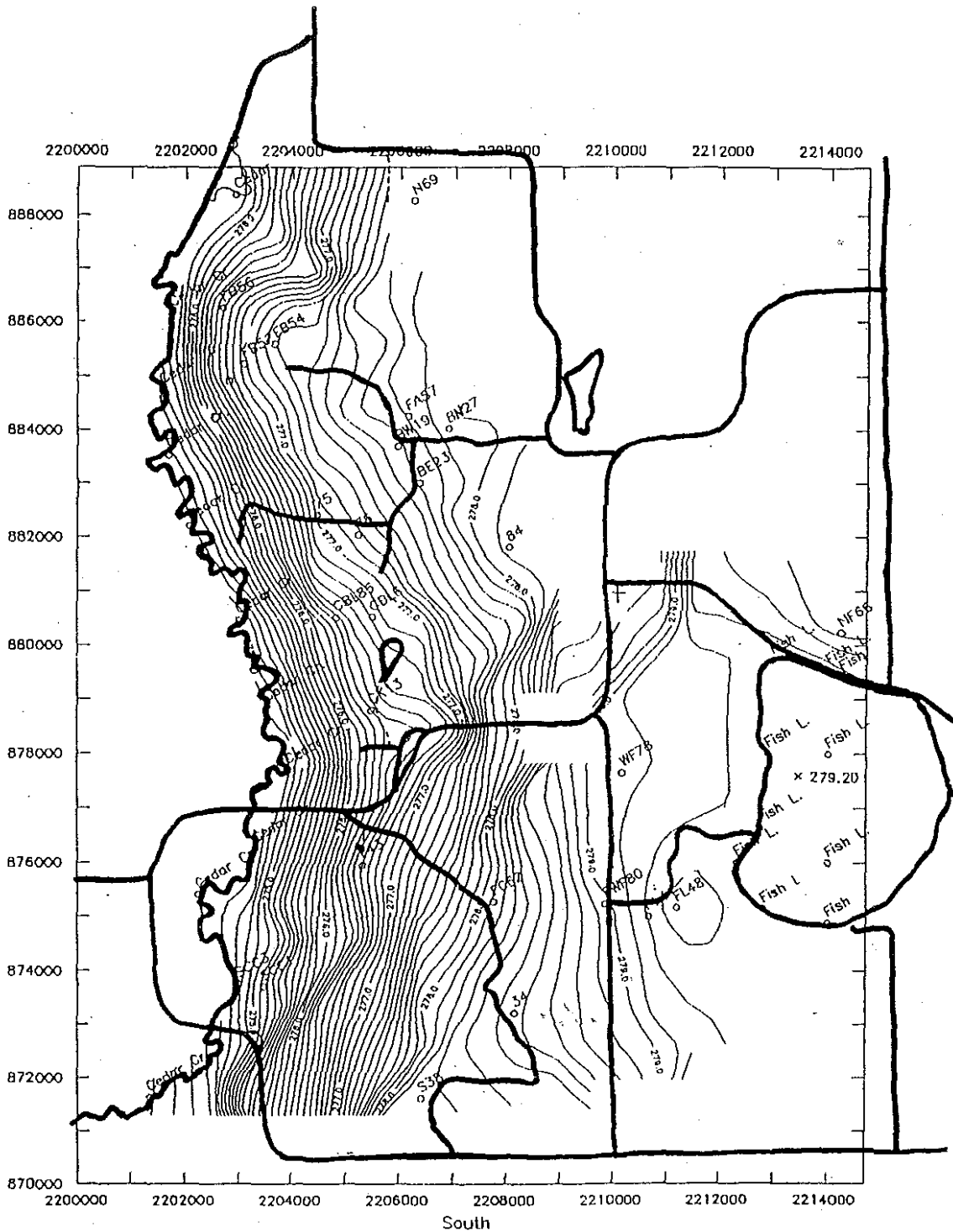
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Fig. 34. Water table depth, 6 October 1990. Lakes, rivers, and roads indicated by bold lines. Legend: well or surface water datum = o; lake elevation = x; grid = MN Coordinate System, south zone (1000 ft intervals); scale = 1:3375; contour interval = 0.1 m.

in understanding savannas will be complemented by this experiment. It will include combinations of herbaceous and woody species characteristic of our savannas. This will allow a more carefully controlled determination of the interactions among both the woody and the herbaceous strata of the savanna. Finally, our work will have implications for prairie and savanna restoration. Both our methods and our results, which will help determine the degree of floristic complexity necessary for a fully functioning system, will be useful to those interested in returning landscapes to their pre-European composition.

Methods

Establishment of the experiment began in summer 1993, and will be completed in spring 1994 using funds from the existing LTER and a Mellon grant to DT. The funds requested here would not be available until 1995, and will be used for data collection and maintenance.

Layout: The experiment contains 210 plots, each 21 m x 21 m, laid out in a 14 by 15 plot block. Plots are contiguous, but the marginal 1 m of each is used for access. In addition, 2 m wide access paths divide the block into seven equal strips, each containing 30 plots. Each plot is divided into two zones. The central 10 m x 10 m "core" will be protected from other manipulations, manually weeded to maintain the imposed diversity treatment, and mainly used for observational sampling. However, each year two 10 cm x 300 cm strips of vegetation will be cut in it. This minor rate of clipping would require 167 years to clip the entire area. The core will be sampled twice each year for insects via sweep netting and pit fall traps. The outer 5.5 m wide strip around the core is available for experimental manipulation, but no more than 1/4 of this will be used for such work.

Plant Species and Functional Groups: The experiment will separate the effects of species richness and of functional groups on observed responses. Plant species from five different functional groups are used. Specifically, we mainly use 4 species of C-4 grasses, 4 species of C-3 grasses, 4 species of forbs, 4 species of legumes and 2 species of woody plants. All species used are common perennial prairie/savanna species, and are: (1) C-4 grasses -- *Andropogon gerardi, Schizachyrium scoparium, Sorghastrum nutans, Panicum virgatum*; (2) C-3 grasses -- *Koeleria cristata, Poa pratensis, Agropyron smithii, Elymus canadensis*; (3) Prairie forbs-- *Asclepias tuberosa, Solidago rigida, Liatris aspera, Aster azureus*; (4) Legumes -- *Lespedeza capitata, Lupinus perennis, Petalostemum purpureum, Amorpha canescens*; and (5) Woody species-- *Quercus macrocarpa, Quercus ellipsoidalis.*

Treatments: The experiment has seven treatment levels of biodiversity:
1. *Bare soil*: Four plots will be maintained with bare soil via frequent cultivation and/or herbicides. Beginning the third year, only the central 5 m x 5 m will be kept bare. The remainder will undergo succession.
2. *Monocultures*: All 18 species listed above will be grown in monoculture, with two replicates per species, or a total of 36 plots.
3. *Two-species plots*: In these plots, the species were chosen to equitably represent all possible combinations of the 5 functional groups. There are 15 combinations of life forms when chosen one or two life forms at a time (5 single life form groups plus 10 combinations of two life forms). There are two replicates of each combination, with the species used in each replicate chosen at random from the list above, or 30 total plots.
4. *Four-species plots*: For these plots, there are 4 possible one-functional-group combinations (because we only have 2 woody species, we do not have plots with only woody species), 10 possible two-functional-group combinations, and 5 possible four-functional-group combinations. This is a total of 19 combinations, each in duplicate, with species for each drawn at random from the list above. Thus there are 38 total plots.
5. *Eight-species plots*: These plots consist of each of the following 6 combinations of functional groups: (1) grasses (both C-3 and C-4); (2) forbs and legumes; (3) grasses, forbs and legumes; (4) grasses and woody; (5) forb, legume and woody; (6) grasses, forbs, legumes and woody. Each combination is replicated 6 times, or 36 total plots.
6. *Sixteen-species plots*: These plots have (1) grasses; (2) forbs and legumes; (3) grasses, forbs and legumes; (4) grasses and woody; (5) forbs,

legumes, and woody; or (6) grasses, forbs, legumes and woody. There will be 3 replicates each of treatments 1-5 and 21 replicates of treatment 6, or 36 plots.

7. *Thirty-two species plots*: The 30 replications of this treatment will include the 16 herbaceous and 2 woody species listed above plus 16 additional species common in Cedar Creek oak savanna.

Establishment and Maintenance: The experiment occupies a 10-ha block of a former *Bromus inermis* field. This was sprayed with a general herbicide (Round-Up) in early August, 1993, and burned in late August after the vegetation was dead and dry. An earth-moving "scraper" removed the upper 8 cm (4 cm - 15 cm) of sod, soil, and seed bank, which was deposited off-site. The remaining soil was plowed with a mold-board plow and then thoroughly disked in late October 1993. Soil samples taken from 36 evenly-spaced sites across the field revealed that seed bank had been reduced by >90%. As soon as the ground is workable in spring of 1994, it will be disked a final time, and then smoothed. It will be sprayed with a general herbicide 3 weeks after this, and planted as soon after that as advisable.

To maintain the plots, they will be sprayed with suitable herbicides and burned during the first 2 years to help eliminate weeds and aid in the establishment of prairie species. Monocultures will be heavily seeded with desired species to further insure establishment. Plots will also be hand weeded and spot sprayed, as needed and as available labor allows. The central 10 m x 10 m portion of each plot will be weeded manually and planted with additional seeds/seedlings, if required, to more fully establish the desired treatments. Hand weeding will continue indefinitely, but the use of herbicides will stop after the second year.

Sampling/Experiments

This experiment will provide a rich source of opportunities for studies of diversity. We have identified core studies that we will begin in 1994, but we will encourage other investigators, with their own funds, to participate in related work at the site.

Vegetation sampling: Each year the percent cover of all plant species will be estimated for two different permanent 1 m x 1 m subplots in the central core area. Such subplots will also be established in the predator (bird) exclosures and the herbivore exclosures that will be installed in each plot. In addition, each year two 10 cm x 300 cm strips of vegetation will be clipped from the core area, but not in the 1 m x 1 m areas. Clipped samples will be composited, sorted to species, dried and weighed. Ecophysiological studies will help provide a mechanistic basis for the effects of biodiversity.

Insect sampling: We will sample insect taxa in each plot twice each year, in mid-June and late August. Sampling will be by sweep netting and pit-fall trapping, with samples sorted to species and enumerated. This task is greatly aided by our on-site collection of over 3000 species. Dr. John Haarstad, our resident insect taxonomist, will sort all samples, and verify new taxa with experts. Observational and mark-recapture techniques will be used for taxa of particular interest. Although sweep netting is not as quantitative as some techniques, it samples a large area, and has provided excellent information on species richness and relative abundances, and acceptable information on annual changes in abundances during the past 12 years.

Soil sampling: Within each core area we will permanently mark 9 evenly spaced locations for soil sampling. We will collect a 2.5 cm x 20 cm soil core from each location in spring 1994. A portion of each will be analyzed for total soil N and C, and the remainder will be dried and archived. We will resample these locations every 4 years, and analyze our archived cores in duplicate with newly pulled cores to quantify changes in soil total N and C. In addition, at one location per plot, soils will be annually sampled for the first four years, and thereafter biennially, by depth (litter, 0-5 cm depth, 5-10 cm, and 10-20 cm) for total C, total N, and pH. Extractable elements (Ca, Mg, K, Na, Zn, P, etc.) will be determined via inductively-coupled plasma spectrometry (ICP) originally and every 4 years on a subsample composited by depth. *In situ* N mineralization will be measured periodically in all plots.

In addition, samples collected in the fourth year will be analyzed for $^{13}C/^{12}C$ ratio to determine effects of C-4 and C-3 grasses, forbs, and trees.

Nutrient flux sampling: We will sample the flux of soil solution from plots using one ceramic cup lysimeter per plot, at a depth of 1.5 m, well below the majority of the rooting zone. Cups will be maintained under ca. 0.5 bar tension, and samples collected twice per month. Samples from each plot will be bulked, proportionally to volume collected, over spring (March, April, May), summer (June, July, August), and autumn (September, October, November). These three bulked samples per plot will be analyzed for NH_4^+ and NO_3^-.

Herbivore exclosures: Within each plot we will establish a permanent 4 x 4 m herbivore exclosure. Wire mesh and aluminum flashing will exclude small mammals. Window screen will minimize insect movement into an exclosure, and exclosures will be periodically sprayed with a broad-spectrum herbicide.

Predator (bird) exclosures: A subset of 60 plots representing a gradient of species and functional group diversity will be used for a predator exclosure experiment. On each selected plot, two 4 x 4 m subplots will be set up. One will be control; the other a predator exclosure, covered during summer with Krylon bird netting and fenced with aluminum flashing coated with teflon lubricant. In July and August each summer, each plot will be sampled for arthropods by sweep-netting and pitfall trapping. Samples will sorted to species, counted, and weighed. To measure cascading effects, percent cover of all plant species will be recorded each year. Every fourth year one 10 cm x 300 cm strip of vegetation will be clipped and sorted per plot.

Small Mammals: This sampling will address the effect of plant species and functional diversity on small mammal habitat choice. These plots are not large enough to support separate populations of small mammals, but differential use of these plots should still reflect the importance of plant diversity to mammalian consumers. We have documented differential use of fertilized 4 x 4 m and even of 1.5 x 4 m plots by *Microtus pennsylvanicus* and *Peromyscus leucopus* (Inouye et al. 1987a), thus we are confident that these plots are large enough to reveal mammal responses to diversity. Plots will be trapped for three consecutive nights twice each year (June and August) using Sherman live traps (2/plot) placed along opposite edges of the core area in each plot, facing into the core area. This will place traps about 6 m from the edge of each plot. Animals will be identified, measured, and released.

Drought experiment: In the fourth and fifth years of this study, we will use a portable rainout shelter, 3 m x 3 m, to impose drought in each of 60 plots (10 per species richness level). We have successfully used such rainout shelters, which have a removable clear plastic cover, to impose droughts that led to biomass responses similar to that of the 1988 drought (Wardenaar, in prep.).

Expected Results

Our biodiversity experiment should determine the effects of plant species richness and plant functional-group richness on (1) stability of primary productivity, (2) composition, stability and diversity of herbivorous and predaceous insects; (3) habitat choice by small mammals; (4) the dynamics of soil nutrients; (5) the composition and biodiversity of soil micro- and macro-organisms; and (6) dynamics of plant diseases. We will not have sufficient funds to accomplish all these goals. However, we consider the biodiversity experiment to be a national research resource that we are establishing. We will encourage others to use it to address questions, like those listed above, for which it is uniquely suited. Although the study has not yet been established, several scientists have already expressed strong interest in using the plots, including Dr. F. Stuart Chapin (Berkeley), Dr. Les Real (Indiana), and Drs. Linda Kinkle and Deborah Allan (Minnesota).

Conclusions

This long-term experimental study of the impacts of biodiversity on ecosystem functioning and stability will provide some of the first direct evidence from a field experiment of the effects of species richness and functional diversity on numerous aspects of population, community and ecosystem dynamics, stability, and functioning.