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## Project Summary

This is a request for renewal of the Cedar Creek Natural History Area Long-Term Ecological Research project. The nine co-investigators of the Cedar Creek LTER are using long-term experimentation, observation and theory to examine (1) the controls of biodiversity, community assembly and ecosystem functioning in upland ecosystems at the prairie-forest boundary, (2) the effects of both biodiversity and community composition on ecosystem processes, and (3) the impacts of major perturbations – including climatic variation, N deposition, elevated CO<sub>2</sub>, predator suppression, and changes in fire frequency – on species composition, diversity and ecosystem functioning. 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. Work proposed here will build on an 18-year record that we have already accumulated at our site.

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, for the next six years, we propose to continue and expand on five major sets of long-term research, including experimental and observational studies of biodiversity, nitrogen addition, fire frequency, trophic interactions, and successional dynamics and land use.

The results of many of our proposed studies are relevant to society because they will provide a better understanding of the long-term impacts of human actions on ecosystems. For instance, our research will help elucidate the both factors that control biodiversity and the effects of the loss of biodiversity on ecosystem functioning. Our studies of the impacts of nitrogen addition, of elevated CO<sub>2</sub>, of fire frequency, and of changes in trophic structure all address issues related to major ways that humans are impacting the environment.

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## Section 1.A. Results of Prior LTER Support

NSF/DEB-9411972, Long-Term Ecological Research (LTER; 1994 – 2000) “**Succession, Biodiversity and Ecosystem Functioning at the Prairie-Forest Border,**” G. David Tilman, Peter Reich, David Grigal, Mark Ritchie and Richard Inouye, original co-PI’s \$560,000 per year

The collective efforts of more than 36 researchers at Cedar Creek Natural History Area (CCNHA) over the past six years have increased understanding of both the consequences and the causes of biodiversity in ecosystems. In addition, our research has addressed the effects that disturbances such as changes in fire frequency, nitrogen (N) enrichment, elevated atmospheric CO<sub>2</sub>, trophic interactions, and climate have on the species composition, productivity, nutrient cycling, and stability of terrestrial ecosystems. We have used long-term observations and experiments to explore these effects in plant, arthropod, avian and mammalian communities, and have measured the feedbacks of species on ecosystem productivity and nutrient cycling. In addition, we have developed, and are now testing, new hypotheses about the mechanisms controlling species composition and diversity in plant and animal communities and the effects of these on community assembly and susceptibility to invasion. The work of the Cedar Creek LTER integrates ecophysiological, community and ecosystem perspectives, and seeks generality via simple mechanistic theories.

Much of our research has contributed information of direct relevance to society and the environment, regarding the loss of biodiversity, increasing global atmospheric CO<sub>2</sub> levels, changes in carbon and N budgets, variation in climate, fire suppression, and overpopulation of mammalian herbivores. Because of their relevance to environmental issues, many of our results have been communicated to the public by the media. We will now explore how these human impacts affect population, community, and ecosystem processes at the continental border between grasslands and forest.

Our work at CCNHA has addressed six fundamental questions related to the inter-relationships between individual species and ecosystem functioning:

1. How do individual species modify ecosystem functioning by influencing abiotic conditions and nutrient budgets?
2. How does plant species richness affect the magnitude, sustainability and stability of productivity in ecosystems?
3. How do elevated levels of CO<sub>2</sub> and N impact species composition and diversity and their feedbacks on ecosystem carbon (C) and N budgets?
4. What mechanisms allow so many species to coexist, and how do these mechanisms influence the effects of individual species and species diversity on ecosystem productivity, nutrient cycling, and stability?
5. How do trophic interactions modify species composition and directly and indirectly modify ecosystem functioning?
6. How do mechanisms of coexistence and feedbacks on ecosystem functioning drive successional dynamics of plants and animals?

These questions were addressed with a coordinated suite of theoretical, field experimental and observational studies, which we highlight below.

### ***Species effects on ecosystem functioning***

Long-term research at Cedar Creek has demonstrated the strong and often opposing feedback effects of plant and consumer species on ecosystem functioning, independent of edaphic factors (Wedin et al. 1995). Our most recent work shows that plant species, in combination with fire, have strong influence on nutrient cycling and productivity. For example, dominant prairie grasses immobilize useable forms of N, and yield more closed N and C budgets with reduced N availability (Wedin and Tilman 1996). Nitrogen-fixers, such as the herbaceous legume *Lathyrus venosus*, greatly increase N inputs, eventually doubling productivity and increasing total soil N by 30-50% after 13 years (Knops et al. 2000) (Fig. 1A), but only when deer are excluded (Ritchie et al. 1998). White pines (*Pinus strobus*) exhibited triple the productivity of C4 grasses and oaks when grown in the same original soil, either because of extensive root foraging or non-symbiotic N fixation (Knops et al. 2000). Woody plants modify soil total C and N, N mineralization, moisture and temperature, which may modify fire intensity and further promote woody plants (Reich et al. 2000). Over the past 60 years, dominance of grasses vs. trees on the same soil type has led to major differences in ecosystem C storage (Johnston et al. 1996) (Fig. 1B).

From experimental garden monocultures of each of 40 common plant species at Cedar Creek, plant ecophysiological traits such as plant tissue turnover and morphology are closely associated with these ecosystem effects (Craine et al. 1999a, 1999b) (Fig. 1C, traits vs. monoculture R\* values for soil nitrate). Indeed, strong trade-offs among plant traits help explain differences in species effects on ecosystem functioning, and appear to apply across different biomes (Reich et al. 1997b, 1998ab, 1999a).

We also have demonstrated that consumers may strongly mediate plant-ecosystem feedbacks (Huntly 1995). Herbivores, such as white-tailed deer (*Odocoileus virginianus*), modify these plant feedbacks through selective feeding on critical "feedback" species such as legumes and woody plants. Protection from deer and insect herbivory for only 6 years increased legume abundance five-fold and doubled available soil N (Ritchie et al. 1998) (Fig. 1D). Pocket gopher digging transported nutrient-poor soil to the surface and created microtopographic variability in soils that affected plant species composition and diversity (Inouye et al. 1997).

These examples underscore the potential effects on ecosystem functioning of losing species from habitat destruction (Tilman et al. 1994b, 1997c) or other causes. They also establish mechanistic links between ecophysiology, species interactions, community composition, succession, plant diversity and ecosystem functioning that we have explored conceptually and theoretically (e.g., Tilman et al. 1994b, 1997b, 1997c, Ritchie and Olff 1999) as well as empirically (e.g., Gleeson and Tilman 1994, Zak et al. 1994, Reich et al. 1995, Wedin et al. 1995, Ritchie and Tilman 1995, Wedin and Tilman 1996, Reich et al. 1997b, Craine 1999a,b).

### ***Effects of biodiversity on ecosystem functioning***

The influence of biodiversity on ecosystem functioning is critical in understanding the consequences of the loss of biodiversity. Individual species effects on ecosystem functioning may translate into strong effects of biodiversity on ecosystem functioning. Our field experiments provided strong evidence of such effects. Greater numbers of plant species in old field grasslands and savannas were associated with greater resistance of plant biomass to a severe drought (Tilman and Downing 1994, Tilman 1996a, 1999a) (Fig. 2A). This relationship held even after controlling for up to 20 different potentially confounding variables that had been simultaneously measured in these 207 plots. These patterns led us to establish two well-replicated, long-term

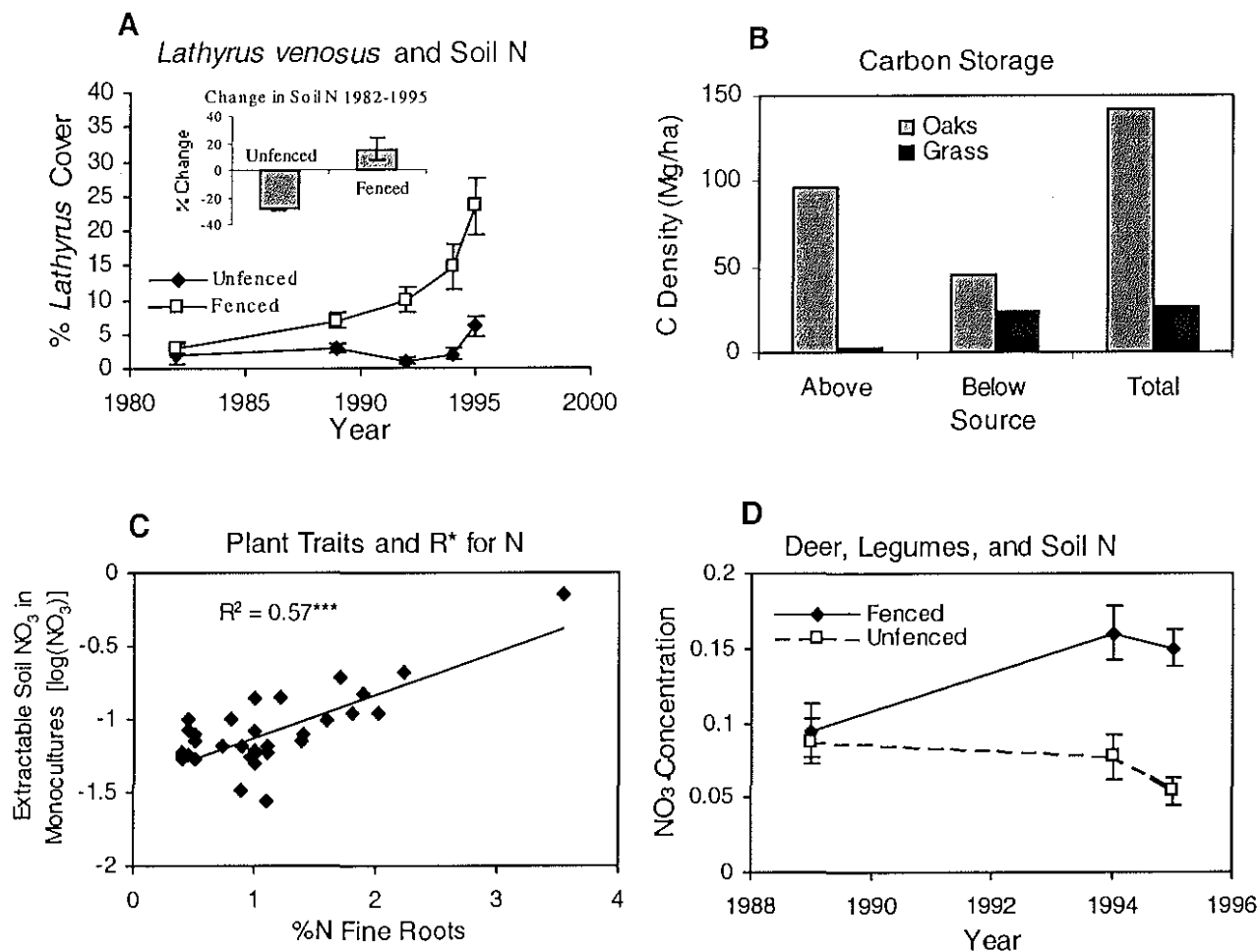


Figure 1. Strong species effects on ecosystem function at Cedar Creek.

(A) Increase in mean ( $\pm$ SE) abundance of a dominant legume species *Lathyrus venosus*, in response to exclusion of white-tailed deer (fenced) in frequently burned oak savanna from 1982-1995 (Ritchie, Tilman, Knops 1998, *Ecology*), showing that deer herbivory strongly limits legumes. Inset graph shows that changes in mean total soil N ( $\pm$ SE) decreased from 1982-1995 where legume abundance is low (Unfenced) and increased where legume abundance is high (Fenced). (Knops, Ritchie, Tilman (2000) *Ecoscience*).

(B) Strong influence of woody species vs. grasses on C storage aboveground (Above), belowground (Below) and in total (Total) in upland environments of similar soil parent material (Johnston et al. (1996) *Forest Ecology and Management*).

(C) Increase in the logarithm of mean available soil nitrate concentration vs. %N of fine root tissue for 33 species of C4 and C3 grasses, forbs, legumes, and woody plants growing in 8 year-old experimental monocultures (unpublished data of J.Craine, D. Wedin, D. Tilman, P. Reich). This shows the influence of species ecophysiological traits on ecosystem function.

(D) Positive effects of legumes on mean extractable soil nitrate ( $\pm$ SE) from 1989-1995. Data are from plots with high legume abundance protected from deer (Fenced) vs. plots with low legume abundance (Unfenced). (Ritchie et al. (1998) *Ecology*).

field experiments. One is a species diversity experiment (147 plots, each 9 m<sup>2</sup>, called Biodiversity I) that manipulates plant species richness independently of species composition. The second experiment, Biodiversity II, simultaneously manipulates species diversity and functional group diversity and composition (249 plots, each 81 m<sup>2</sup>). We found that total plant cover increased significantly with plant species richness (Fig. 2B). Furthermore, the main limiting nutrient, soil mineral N, was used more completely when there was a greater diversity of species (Fig. 2C), leading to lower leaching loss of N (Tilman et al. 1996b). Subsequently, we found that the diversity of functional groups (legumes, C<sub>4</sub> grasses, etc.) was the most important component of biodiversity that affected productivity (Tilman et al. 1997a, Symstad et al. 1998). Functional diversity implied strong differences in species capture and use of N, and its effects on N inputs, losses and recycling (legumes vs. C<sub>4</sub> grasses), which may lead to complementary, and thus more sustainable, use of N.

These direct effects of plant diversity cascaded into effects on other ecosystem characteristics. Both the biomass (Fig. 2D) and species diversity of invading weeds were significantly lower in plots with more plant species (Knops et al. 1999). Fungal diseases of 4 plant species were significantly less abundant in more diverse plots in Biodiversity II (Knops et al. 1999, Mitchell et al. *in prep.*) (Fig. 2E). Likewise, species diversity of all arthropods (Fig. 2F) and of many trophic groups of arthropods (e.g., predators/parasitoids, herbivores) was positively correlated with plant species diversity (Siemann et al. 1998, Knops et al. 1999). Unexpectedly, insect abundance declined with increasing functional diversity but increased with increasing species richness (Haddad et al. *ms*). Greater plant diversity therefore appears to diversify and weaken the impacts of higher trophic levels.

These experiments sparked the development of theory that explored how diversity might impact productivity (Tilman et al. 1997b, 1998; Tilman 1999a), ecosystem reliability (Naeem and Li 1997, 1998), stability (Tilman et al. 1998, Tilman 1999a, Lehman and Tilman, *in review*) and susceptibility to invasion (Tilman 1999a and Davis, Grime and Thompson, *in review*). In addition, we helped organize two major workshops on biodiversity and ecosystem functioning, a GCTE - Focus 4 workshop at Cedar Creek in September 1995, and one at NCEAS in May 1999. These led to a book synthesizing experimental and theoretical approaches to diversity and ecosystem functioning (Kinzig, Pacala and Tilman, Eds., *in prep.*).

### ***Effects of modifying C and N budgets***

The strong influence of species on ecosystem functioning implies that species composition and diversity may have dramatic effects on the consequences of global changes in C and N budgets. Our work suggests that grassland-forest transition ecosystems may be capable of storing significant C, but are vulnerable to N deposition and perhaps greater atmospheric CO<sub>2</sub> concentration.

In a 12-year experimental study of N deposition on Minnesota grasslands, plots dominated by native C<sub>4</sub> grasses shifted to low-diversity mixtures dominated by cool-season grasses at all but the lowest N addition rates. This shift was associated with decreased plant C and C:N ratios, increased N mineralization (Fig. 3A), high N losses, and low C storage (Wedin and Tilman 1996). In addition, plots originally dominated by nonnative C<sub>3</sub> grasses retained little added N and stored little C, even at low N input rates (Fig. 3B). Thus, grasslands with high N retention and C storage rates were the most vulnerable to species losses and major shifts in C and N cycling.

Sampling of soils within the old field chronosequence of 22 fields that range from about 1 to 60 years in age provides additional evidence of the C and N dynamics of natural ecosystems

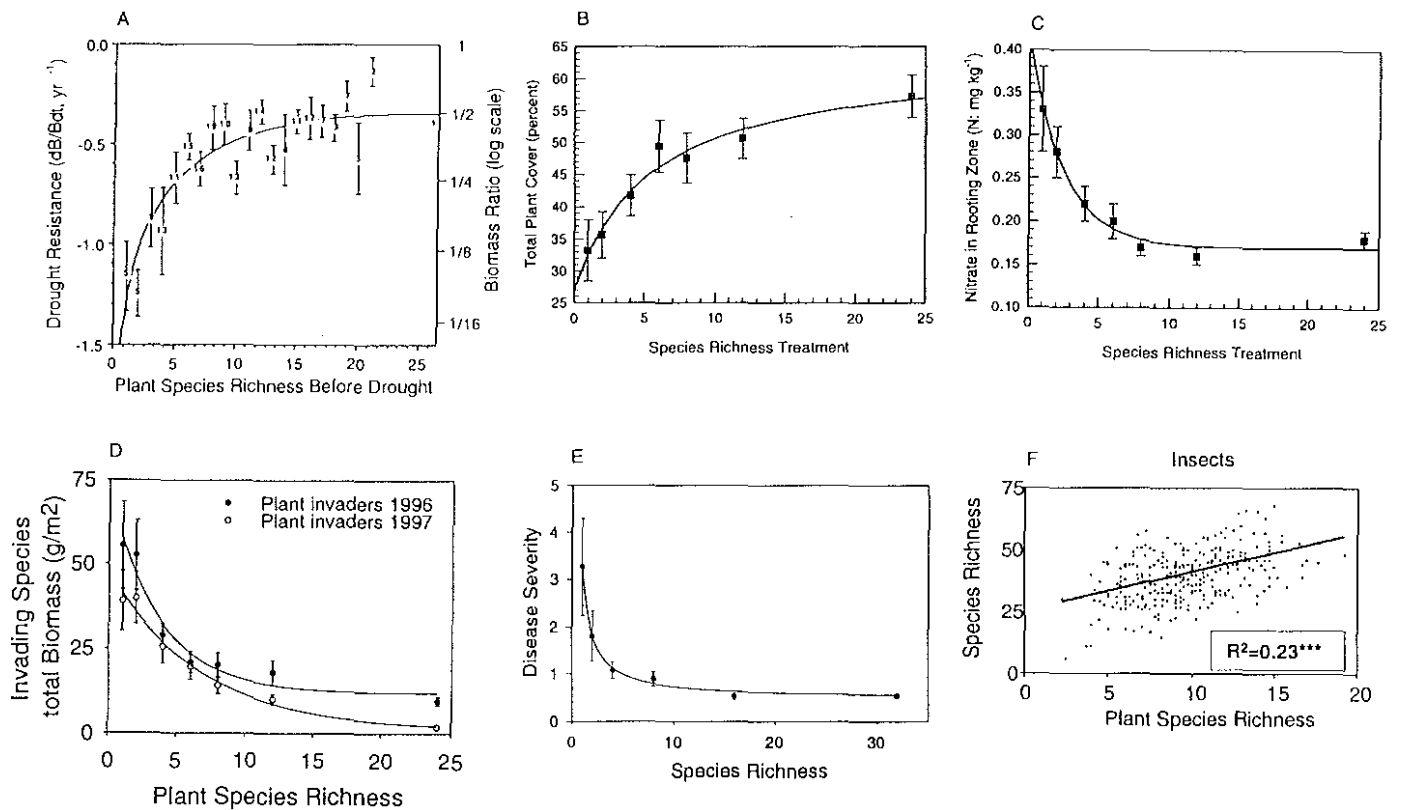


Figure 2. (A) Relationship between drought resistance of grassland plots and plant species richness ( $SR_{86}$ ) preceding a severe drought. Mean, standard error and number of plots with a given species richness are shown. Drought resistance was measured as  $dB/Bdt$  ( $yr^{-1}$ ), that is, as  $0.5 \ln [biomass_{1988}/biomass_{1986}]$ ; left-hand scale). The right-hand scale shows the proportionate decrease in plant biomass associated with the  $dB/Bdt$  values. (Tilman and Downing (1994) *Nature*). (B) Total plant cover is the sum of cover of all vascular species in a plot. Fitted curve is  $y = 27 + 36.4x/(5.48 + x)$ ,  $R^2 = 0.18$ ,  $n = 147$ ,  $P < 0.001$ . (Tilman, Wedin and Knops (1996) *Nature*.) (C) Soil nitrate (as mg of N per kg of dry soil) at 0-20 cm depth, where 79.8% of roots occur. Fitted curve is  $y = 0.17 + 0.24e^{-0.41x}$ ,  $R^2 = 0.22$ ,  $n = 147$ ,  $P < 0.001$ . (D) Invading external plant richness as number of invading species (excluding the 24 planted species), fitted curve is  $y = 1.92 + 5.94e^{-0.105x}$ ,  $F=51.1$ ,  $R^2 = 0.283$ ,  $n=147$ ,  $P<0.001$ , sample size 20 - 24. All results plotted are means  $\pm$  SEM. Note that the biomass of the smaller *Crepis* plants is multiplied by three to provide a similar scale of that of *Digitaria* for purposes of illustration. (Knops et al. (2000) *Ecology Letters*.) (E) Effects of biodiversity on relative disease severity across four plant diseases in three sampling periods in E120 in 1997. Relative disease severity was calculated as the average percent leaf area covered by disease, standardized by disease and sampling period. Data shown are means  $\pm$  SEM; fitted curve is  $y=0.490+2.77x^{-1.06}$  ( $R^2=0.24$ ,  $P<0.001$ ). (F) Increase in species richness of all insects with increasing plant species richness in the Biodiversity II experiment. (Haddad et al. *ms*, Siemann et al. (1998) *American Naturalist*.)



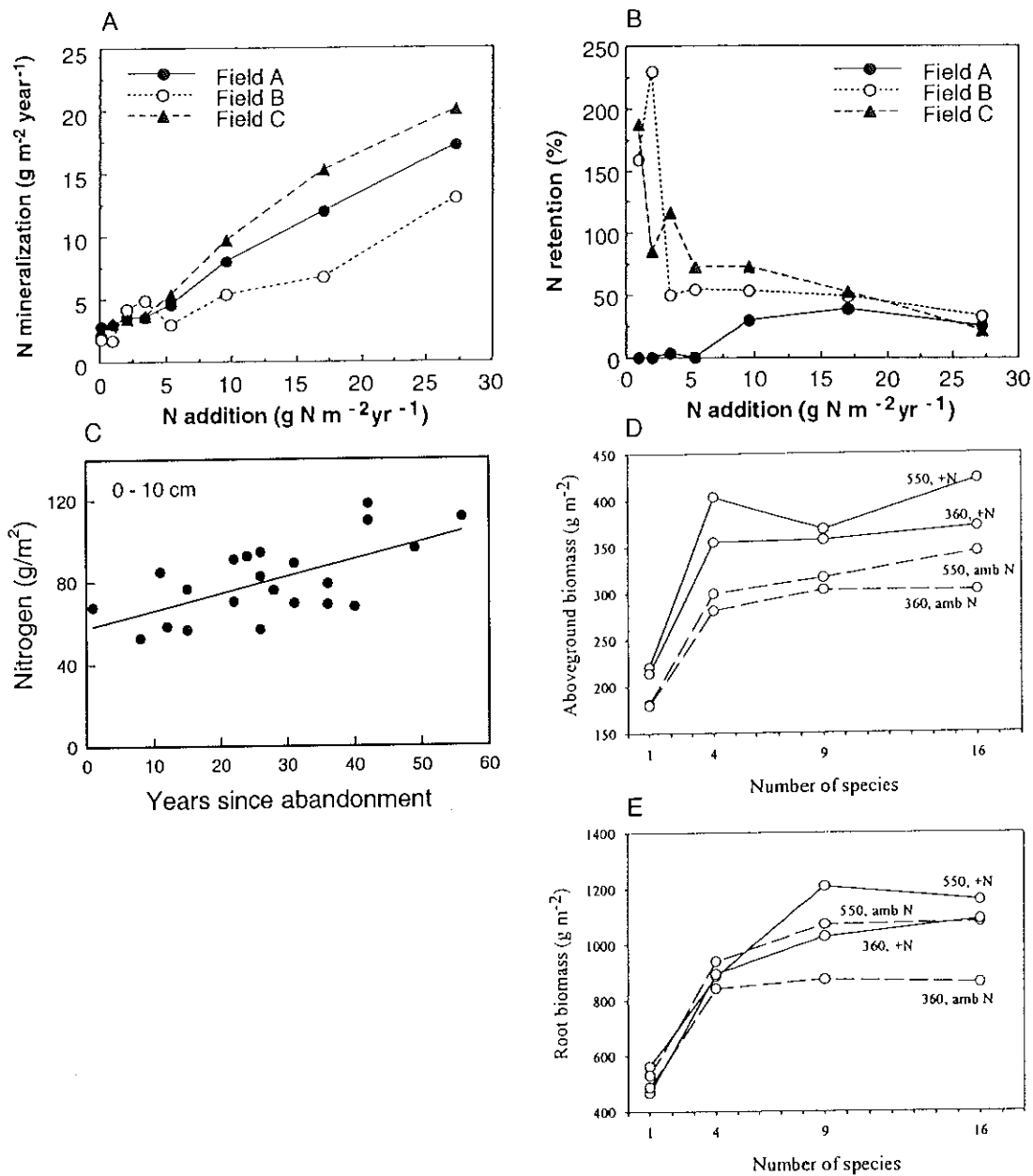


Figure 3. (A and B) Nitrogen dynamics after 12 years of N addition. (Wedin and Tilman (1996) *Science*.)

(A) Annual in situ net N mineralization, and (B) net N retention after 12 years estimated as the change in total system N (relative to controls) divided by the sum of experimental N additions.

(C) Soil nitrogen in g/m<sup>2</sup> from 0-10 cm deep. This data is based on Inouye et al. (1987a, b), who reported mass-based data from a subset of the fields presented here. Data are averaged by field ( $n = 8$  per field) and the regression slope is from a linear regression: 0-10 cm df = 1, 20,  $F = 13.17$ ,  $P = 0.002$ ,  $R^2 = 0.367$ . (Knops and Tilman (2000) *Ecology*.)

(D and E). Result from BioCON. Total aboveground and belowground biomass for plots with either 1, 4, 9 or 16 species, grown at four combinations of ambient and elevated CO<sub>2</sub> and N ( $n=296$ ). Biomass data were averaged per plot for four harvests (June and August in both 1998 and 1999). (Reich et al., in review.)

(Fig. 3C). Intensive agriculture and associated destruction of plant communities results in major losses of C and N, even 61 years after abandonment of agriculture (Johnston et al. 1996, Knops and Tilman 2000). Projections suggest that pre-agriculture C and N levels will not be achieved for another 180 to 230 years. New work assessing C and N storage across an experimental fire gradient in oak savanna is exploring the potential effects of fire suppression on C storage (Tilman et al. 2000; D. Wedin et al. in prep.).

A new experiment (E141, BioCON) explores the effects of enhanced atmospheric CO<sub>2</sub> and N deposition to 371 plots (4 m<sup>2</sup>) containing different numbers of plant species. Early results show that plots with more plant species show greater productivity when supplied with more N or CO<sub>2</sub> (Fig. 3D,E). This result suggests that biodiversity losses may interact with atmospheric global change: ecosystems with greater species richness may respond to elevated CO<sub>2</sub> and N deposition with greater CO<sub>2</sub> uptake and storage, whereas low-diversity ecosystems may not.

### ***Mechanisms of species coexistence***

Work at Cedar Creek has identified two major new mechanisms that potentially explain how multiple species coexist on a few limiting resources. First, a trade-off between species' competitive ability for limiting nutrients and the ability to colonize new sites allows many species to coexist (Tilman 1994, Tilman 1997a, Lehman 1999). This hypothesis appears to explain the lack of local saturation of plant communities and the role of regional diversity in the control of local diversity (Fig. 4A). Second, partitioning of the environment according to body size is predicted to allow multiple species to coexist on a single limiting resource (Ritchie and Olff 1999). Size differences among smaller species are expected to be greater than those among larger species (Fig. 4B). This helps explain why the smallest and largest individuals are represented by fewer species than intermediate-sized individuals (Fig. 4C) and why particular taxa have a distinct body size at which both species richness and number of individuals are highest (Fig. 4D) (Siemann et al. 1996). These advances provide a framework for evaluating the consequences of habitat fragmentation for biodiversity, and hint at a general, size-invariant rule for the relations among colonization limitation, habitat structure and fragmentation, interspecific resource division, abundance and diversity.

Other work confirms the role of resource diversity in promoting species diversity (Siemann et al. 1998, Haddad et al. *ms*), as insect diversity in the Biodiversity II experiment increased with plant species diversity (see Fig. 2F).

### ***Trophic interactions and indirect effects on ecosystem functioning***

Several experiments suggest that trophic interactions may involve a relatively small fraction of primary productivity, but are nevertheless important in determining plant community composition, succession, and ecosystem functioning. Impacts of major vertebrate predators (lizards, birds) on grasshoppers, the dominant herbivorous insects, over 11 years appear weak compared to the effects of annual weather and N limitation of plant quality (Ritchie 2000, Pitt 1999, Haddad et al. *ms*) (Fig. 5A,B). Despite consuming less than 10% of plant production, herbivores selectively feed on a few legume (Fig. 1A) and woody species that would otherwise enhance productivity and accelerate N availability in favor of shade-tolerant forbs and woody plants (Ritchie and Tilman 1995, Ritchie et al. 1998) (Fig. 5C). These results imply that herbivores indirectly reduce productivity and retard succession through their selective impact on plant species that have large impacts on ecosystem functioning. These Cedar Creek results fit within the framework of a new general model that explains plant-herbivore interactions as a

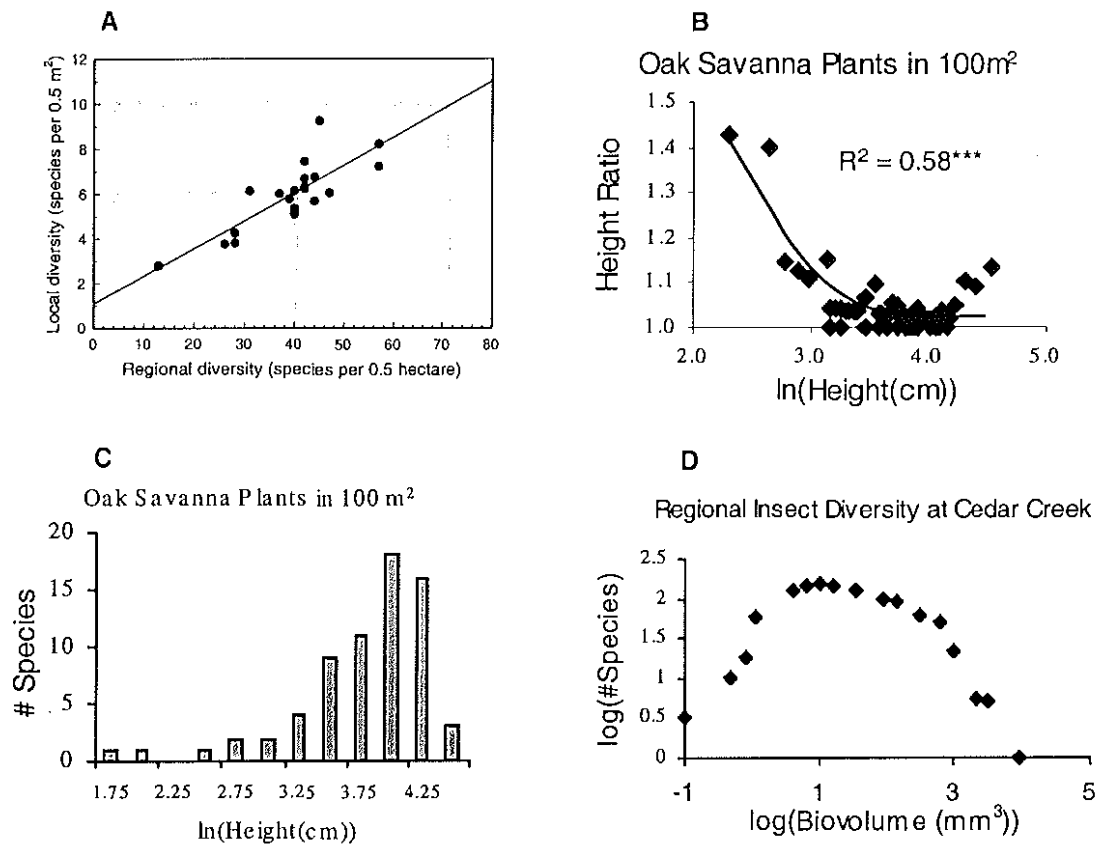


Figure 4. Species diversity patterns appear to be governed by a variety of mechanisms at Cedar Creek.

(A) Plant species richness within  $0.5 \text{ m}^2$  plots is correlated with species richness in the entire field, for each of 22 old fields of different successional age, indicating the potential importance of colonization limitation in controlling plant diversity (Tilman (1999) *Science*).

(B) Ratio of the heights of pairs of oak savanna plant species adjacently-ranked by height vs. height of the larger of the two species in each pair. This declining pattern is consistent with that expected if plant coexistence is determined by size-dependent niche partitioning in competition for light or soil resources (Ritchie and Olff (1999) *Nature*).

(C) Distribution of species richness for different oak savanna plant height classes, as predicted by a model of size-dependent niche partitioning.

(D) Distribution of insect species richness vs. size (both log-transformed) for all insects sampled in 2 old fields at Cedar Creek, showing the existence of an optimal body size for species representation. This pattern is predicted by the scaling relationship between species richness ( $S$ ) and abundance ( $I$ ):  $S = I^{0.5}$  expected from a neutral model of species coexistence (Siemann, Tilman, Haarstad (1996) *Nature*).

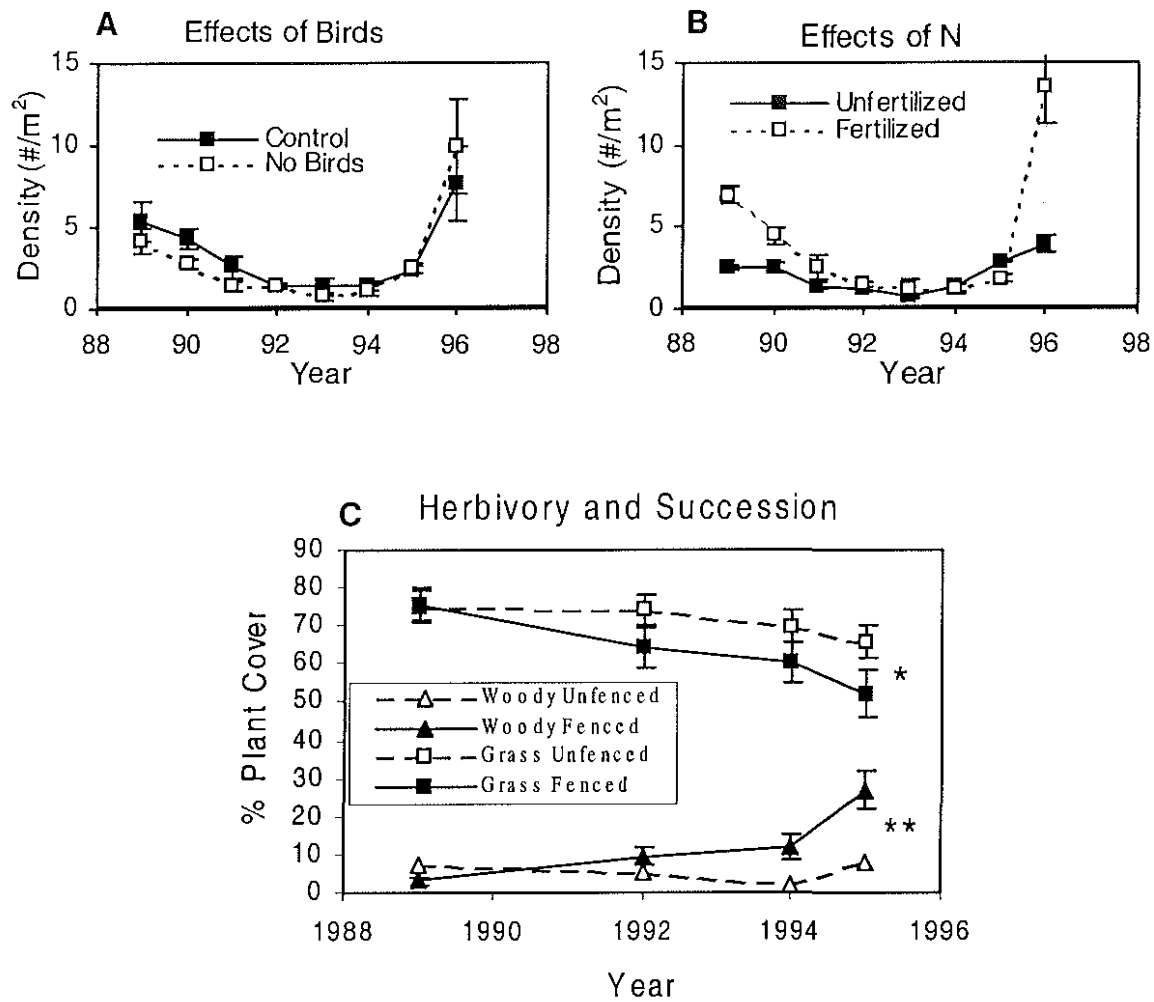


Figure 5. (A and B) Strong influence of bottom-up as opposed to top-down trophic influences on grasshopper abundance from 1989-1996.

(A) Weak, intermittent effects of excluding birds, a major vertebrate predator vs. (B) strong effects of adding  $17 \text{ g m}^{-2} \text{ yr}^{-1}$  of N on grasshopper densities in a single old field, especially following the warm summers of 1988 (drought year) and 1995 (Ritchie 2000 *Ecology*).

(C) Influence of deer herbivory on succession within a grassland opening in frequently burned oak savanna. Data are mean percent cover ( $\pm$  SE) of all woody plants (triangles) and grasses (squares) inside and outside deer fences for the period 1989-1995 (Ritchie et al. 1998, *Ecology*). These data suggest that deer strongly retard succession despite consuming less than 6% of aboveground biomass.

function of water availability and soil fertility (Olf and Ritchie 1998, Ritchie and Olf 1999). This idea was tested with a cross-site study of the effects of mammalian grazers on grassland biodiversity and ecosystem functioning, established at 7 sites across North America.

### ***Mechanisms of succession and community assembly***

Cedar Creek has a long history of work on the patterns and mechanisms of succession and plant invasions. During the past six years, we found several important and previously unappreciated mechanisms of succession. These mechanisms suggest that succession in the absence of fire proceeds through the interactions of colonization, competition, and herbivory.

Colonization limitation may be a major factor limiting species replacement during succession from abandoned fields to grasslands (Tilman 1994, 1997a) via dispersal limitation and seed predation by insects (Kitajima and Tilman 1996). Consequently, species that are strong resource competitors, such as *Schizachyrium* may be delayed in colonizing a locality where they would eventually outcompete early successional species (Fig. 6A) (Foster and Tilman *ms*). Succession from grassland to forest also may be mediated by competition for water with herbaceous vegetation. Survival of oak seedlings (*Quercus macrocarpa* and *Q. ellipsoidalis*) was much more closely related to net soil water supply (gross supply minus evapotranspiration through herbaceous vegetation) than neighbor biomass or gross water supply (Davis et al. 1998) (Fig. 6B). Herbivory by insects and deer also appear to retard succession in a complex interaction where competition from herbaceous plants slows the growth of tree seedlings and makes them vulnerable to herbivory for decades (Inouye et al. 1994).

Using the 36 year old savanna prescribed burning experiment, we have found that fire frequency can have profound effects on ecosystem C storage (Fig. 7A; Tilman et al. in review). Savanna ecosystems experiencing fire suppression stored twice as much C as those experiencing the pre-settlement fire frequency. Because fire suppression has been national policy in the U.S. since the 1920's (Fig. 7B), the resulting shifts in ecosystem composition and C storage may explain a portion of the 'missing' C that is hypothesized to be stored in North America.

### ***Connection to future research***

Our work on the causes and consequence of biodiversity and on the effects of individual species on ecosystem functioning suggest that species influence the impacts of impending environmental change at regional and global scales. While the impact of single factors (e.g., enhanced CO<sub>2</sub> or N deposition) are becoming well-known, interactions among these factors remain largely unknown, despite being critical in assessing the consequences of collective global change. Exploring the interactions among environmental change factors will require the continuation of many of our experiments, the most critical of which are in their early stages. Several long-term experiments, such as long-term N fertilization in old fields and savannas, continue to provide insights into chronic effects of low-level N addition and into how species effects are modified by climatic variation. In addition they allow us to observe changes to ecosystems as environmental changes, such as climate change, happen. Because of the legacy of ideas and long-term field experiments at Cedar Creek, we are uniquely poised to explore interactions between several factors, including CO<sub>2</sub> enhancement, N deposition, fire suppression, loss of regional pools of species that impact ecosystem functioning, and human modification of large mammalian herbivore populations.

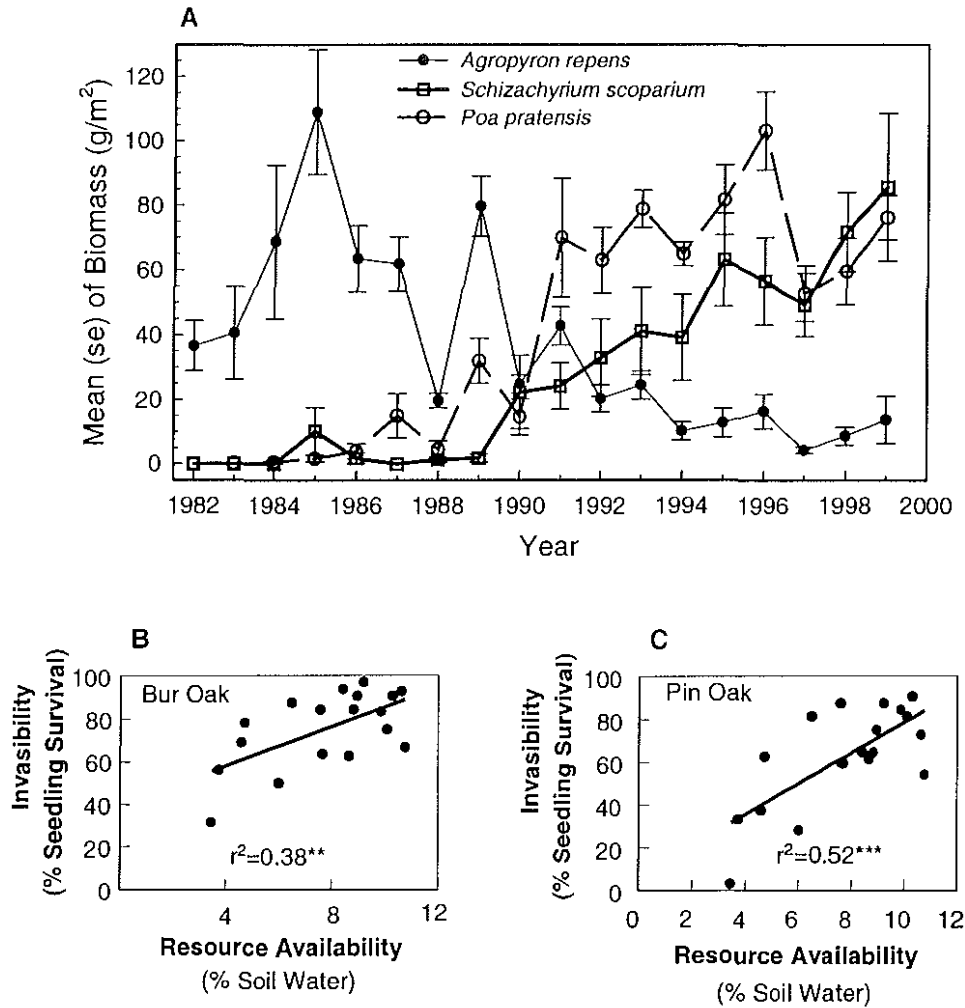


Figure 6. Plant succession is controlled by local competition for soil resources among plant species, and strong colonization limitation of better competitors.

(A) Long-term successional dynamics observed in the control (unfertilized) plots of the nitrogen addition, E001, experiment in a 14-year-old successional field. Of the three major species, *Agropyron repens* declines as first *Poa pratensis* and then *Schizachyrium scoparium* invade and increase in abundance.

(B and C) Water availability, as controlled by biomass and species composition of herbaceous vegetation in an old field, is important in controlling woody plant establishment during succession (Davis et al. 1998 *Journal of Ecology*), as judged from the increased survival of germinated seedlings of two oak species (B) *Quercus macrocarpa* (bur oak) and (C) *Q. ellipsoidalis* (pin oak) across an experimental water gradient.

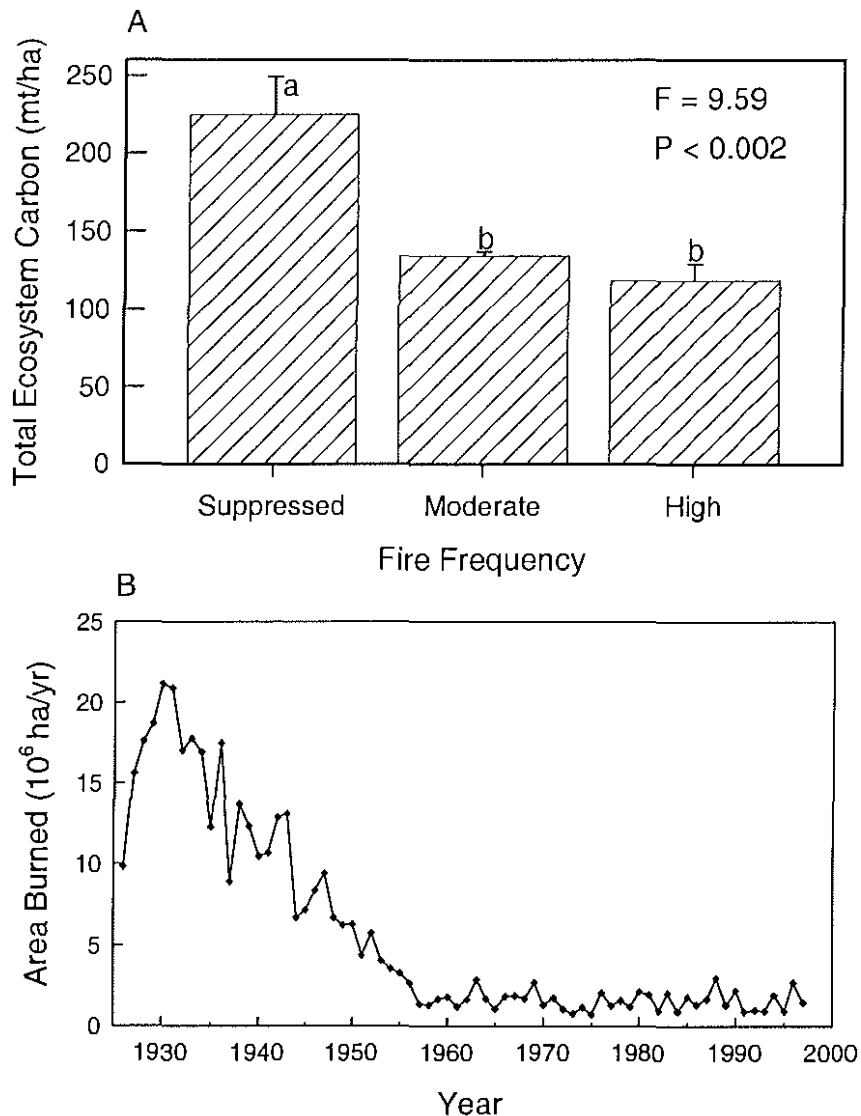


Figure 7.

(A) Total stores of carbon (as C) in all forms (summed, on an aerial basis, for soil plus fine roots, coarse roots, forest floor litter, coarse woody debris, trees, and other vegetation) in the three fire treatments in oak savanna/forest of Cedar Creek Natural History Area. The 8 fire-suppressed plots had a mean fire frequency of  $0.025 \text{ yr}^{-1}$  (i.e., one fire per 40 years), the 4 moderate fire frequency plots had a fire frequency of  $0.24 \text{ yr}^{-1}$  (a fire about every 4 years) and the 7 high fire frequency plots had a mean fire frequency of  $0.62 \text{ yr}^{-1}$  (fire in about 2 of every 3 years). Results for an ANOVA of the effects of the fire frequency treatments on total ecosystem carbon are shown. Means sharing the same lower-case letter do not differ significantly ( $P > 0.05$ ) based on Student-Newman-Keuls multiple comparison test. Units of  $\text{mt ha}^{-1}$  and  $\text{Mg ha}^{-1}$  are equivalent. (Tilman et al., in review, *Ecology*.)

(B) Extent of ecosystem burning in United States (millions of hectares per year) from 1926 to 1997, based on data reported for 1926 through 1969 in the US Census Bureau's "Historical Statistics of the United States," a CD-ROM distributed in 1997 by Cambridge University Press, NY, and, for 1970 through 1997, in annual issues of "Wildfire Statistics," US Forest Service, Government Printing Office, Washington, DC.

## Section 1.B. LTER Publications

### *Refereed Journal Articles*

1. Frank, D. A. and R. S. Inouye. 1994. Temporal variation in actual evapotranspiration of terrestrial ecosystems: patterns and ecological implications. *Journal of Biogeography* 21:401-411.
2. Gleeson, S. K. and D. Tilman. 1994. Plant allocation, growth rate, and successional status. *Functional Ecology* 8:543-550.
3. Grigal, D. F. and P. S. Homann. 1994. Nitrogen mineralization, groundwater dynamics, and forest growth on a Minnesota outwash landscape. *Biogeochemistry* 27:171-185.
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6. Inouye, R. S., T. D. Allison and N. C. Johnson. 1994. Old field succession on a Minnesota sand plain: effects of deer and other factors on invasion by trees. *Bulletin of the Torrey Botanical Club* 121(3):266-276.
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16. Davis, M. A., B. Ritchie, N. Graf and K. Gregg. 1995. An experimental study of the effects of shade, conspecific crowding, pocket gophers and surrounding vegetation on survivorship, growth and reproduction in *Penstemon grandiflorus*. *American Midland Naturalist* 134:237-243.
17. Faber-Langendoen, D. and M. A. Davis. 1995. Fire frequency and its effects on woody plant cover at Allison Savanna, East-Central Minnesota. *Natural Areas Journal* 15:319-328.
18. Inouye, R. S. and D. Tilman. 1995. Convergence and divergence of old-field vegetation after 11 yr of nitrogen addition. *Ecology* 76:1872-1887.
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106. Craine, J.M., D.A. Wedin and F.S. Chapin III. Comparison of diameter-specific root tissue density in four prairie species. *New Phytologist, in review.*
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108. Faber-Langendoen, D. and M. A. Davis. Fire management and its effect on plant community structure and composition at Allison savanna, east-central Minnesota. *In review*.
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122. Symstad, A.J. and D. Tilman. Removal experiment and recruitment limitations of ecosystem functioning. *In review*.
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**Book Chapters**

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## Section 1.C. Long-term Electronic Data Sets

Our long-term data sets cover all of the core LTER studies discussed in the following pages of this proposal, all data gathered in related mechanistic studies at Cedar Creek, as well as meteorological observations, ground water levels, information on archived samples, species lists, and other data. Each of these data sets is electronic. As discussed in Section 4 of this proposal (Data Management) each of these data sets includes extensive metadata as well. All LTER data, no matter how they might be collected, are stored and used in electronic form on our central LTER data base (housed on the U of Minnesota's Twin City campus) and in an identical copy that we maintain, via nightly backup, on our Sun Ultra 450 at Cedar Creek Natural History Area. This data base is huge, having been gathered by the collective efforts, during the past 6 years alone, of 11 faculty researchers, 13 post-doctoral researchers, and 13 graduate student researchers (counting only those in each group whose work has led to a peer-reviewed publication during the past 6 years), and with the assistance of about 4 technicians and 30 undergraduate field assistants each summer. In electronic form these data occupy 4,138 data and meta-data files containing 159.6 Mbytes and 2,061,316 lines of columnar data.

**Data Sets Available on the WWW:** The metadata on all the core long-term LTER studies and on most related studies are available at our WWW site, [www.lter.umn.edu](http://www.lter.umn.edu). In addition, we have worked to make core data directly accessible to others without the use of proprietary software or need of assistance from the Data Manager. To do this, we have distilled the majority of these data sets, especially those from our core LTER studies, down to sizes that are reliably handled by those who are not data managers. By doing this, we decrease the number of times that a non-LTER scientist might have to call upon our Data manager or a PI to gain access to data sets of interest to them. These distilled data sets also are proving useful to Cedar Creek researchers. These data sets, listed below, are available on the WWW at [www.lter.umn.edu/data](http://www.lter.umn.edu/data).

- **Weather.** Historical regional weather data for Fort Snelling, MSP, MN, 1837-1981, the oldest weather record for the state; Cedar, MN (NOAA weather station), 1982-1999; daily precipitation and temperature. Cedar Creek meteorological station, 1988-2000; hourly precipitation, temperature, radiation, wind, and other measurements.
- **Rainfall chemistry.** National Atmospheric Deposition Program (NADP) and Minnesota Pollution Control Agency (MPCA), 1996-1999. Includes precipitation acidity and conductivity. (Data also available at <http://nadp.sws.uiuc.edu>, Site MN01.)
- **Ground water levels.** in 83 Cedar Creek monitoring wells, 1988-1999.
- **Photographic Insects of Cedar Creek,** by John Haarstad, illustrating photographically and/or listing the over 4000 species of insects collected on site and archived in the Cedar Creek entomological collections; data on emergence, life history, abundance, and so forth are also available at ([www.lter.umn.edu/insects](http://www.lter.umn.edu/insects), 1500 web pages, 1500 images).
- **Photographic Herbarium** has photographs and scanned images of the more abundant plant species of Cedar Creek as an aid in plant identification ([www.lter.umn.edu/herbarium](http://www.lter.umn.edu/herbarium), 150 web pages, 400 images, under development).

- **Flora** of Cedar Creek, by John Moore ([www.lter.umn.edu/flora](http://www.lter.umn.edu/flora), 100 web pages, 300 images).
- **Birds** of Cedar Creek, by James Horowitz and David Bosanko ([www.lter.umn.edu/birds](http://www.lter.umn.edu/birds), 80 web pages).
- **Arthropod size and diversity (E122)**: Arthropod samples, each identified to species and enumerated, collected at 7 to 9 times during the 1992 growing season in each of 48 successional fields or savanna; and body sizes (length, width, depth) of each of the 1100 insect species, as well as abundances across all fields and sampling dates.
- **Effects of nitrogen supply on ecosystem dynamics (E001)**: Biomass by species (treatment means) 1982-1999. Plant biomass and light penetration (treatment means), species richness and its derivatives, 1982-1999.
- **Effects of fire frequency on old field vegetation (E012)**: Biomass by species (treatment means), 1983, 1987, 1991. Plant biomass and light penetration (treatment means), species richness and its derivatives, 1983, 1987, 1991.
- **Successional dynamics in a resampled chronosequence (E014)**: Percent cover by species (field means), 1983, 1989, 1994, 1997, and associated total soil N and C.
- **Productivity in an old-field chronosequence (E054)**: Biomass by species (field means), 1988-1999.
- **Species and functional diversity (E120, Biodiversity-II)**: Percent cover by species (treatment means), 1996-1999. Aboveground biomass, root biomass, total percent plant cover, soil nutrients, light penetration (treatment means), species richness and its derivatives, 1996-1999.
- **Biodiversity, productivity, and nutrient dynamics (E123, Biodiversity-I)**: Percent cover by species (treatment means), 1995-1999. Aboveground biomass, root biomass, total percent plant cover, soil nutrients, light penetration (treatment means), species richness and its derivatives, 1995-1999.
- **Archived samples**. Records of over 30,000 soil, plant tissue, and litter samples archived for access by researchers of the future. Archived samples are stored in archival-quality containers labeled and curated in a room dedicated solely to this task, much as is a library.

All of the above data are directly available without delay to any researcher using the web who registers through a code-of-ethics page ([www.lter.umn.edu/data/register.html](http://www.lter.umn.edu/data/register.html)). In addition, other data may be obtained with the assistance of the Data Manager or a PI after such registration.

**Non-LTER Users of Cedar Creek Data:** The documented uses, to date, of our electronic data by investigators not directly associated with the Cedar Creek LTER program include:

- **Nitrogen addition, primary productivity, and diversity data** (E001, 1982-1996), used at the NCEAS productivity workshop, Santa Barbara, September 10-20, 1996, for studies on the relationship of productivity and diversity, and published in  
Gough, Osenberg, Gross, and Collins. 2000. *Oikos*, in press.  
Gross, Willig, Gough, Inouye, and Cox. 2000. *Oikos*, in press.
- **Biodiversity data** (E120, 1996-1998), including data on abundances of individual species and total community biomass for the Biodiversity II experiment, used by G. Burt-Smith and J. P. Grime, Sheffield, UK. for a study of plant diversity and ecosystem functioning; manuscript in prep.
- **Primary productivity data** (E001, 1983-1998), and **meteorological data** (E080, 1983-1998), currently are being used by Alan Knapp and Melinda Smith of Kansas State University for a cross-site comparative study of the relationship between productivity and precipitation/climate.
- **Plant biomass data** from a full-factorial N addition by disturbance experiment (E052, 1991), used by Nancy Johnson of Northern Arizona University for a study of mycorrhizal fungal community structure and dynamics in relation to plant community composition and diversity.
- **Flora of Cedar Creek** in Field D, including relative abundance patterns, used by Jane Bock of the University of Colorado for a cross-site study of biodiversity patterns.
- **Meteorological data**, used by David Greenland of the University of North Carolina at Chapel Hill for comparative studies of climate and ecosystem responses.
- **Complete Cedar Creek plant and arthropod species lists**, used by Bob Waide of the LTER central office for work on biodiversity patterns.



## Section 2. Biodiversity, Disturbance and Ecosystem Functioning at the Prairie-Forest Border

### A. Conceptual Framework

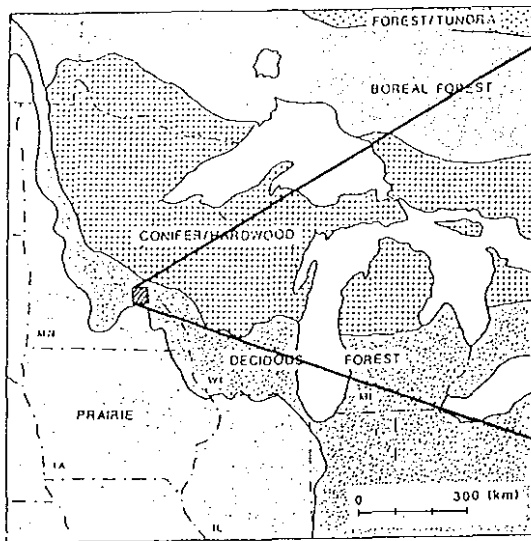
**Research Philosophy:** Since its inception in 1982, the overarching philosophy of the Cedar Creek LTER has been, and remains, the synthesis and integration of the principles and processes of population, community and ecosystem ecology. In our original (1981) LTER proposal we said:

*Population and community ecology can be greatly strengthened by consideration of the long-term effects, the indirect effects and the feedback effects that the ecosystem approach emphasizes. Similarly, ecosystem ecology can be strengthened by detailed studies of the dynamics of interactions among individual species that play such a key role in the processes of productivity, energy flow and nutrient cycling. We believe this synthesis will only be possible when long-term experimental research combines population, community and ecosystem perspectives.*

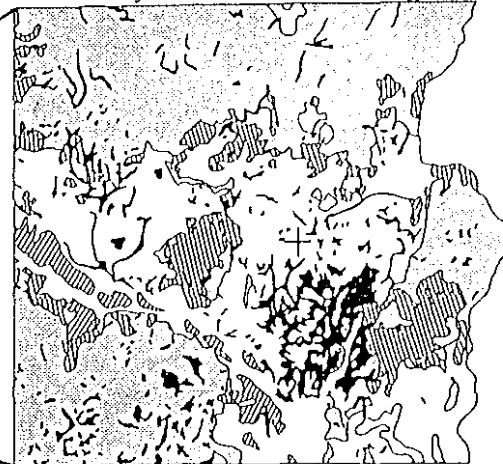
This philosophy has led us to simultaneously collect, from the same observational and experimental sites, long-term, detailed information on the abundances, dynamics and diversity of species on several trophic levels, on the controls of the pool sizes and dynamics of such ecosystem traits as soil C and N, on above and below ground primary productivity, on N mineralization, and on disturbance regimes. It has led us to seek ways to scale up from ecophysiology and interspecific interactions to their effects on ecosystem stability, productivity, nutrient dynamics, and susceptibility to invasion. It has led to long-term experiments that explore the impacts on species abundances, diversity, and ecosystem functioning of the major driving variables at Cedar Creek: soil N, trophic structure, fire frequency, and human land use. The results of these on-going experiments have, themselves, led to new long-term experiments that explore the effects of species composition and biodiversity on ecosystem functioning, and the joint effects of biodiversity, elevated CO<sub>2</sub>, and N deposition on population, community and ecosystem processes. In all this work, we seek to identify potentially generalizable ecological principles through the synthesis of population, community and ecosystem processes, patterns, and mechanisms.

**Context:** All work is performed within the context of our 22 km<sup>2</sup> site, Cedar Creek Natural History Area. Cedar Creek is unique among the LTER sites because of its location on the climatically, edaphically, and disturbance controlled boundary between North America's prairie and forest (Fig. 8). As Curtis (1959) suggested, the oak savanna vegetation that characterizes this "tension zone" between forest and prairie is highly sensitive to climatic variation (Tilman and El Haddi 1992, Faber-Langendoen and Tester 1993, Tilman and Downing 1994, Tilman 1996, 1999). It is also strongly impacted by edaphic factors, especially soil N 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, Peterson and Reich 2000a, Reich et al. 2000) and by herbivores and predators (Inouye et al. 1987a, 1987b, Huntly and Inouye 1984, 1987, 1988, Ritchie and Tilman 1992, 1993, Ritchie et al. 1998, Ritchie 2000). Cedar Creek contains large tracts of native oak savanna, of prairie and successional grasslands, and of oak forest, and smaller stands of basswood-sugar maple, white pine, jack pine, and red pine. This diverse mosaic of upland ecosystems has been shaped by the soil parent materials, by a variety of

A. The Prairie-Forest Boundary



B. Ecosystems of CCNHA Region



- 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)

Figure 8. 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.

landscape features that influenced fire frequency, by the pattern and history of physical disturbances, and by European settlement and agriculture. These upland ecosystems also are species rich. A m<sup>2</sup> of savanna contains 10-40 plant species, and a hectare about 200 plant species. Over 1200 insect species, including 577 species of herbivores, 226 species of predators, 281 species of parasites, and 141 species of detritivores, were found in a quantitative survey of successional grasslands and savanna (Siemann et al. 1996, 1999a). About 4000 insect species are in our on-site collection, which, like our herbarium, is accessible at [www.lter.umn.edu](http://www.lter.umn.edu). The species-rich successional grasslands and savannas of Cedar Creek are the focus of the LTER program. Our research explores the various physical factors (climate and its variation, soil N, fire, and various disturbances), species interactions, and feedback effects that have shaped various aspects of these ecosystems, including their species diversity, species composition, productivity, nutrient dynamics and stability.

**Research Themes:** The Cedar Creek LTER has evolved since its founding to address both elaborations on its initial themes and new themes inspired by our results and their relevance to the work of others. We were initially interested in the causes of high plant and insect diversity, in the controls of community assembly, and in processes controlling the responses of species and ecosystems to disturbances. These interests were linked by our search for underlying mechanisms, and by the hypothesis that similar mechanisms would be involved in all three. After all, successional dynamics are the dynamics of community assembly after disturbance, and diversity is one component of the type of ecosystem created by the assembly process. Our long-term studies continue to address succession and community assembly, the controls of diversity, and the impacts of disturbances on population, community and ecosystem traits, processes and dynamics. Our studies of succession continue to give us insights into community assembly. The process of community assembly is of interest in its own right and is directly relevant to an emerging area of interest for many Cedar Creek researchers and collaborators – the processes controlling abundances of exotic or invasive species. Moreover, such questions are deeply intertwined with the mechanisms of multi-species coexistence because species persistently coexist only if each species can invade communities from which it is absent.

As our understanding of the ecosystems of Cedar Creek has grown, we have broadened our perspectives and used long-term studies to address a variety of additional questions. One of these – the consequences of the loss of biodiversity for ecosystem functioning – has grown into a major theme. We proposed two long-term experiments on the ecosystem effects of biodiversity and functional group composition in our 1994 LTER renewal, and have since started (mainly with funds from another grant) a third experiment that explores the joint and interactive effects of biodiversity, N deposition, and elevated atmospheric CO<sub>2</sub>. Moreover, our ongoing work is raising many new questions about the consequences of N deposition, elevated atmospheric CO<sub>2</sub>, changes in fire frequency, agricultural land use and abandonment, loss of biodiversity, and changes in trophic structure. These disturbances are human-caused. As such, our initial and continuing interest in and focus on disturbance and diversity, combined with the expanding global impacts of human society, have resulted in an increasing focus on the effects of human ecosystem domination (e.g., Vitousek 1994, Vitousek et al. 1997). In total, we now have four major questions, and a host of subsidiary issues, that provide the interdependent themes for Cedar Creek research:

**Theme 1:** *What are the impacts of major perturbations -- especially climatic variation, N deposition, land use history, changes in fire frequency, elevated CO<sub>2</sub>, exotic species, and changes in trophic structure -- on species composition, diversity and ecosystem functioning?*

**Theme 2:** *What processes, interactions and positive and negative feedbacks control species abundances, community assembly, and community composition, diversity and dynamics in Cedar Creek grasslands and savanna?*

**Theme 3:** *How do composition and biodiversity directly and indirectly impact ecosystem functioning?*

**Theme 4:** *What general principles allow integration across scales ranging from ecophysiological and population processes to ecosystem functioning; from single trophic levels to whole foodwebs; from single plots to landscapes; and from snapshots in time to long time series?*

We are pursuing these four themes in five inter-related types of long-term studies that form the heart of the Cedar Creek LTER. Each is guided by our research philosophy and each addresses several themes. LTER funding supports this core long-term work and the research infrastructure of Cedar Creek (computer network, analytical chemistry laboratory, herbarium and insect collections, data management and software development, and shared research equipment). Additional grants allow deeper pursuit of questions. For instance, L. Kinkle and colleagues are working on soil microbial dynamics in the long-term N addition experiments using their NSF 'Microbial Observatory' grant. A DOE-funded grant is allowing us to expand work on the effects of biodiversity to include an experiment in which we factorially vary N deposition, CO<sub>2</sub>, and biodiversity. A grant from the Andrew Mellon Foundation is supporting parallel work on community assembly and invasibility both at Cedar Creek and, in collaboration with Jim Reichman, in the oak savannas of U. C. Santa Barbara's Sedgwick Ranch. Nancy Johnson of Northern Arizona University has an NSF grant to work on the interactions of plant diversity and mycorrhizal fungi at Cedar Creek. The British NERC is supporting work by J. P. Grime and Graham Burt-Smith to test the ability of Grime's theory to predict the observed effects of plant diversity on productivity. Indeed, there are currently 17 grants from diverse funding sources supporting work related to LTER by 25 researchers, many of whom are not directly supported by LTER. Thus, by establishing, maintaining, and collecting core data in long-term studies, the LTER provides a data-rich environment that attracts additional researchers. Just as greater plant diversity increases primary productivity, so may the greater intellectual diversity that results from having many others work at Cedar Creek lead to greater scientific creativity and productivity.

Our five types of long-term studies, which are described in detail below, are: (1) experimental manipulations of plant diversity; (2) N addition experiments; (3) fire frequency experiments; (4) experimental manipulations of herbivore and predator trophic levels; and (5) long-term observations of soils, plants, insects and mammals in a successional chronosequence and savanna (Table 1). Each of these five types of studies is designed to give insights into two or more of our four themes. For instance, the diversity experiments directly illustrate the ecosystem consequences of plant diversity (Theme 3), and also address both Theme 1 via long-term observations of the effects of climatic variation on species composition, diversity and ecosystem functioning, and Theme 2 through the observed process of species coexistence and community assembly (reflected in how the abundance of each plant species depends on the identities and diversity of the other species planted in the same plot). The N addition experiments and the burning experiments are directly relevant to Theme 1 because N deposition and fire suppression

are perturbations and their long-term data allow determination of the effects of climatic variation. Moreover, they also are directly relevant to Theme 2 because N is the major limiting resource of Cedar Creek and its availability influences plant, herbivore and predator composition and diversity, just as does fire frequency. Moreover, by influencing diversity, N addition also gives insights into the effects of diversity on ecosystem functioning. The experimental manipulations of higher trophic levels demonstrate direct effects of these on plant community composition, diversity and dynamics (Theme 2), and indirect effects mediated through their impacts on ecosystem processes. Finally, our long-term observations describe successional and community assembly patterns and processes that are directly relevant to Themes 1 and 2. Because sites within and among fields differ in diversity and composition, they give insights into Theme 3. They also provide data on our broadest spatial and temporal scales, and thus provide opportunities to test alternative ways to scale up from the smaller plots, shorter time scales, and underlying mechanisms to larger temporal and spatial patterns (Theme 4). In total, our overarching philosophy of synthesis of population, community and ecosystem perspectives guides our work in these five types of long-term studies, as do our four unifying themes. In the following sections we describe in more depth these five types of long-term studies.

## **Section 2.B. The Five Core Sets of Long-Term Studies at Cedar Creek**

The five sets of studies summarized below represent the core long-term projects of the Cedar Creek LTER. Although each set is discussed separately, all are interrelated components of our approach to addressing our four themes (Table 1). Each set has generated short-term mechanistic studies and theory that seeks to generalize the work and synthesize it with our other projects and with the literature. We summarize these related projects and theory, and our proposed research, in each section below. In a later section we propose additional long-term projects.

### *Set 1. Effects of Biodiversity*

**A. Introduction.** The pioneering work of Elton (1958), May (1972), McNaughton (1978), Pimm (1979, 1984) and others on the diversity-stability hypothesis, the ideas raised in Schulze and Mooney (1993), and the coincidence of a major drought with our collection of long-term data led us to explore the diversity-stability hypothesis (Tilman and Downing 1994, Tilman 1996a, 1999a). This led to two experiments exploring the effects of plant diversity on productivity and N dynamics (Fig. 9; Tilman et al. 1996b, Tilman et al. 1997a), on plant invasion (Fig. 10), on insect diversity (Fig. 11) and on plant diseases (Fig. 12) (Knops et al. 1999, Siemann et al. 1998, Haddad et al. , in review). We also explored conceptual and theoretical bases for the effects of diversity and composition on population and ecosystem stability (Tilman et al. 1998; Tilman 1999a; Lehman and Tilman, in review) and on productivity or standing crop and limiting resources (Tilman et al. 1997b). Our work is motivated both by an interest in how diversity, composition, and other factors influence ecosystem processes and by the potential relevance of such work to human-caused ecosystem simplification. Our work is contributing to a growing literature on the effects of diversity and composition (e.g., Frank and McNaughton 1991, Ewel et al 1991, McNaughton 1993, Vitousek and Hooper 1993, Naeem et al. 1994, 1996, Hooper and Vitousek 1997, McGrady-Steed et al. 1997, Naeem and Li 1997, Loreau 1998a, 1998b, Doak et al. 1998, Lawton et al. 1998, Symstad et al. 1998, Ives et al. 1999, Hector et al.

## The Core Long-Term Studies of the Cedar Creek LTER

### 1. Biodiversity Experiments

1. **E123** – Biodiversity I; 147 plots, each 3 m x 3 m; the number of planted species is the experimental variable; started 1994
2. **E120** – Biodiversity II; 245 plots, each 9 m x 9 m; species diversity, functional group composition, and functional group diversity are the experimental variables; started 1994
3. **E141** – BioCON, a Free Air Carbon dioxide Enrichment (FACE) experiment in CO<sub>2</sub>, N deposition, and plant diversity are varied

### 2. Nitrogen Addition Experiments

1. **E001** – N addition at one of 8 rates to 207 plots in 3 successional fields and in native savanna; started in 1982
2. **E002** – A similar experiment, but on initially disturbed (disked) soil, now converted to study effects of cessation of N addition or of interactions between N addition and fire; started in 1982
3. **E095** – N addition in oak savanna; 3 replicates each of control and 2 rates of N addition; 20 m x 50 m plots; started in 1983

### 3. Fire Frequency Experiments

1. **E012** – Grassland burning every 0, 1, 2, or 4 years; 8 m x 8 m plots, 6 replicates of each treatment; started in 1983
2. **E015 and E133** – Prescribed fire experiment imposed on large blocks of oak savanna/woodland beginning in 1965

### 4. Trophic Interactions

1. **E007** – Deer exclosures, 10 x 30 m each; begun in 1983; 3 exclosures and 3 controls per field, in 3 fields
2. **E061** – Bird predation and grasshopper and plant responses; 12 plots, each 9 m x 9 m; treatments are 0 or +N, birds or no birds
3. **E140** – Deer exclosures in savanna; 12 plots, each 30 x 30 m, 6 fenced; started in 1995

### 5. Successional Dynamics and Land Use History

1. **E014** – Chronosequence of 22 abandoned agricultural fields; 100 permanent sampling points per field; started in 1983
2. **E054** – Annual biomass dynamics in a 14 field subset of E014

Table 1

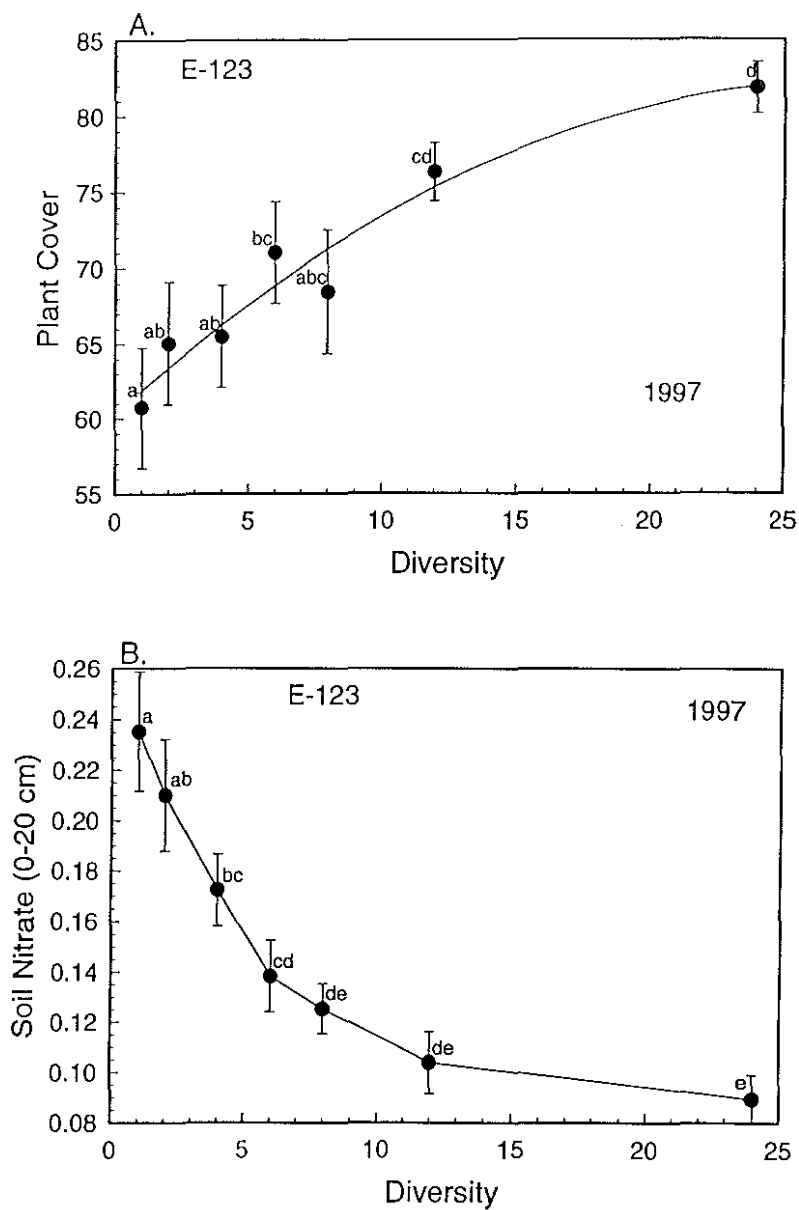


Figure 9. From Tilman (1999) *Ecology*.

(A) Total plant cover, a measure of total community plant biomass, for the Biodiversity I experiment (E123) at Cedar Creek. Results are for 1997, the fourth year of the experiment. Mean responses ( $\pm$  SE) are shown, as are results of contrasts. Means that differ significantly at the  $P < 0.05$  level do not share any lowercase letter. The curve shown is fitted through all of the data.

(B) The dependence of soil nitrate on diversity for this same experiment, shown similarly, for soil cores from a depth of 0-20 cm.

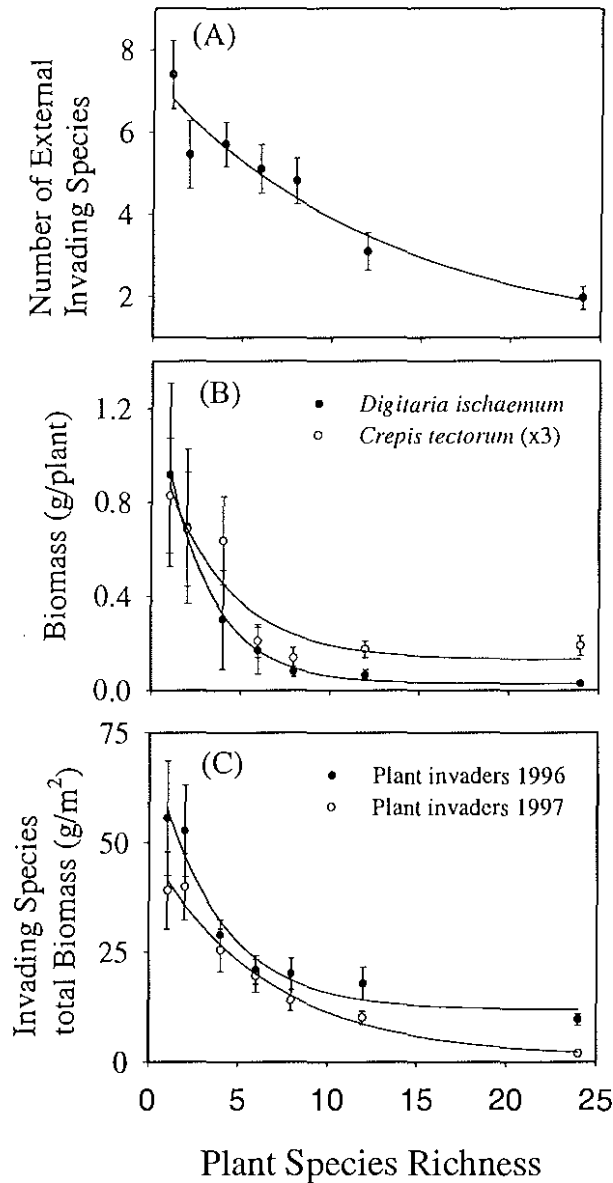


Figure 10. Plant invasions, from Knops et al. (1999) *Ecology Letters*, for Biodiversity I, E123.

(A) Number of invading plant species (invading external plant richness, excluding the 24 planted species) depends significantly on the experimentally controlled plant species richness of plots. Fitted curve is  $y = 1.92 + 5.94e^{-0.105X}$ ,  $F = 51.1$ ,  $R^2 = 0.283$ ,  $n = 147$ ,  $P < 0.001$ . All results plotted are means  $\pm$  SEM. Note that the biomass of the smaller *Crepis* plants is multiplied by three to provide a similar scale of that of *Digitaria* for purposes of illustration.

(B) *Digitaria ischaemum* and *Crepis tectorum* average aboveground plant size. Fitted curve for *Digitaria* is  $y = 0.095 + 0.786e^{-0.439X}$ ,  $F = 15.7$ ,  $R^2 = 0.094$ ,  $n = 137$ ,  $P < 0.001$ , sample size 18 - 22. and *Crepis* is  $y = -0.0136 + 0.193/(x^{0.5})$ ,  $F = 13.4$ ,  $R^2 = 0.112$ ,  $n = 109$ ,  $P < 0.001$ , sample size 12 - 20.

(C) Total invading plant biomass. Fitted curve for 1996 is  $y = 11.7 + 60.8e^{-0.271X}$ ,  $F = 41.0$ ,  $R^2 = 0.230$ ,  $P < 0.001$  and 1997 is  $y = 0.93 + 47.0e^{-0.150X}$ ,  $F = 52.5$ ,  $R^2 = 0.271$ ,  $n = 147$ ,  $P < 0.001$ , sample size 20-24.



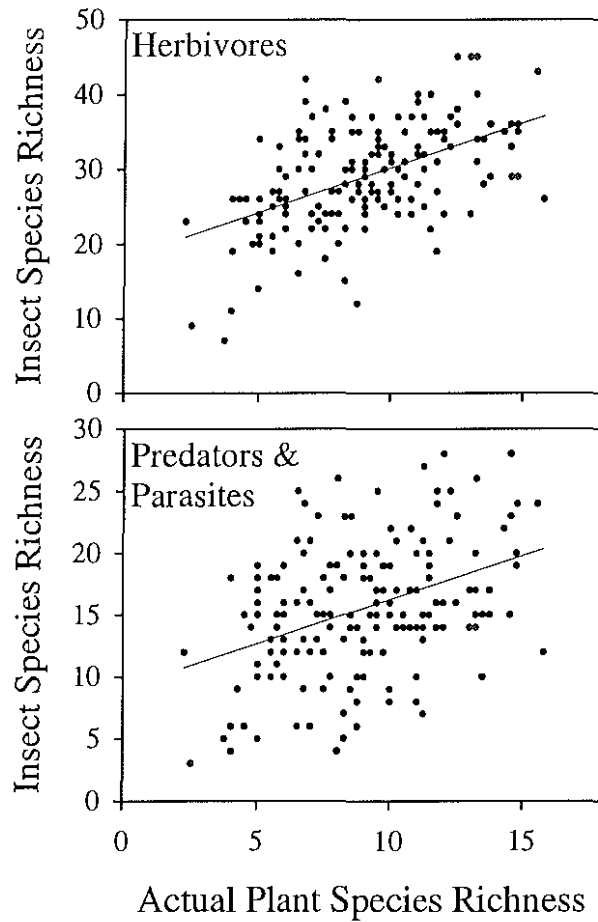


Figure 11. Herbivore and predator and parasite richness from Knops et al. (1999) *Ecology Letters*, for Biodiversity I, **E123**. Each point represents the total number of species collected in three samples in each experimental plot. Linear regressions are against actual plant species richness for (A) herbivore species richness ( $F = 57.7$ ;  $R^2 = 0.26$ ;  $P = 0.001$ ;  $n=163$ ;  $y = 1.20x + 18.28$ ). (B) predator and parasite species richness ( $F = 30.07$ ;  $R^2 = 0.16$ ;  $P = 0.001$ ;  $n=163$ ;  $y = 0.71x + 9.15$ ).

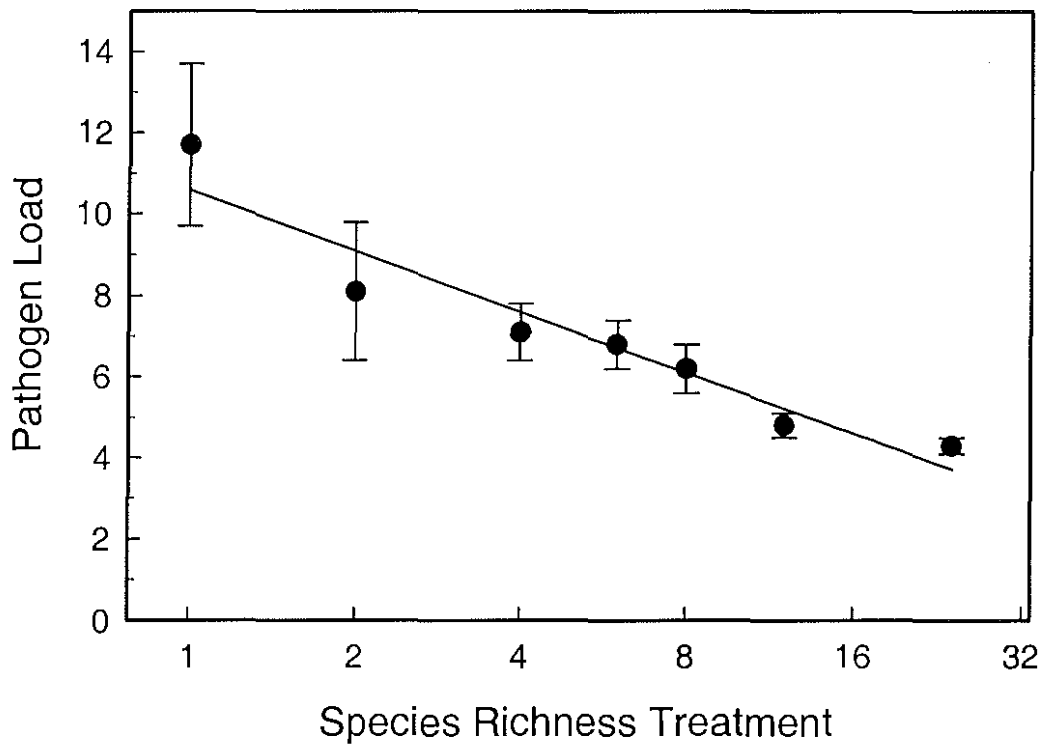


Figure 12. Effects of biodiversity on pathogen load across the entire plant community (24 diseases) in Biodiversity I, E123 in 1998. Pathogen load was calculated as the weighted average of the percent leaf area of each species covered by disease, weighted by the percent cover of each species. Data shown are means  $\pm$  SEM ( $R^2=0.181$ ;  $P<0.001$ ). (From C. Mitchell, in prep.)

1999). We are members of an NSF-supported team of Japanese, US, and UK scientists, led by Simon Levin, doing collaborative research on biodiversity and ecosystem functioning.

Recent research on biodiversity and ecosystem functioning has raised many questions, including disagreements about data interpretation and causes of observed results (e.g., Givnish 1994, Huston 1997, Aarssen 1997, Hodgson et al. 1998, Doak et al. 1998) and contradictions between experimental and observational studies (Wardle et al. 1997a, 1997b, Grime 1997). These critiques and alternative hypotheses have been met with various replies, but the best resolution to these debates may come from long-term field experiments in which diversity is directly controlled and detailed observations and related ecophysiological studies allow determination of underlying mechanisms. The Cedar Creek LTER began two such experiments, dubbed Biodiversity I and II, in 1994, and initiated a third, dubbed BioCON, in 1997.

## B. Description of Experiments and Methods

**Biodiversity I (E123;** <http://www.lter.umn.edu/research/exper/e123/e123.html>); Tilman, Wedin and Knops 1996; Fig. 13) manipulates species diversity independently of composition. It has 147 plots, each 3 x 3 m, separated by 1-2 m paths. Plots were randomly assigned to have 1, 2, 4, 6, or 8 species (n=20 replicates each), 12 species (n=23), or 24 species (n=24). The species added, as seed, to each plot were chosen by separate, random draws from a pool of 24 grassland species.

**Biodiversity II (E120;** <http://www.lter.umn.edu/research/exper/e120/e120.html>); Tilman et al. 1997a; Fig. 14) simultaneously manipulates species diversity, functional group diversity, and functional group composition. Its 245 plots, each 9 m x 9 m, were planted with 1, 2, 4, 8, or 16 species that were in either the C4 grass, C3 grass, legume, other forb, or woody functional groups. The composition and diversity of each plot was chosen randomly, but constrained to provide even coverage of all possible combinations of species and functional-group diversity.

**BioCON (E141;** <http://www.lter.umn.edu/research/exper/e141/e141.html>;) directly controls plant diversity (1, 4, 9 or 16 perennial species randomly chosen from a pool of 16 species, planted as seed in 1997), N availability treatments (ambient soil vs. ambient soil + 4 g m<sup>-2</sup> yr<sup>-1</sup> N), and atmospheric CO<sub>2</sub> concentrations (ambient vs 550 ppm, beginning in 1998) in a well-replicated split-plot experiment consisting of a full factorial combination of treatment levels in a completely randomized design. Its 296 individual plots, each 2 x 2 m, occur in six 20-m rings, three exposed to ambient CO<sub>2</sub> and three to elevated CO<sub>2</sub> using free-air CO<sub>2</sub> enrichment (Lewin et al 1994). BioCON is an integral part of the LTER but mainly is funded by DOE.

*Sampling methods for these experiments:* Plant abundances are estimated via total plant cover (identified to species). The proportion of incident light intercepted by vegetation is measured. Biomass is measured once or twice per year by clipping, sorting, drying, and weighing vegetation in a 0.1 x 1.0 m strip per plot in Biodiversity I and BioCON, or four 0.1 m x 3.0 m strips per plot in Biodiversity II. Root mass is from three 5 cm diameter by 40 cm deep soil cores per clip strip, gently rinsed on a fine screen, dried and weighed. Soils are sampled for 0.01 M KCl extractable NO<sub>3</sub> and NH<sub>4</sub> and for total soil N using four 2.5 cm diameter by 20 cm deep soil cores per plot. Soil NO<sub>3</sub> and NH<sub>4</sub> at 40-60 cm depth are sampled to estimate leaching losses.

## C. Key Results

◆ Plant total cover and standing crop (correlates of productivity) were significantly increasing functions, and levels of unconsumed soil nitrate both in the rooting zone and below the rooting zone, were significantly decreasing functions of plant species diversity in both Biodiversity I (Fig. 9, 15A; Tilman et al. 1996a; Tilman 1999a) and Biodiversity II (Fig. 15B; Tilman et al.

Boug 1 Schs 4	24 s 1 4 2	Andg 1 Anec 4	12 s 1 4 4	24 s 1 4 5	12 s 1 4 6	8 s 1 4 7
Bucd 1 Anec 4 Soln 0 Aste 0	24 s 1 3 0	12 s 1 3 8	8 s 1 3 7	Koec 1 Andg 3 Sorn 6	6 s 1 3 5	Sorn 1 Asta 3 Eupc 4 Liaa 4
Anec 1 Asta 2 Soln 7 Lesc 7	Andg 1 2 8	24 s 1 2 0	Ascl 1 3 0	24 s 1 3 1	12 s 1 3 2	12 s 1 3 3
6 s 1 2 0	Lesc 1 Petp 2 5	24 s 1 2 4	8 s 1 2 3	8 s 1 2 2	Spoc 1 Schs 2 Sorn 1 Corp 1	12 s 1 2 0
Ascl 1 Vicv 3	Bucd 1 4 4	8 s 1 5 5	8 s 1 6 6	24 s 1 7 7	12 s 1 8 8	12 s 1 9 0
Spoc 1 Sorn 1 Asta 2 Eupc 2	24 s 1 1 1	12 s 1 1 0	Koec 1 Astm 1 Lesc 9 Petp 9	8 s 1 0 8	24 s 1 0 7	6 s 1 0 0
6 s 0 0 0	8 s 1 0 0	24 s 1 0 1	6 s 1 0 2	Sorn 1 0 3	8 s 1 0 4	6 s 1 0 5
6 s 0 8 8	Agrs 9 Astm 7	12 s 0 6 6	12 s 0 5 5	24 s 0 4 4	12 s 0 3 3	Elyc 9 Poap 9
24 s 8 5 5	Sorn 8 Vicv 6	Schs 8 7 7	24 s 8 8 8	Panv 8 Sorn 8 Rudh 9	Spoc 0 0 0	Sorn 0 Rudh 1 Aste 1 Vicv 1
24 s 8 4 4	Agrs 8 Eupc 3	6 s 8 2 2	Koec 8 Lesc 1	6 s 8 0 0	Petp 7 9 9	6 s 7 8 8
Sorn 7 Asta 1	8 s 7 2 2	Koec 7 Sorn 3 Astm 3	12 s 7 4 4	24 s 7 5 5	Panv 7 0 0	8 s 7 7 7
6 s 7 0 0	6 s 6 9 9	12 s 6 8 8	Sorn 6 Rudh 7	Koec 6 Eupc 6	Bucd 6 Panv 6 Liaa 5 Aste 5	12 s 6 4 4
12 s 5 7 7	Koec 5 Spoc 5 Bucd 8 Petp 7	Anec 5 0 0	6 s 5 0 0	6 s 5 1 1	12 s 5 2 2	24 s 5 3 3
8 s 5 6 6	Schs 5 5 5	Elyc 5 Spoc 5 Anec 4 Vicv 4	Koec 5 Sorn 5	6 s 5 2 2	8 s 5 1 1	8 s 5 0 0
Eupc 4 3 3	12 s 4 4 4	8 s 4 5 5	12 s 4 0 0	24 s 4 7 7	8 s 4 8 8	Andg 4 9 9
Koec 4 Boug 4 Liaa 2 Aste 2	24 s 4 1 1	8 s 4 0 0	Eupc 4 9 9	Elyc 4 Spoc 3 Anec 8 Asta 0	Schs 3 7 7	Astm 3 6 6
6 s 2 9 9	Koec 3 Rudh 3 Petp 0 Vicv 0	8 s 3 1 1	6 s 3 2 2	Elyc 3 Andg 3 Sorn 3 Corp 3	24 s 3 4 4	Panv 3 Corp 3 Aste 3 Lesc 3
24 s 2 8 8	Bucd 2 Soln 7	12 s 2 6 6	Koec 2 Aste 5	6 s 2 4 4	8 s 2 3 3	6 s 2 2 2
24 s 1 3 3	12 s 1 6 6	24 s 1 7 7	Koec 1 Sorn 1 Liaa 8 Vicv 8	24 s 1 9 9	Spoc 2 Asta 0	Astm 2 1 1
Elyc 1 Schs 1 Asta 5 Lesc 5	12 s 1 4 4	Bucd 1 Asta 2	Asta 1 1 1	Panv 1 0 0	6 s 0 9 9	Spoc 8 Panv 8 Sorn 8 Vicv 8
12 s 1 1 1	8 s 2 2 2	Boug 3 Astm 3	Anec 4 4 4	Andg 5 Vicv 5	Lesc 6 6 6	24 s 7 7 7

### EXPERIMENT 123—BIODIVERSITY I

Started 1994

#### Cedar Creek Natural History Area

This experiment was designed to determine the effects of plant species diversity on primary productivity, on soil carbon and nitrogen dynamics, on nitrogen leaching rates, on ecosystem invasibility, and on the stability of productivity and species abundances in response to climatic and biotic perturbations. Individual plots contain either 1, 2, 4, 6, 8, 12, or 24 randomly selected species drawn from five functional groups of common prairie-savannah plants. Each plot represents a separate random and independent draw of a certain number of species from the species pool. Treatments are maintained by periodic manual weeding.

Abbr.	Species	Group
Astm	<i>Achillea millefolium</i>	Forb
Agrs	<i>Agropyron smithii</i>	C <sub>3</sub> grass
Andg	<i>Andropogon gerardi</i>	C <sub>4</sub> grass
Anec	<i>Anemone cylindrica</i>	Forb
Ascl	<i>Asclepias tuberosa</i>	Forb
Asta	<i>Aster azureus</i>	Forb
Aste	<i>Astragalus canadensis</i>	Legume
Boug	<i>Bouteloua gracilis</i>	C <sub>4</sub> grass
Bucd	<i>Buchloe dactyloides</i>	C <sub>4</sub> grass
Corp	<i>Coreopsis palmata</i>	Forb
Elyc	<i>Elymus canadensis</i>	C <sub>3</sub> grass
Eupc	<i>Euphorbia corollata</i>	Forb
Koec	<i>Koeleria cristata</i>	C <sub>3</sub> grass
Lesc	<i>Lespedeza capitata</i>	Legume
Liaa	<i>Liatris aspera</i>	Forb
Panv	<i>Panicum virgatum</i>	C <sub>4</sub> grass
Petp	<i>Petalostemum purpureum</i>	Legume
Poap	<i>Poa pratensis</i>	C <sub>3</sub> grass
Rudh	<i>Rudbeckia hirta</i>	Forb
Schs	<i>Schizachyrium scoparium</i>	C <sub>4</sub> grass
Soln	<i>Solidago nemoralis</i>	Forb
Sorn	<i>Sorghastrum nutans</i>	C <sub>4</sub> grass
Spoc	<i>Sporobolus cryptandrus</i>	C <sub>3</sub> grass
Vicv	<i>Vicia villosa</i>	Legume

Figure 13.

## Biodiversity II - E120

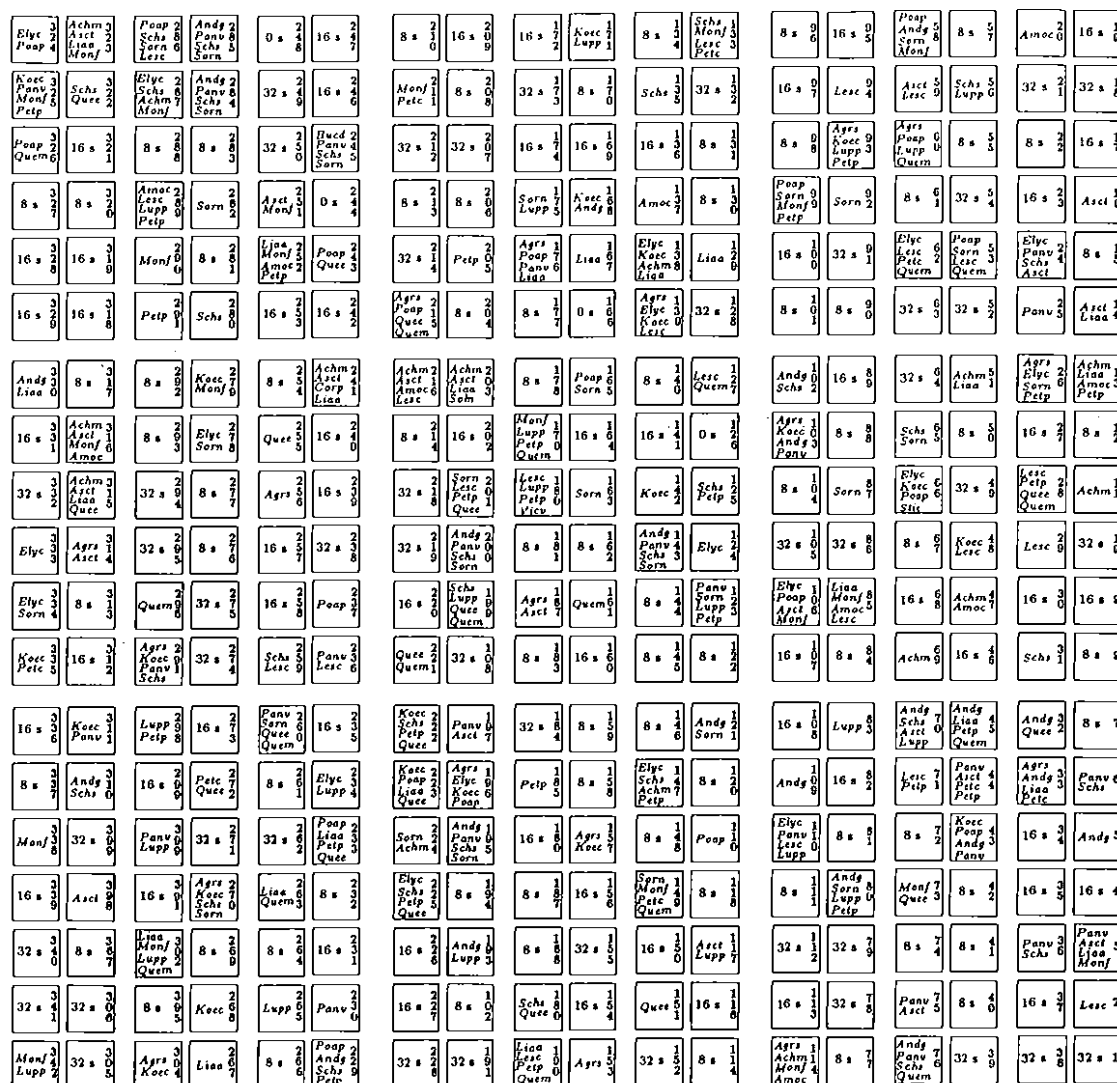


Figure 14. Biodiversity II (E120) is contained within a block of 342 plots adjacent to Biodiversity I. The central 9 m x 9 m of each plot is actively maintained by weeding and used for sampling. Plots were planted with grassland perennial herbaceous and savanna woody species in either the C4 grass, C3 grass, legume, other forb, or woody functional groups. Composition was chosen randomly subject to the constraint of having full coverage of possible combinations of species diversity, functional group diversity and functional group composition. First the species composition of 163 plots was determined by separate random draws of the appropriate number of species (1, 2, 4, 8, or 16 plant species) from a pool of 19 species. Then 82 additional plots were chosen to create all possible randomly-chosen combinations of having 1, 2, 4, or 8 species per plot with having 1, 2, 3, 4 or 5 functional groups per plot, with at least 11 replicates for each combination. These 245 are used to evaluate the effects of species diversity, functional composition and functional diversity on ecosystem processes. Four additional plots are weeded to keep them free of vegetation.

1997a).

- ◆ Plant species diversity and plant functional group composition were approximately equally important determinants of plant community biomass and of levels of unconsumed soil nitrate.
- ◆ Our results in Biodiversity I and II provide tests of two alternative hypotheses for the effects of plant diversity on productivity and limiting nutrients: the sampling effect model (Huston 1997, Aarsen 1997, Tilman et al. 1997b) and the niche differentiation model (Swift and Anderson 1993, Naeem et al. 1994, 1995, Tilman et al. 1997b). As predicted by niche models but not by the sampling effect, results showed that (1) planted species coexisted but the sampling effect predicts displacement of all but one species; (2) many higher-diversity plots have greater standing crop than any plots of lower diversity (Fig. 15A, B); (3) species significantly were inhibited mainly by species in their own functional group, and either not impacted by or positively impacted by species of other functional groups.
- ◆ In Biodiversity I, greater plant diversity was associated with a significantly lower number and biomass of invading weedy species (Fig. 10; Knops et al. 1999). Multiple regressions suggested that effects of diversity on invading species came mainly from lower soil  $\text{NO}_3$  in higher-diversity plots. Other analyses showed neighborhood distances to competitors and sizes of competitors also influenced the success of invaders (Naeem et al. 2000b).
- ◆ The species diversity of the arthropod community of Biodiversity II increased as both plant species and functional diversity increased (Fig. 11; Siemann et al. 1998, Knops et al. 1999). The diversity of herbivorous arthropods depended both on plant diversity and on the diversity of predatory and parasitoid arthropods, suggesting the importance of multi-trophic-level effects. Haddad et al. (in review) found that the effects of plant diversity on arthropod diversity seemed to result from greater plant biomass at higher diversity and the resulting greater number of insects.
- ◆ In BioCON, species diversity, elevated  $\text{CO}_2$  and N deposition all had significant effects and interactions on composition and ecosystem functioning during the 1998 and 1999 growing seasons (Fig. 3 D, E; Reich et al, in prep.). Primary productivity and its response to added  $\text{CO}_2$  or N both increased with diversity, i.e., the community response was much greater than the average species response (Reich et al. in prep.). The stimulation of plant C stocks by elevated  $\text{CO}_2$  was four- to twenty-fold greater in 16-species plots than in monocultures. These data suggest that the reduction of diversity occurring globally may profoundly influence the ability of ecosystems to store C in response to increasing atmospheric  $\text{CO}_2$  and N deposition, and hence on the ability of ecosystems to be C sinks in the face of increasing atmospheric  $\text{CO}_2$  and N deposition.

**D. Mechanistic, Synthetic and Related Studies:** The biodiversity experiments are the focus of many related studies. G. Burt-Smith and P. Grime are growing the Biodiversity I species under controlled conditions in Sheffield, UK to determine which plant traits are best correlated with observed species abundances in Biodiversity I. Joe Craine, a Ph. D. student of F. S. Chapin, is studying the roles of root and leaf longevity, respiration rates, photosynthetic rates, and other traits on abundance patterns in the chronosequence, in Biodiversity I and II, and in BioCON. We are determining effects of plant diversity on the decomposer foodweb by measuring microbial densities (DAPI epifluorescent enumeration) (Porter and Feig 1980), sole source C use profiles (Ecolog plates, Biolog Corp.) (Garland and Mills 1994), and microbial biomass (Islam and Weil 1998a, 1998b) in Biodiversity I.

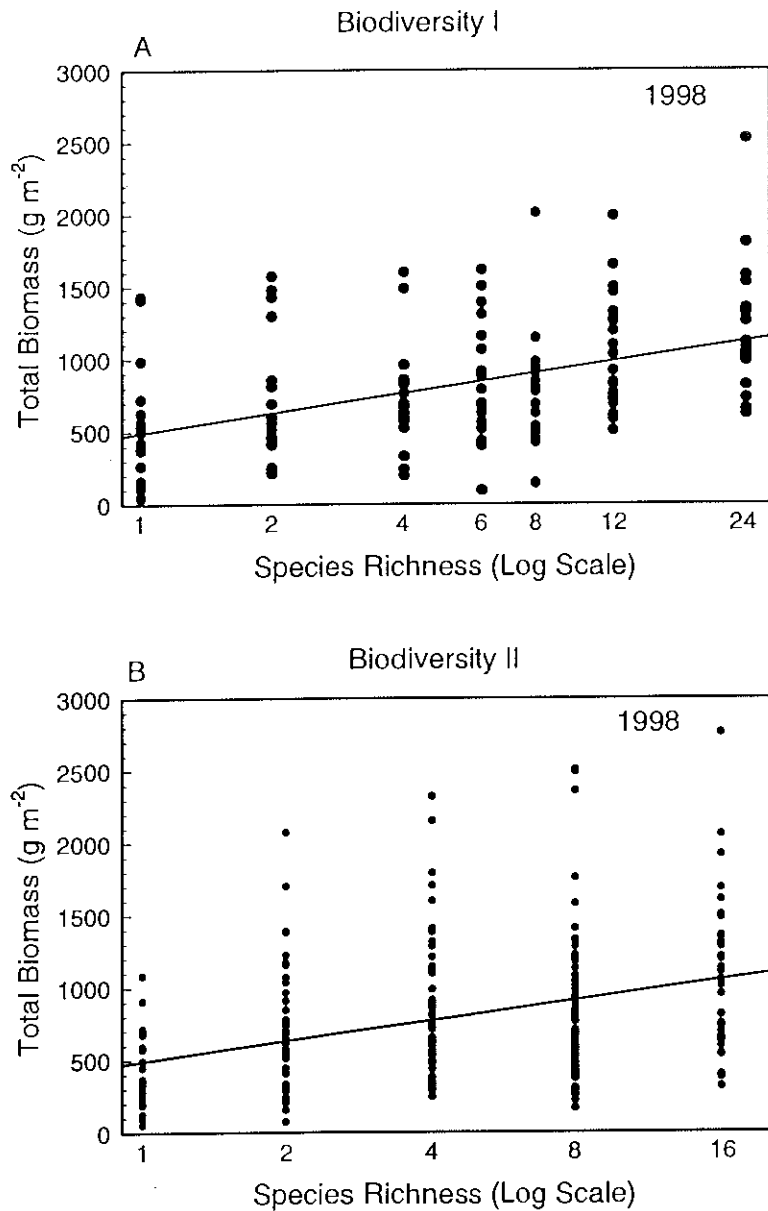


Figure 15.

(A) The dependence of total plant biomass (aboveground plus belowground plant biomass) on the number of planted species for Biodiversity I (E123) in 1998, the fifth year of the experiment. Each dot is the response of a single plot, with all 147 plots shown.

(B) Similar results, but for Biodiversity II (E120), with results for all 245 plots shown. For Biodiversity II, the *average* total biomass of the plots planted to 16 species is greater than the *single monoculture* with the greatest total biomass. Note, for both cases, that the upper bound is an increasing function of plant diversity, which refutes the sampling effect model but supports the predictions of niche differentiation models (from Tilman et al., in prep.).

**E. Future Research:** These are the best replicated and most long-term biodiversity experiments in existence. They already have yielded insights, but their greatest contributions are likely to come in the next 5 to 10 years because they are just attaining asymptotic biomasses and compositions. For the next 6 years we will continue gathering the variables listed above and the related mechanistic studies. In addition, we will pursue a series of related questions:

◆ *How does diversity influence population and ecosystem stability?* We explored this with the N addition experiment (Tilman and Downing 1994, Tilman 1996a), but it lacks direct control of diversity, necessitating control of confounding variables by multiple regression. However, measurement of year-to-year fluctuation in total biomass and species abundances in plots in all three biodiversity experiments will directly assess the effect of diversity and composition on stability. Given normal climatic variation, 6 added years of data will provide a strong test of the diversity-stability hypothesis.

◆ *Why does diversity influence productivity?* Current analyses support niche differentiation over sampling effects, but give no insight into the type of differentiation. We will work to determine the interspecific differences that cause diversity, thus addressing the mechanisms of coexistence.

◆ *How do plant diversity and composition impact the rest of the food chain?* We will continue annual arthropod sampling (counted, to species; begun in 1996) in Biodiversity II (Siemann et al. 1998) to see the effects of plant diversity and composition on arthropod abundances, food chain structure, and stability, and possible feedback effects of arthropods on plant dynamics

◆ *How do plant diversity and composition impact microbial diversity and composition and microbially-mediated processes?* Ecosystem processes are ultimately a function of microbial regulation of N, C and P cycles, but the significance of the extraordinary microbial diversity is poorly understood (Wall and Moore 1999). In Section 2. C. we describe how we will use the biodiversity experiments to explore the effects of plant diversity and composition on the diversity and composition of the soil microbial community.

◆ *How do plant diversity and composition influence the susceptibility of a community to invasion by exotic species?* Biological invasion is widespread, but the mechanisms controlling susceptibility to invasion are debated (Robinson et al. 1995, Levine et al. 1995, Planty-Tabacchi et al. 1996, Wisser et al. 1998, Levine and D'Antonio 1999, Stohlgren et al. 1999, Tilman 1999a). We propose a multi-investigator, multi-pronged approach to this question. Our team includes C. Brown, S. Naeem, M. Davis (in collaboration with P. Grime and K. Thompson), J. Knops, and D. Tilman. We will explore mechanisms of neighborhood interaction (Harper 1977, Pacala and Silander 1985, Goldberg 1987, Naeem et al. 2000b), the role of limiting resources (Tilman 1999a, Davis et al., in review), the effects of disturbance and climatic variation, and the relations between the traits of potential invaders versus established plants.

## ***Set 2. Dynamics Effects of N on Populations, Communities and Ecosystems***

**A. Introduction:** Because NPP at Cedar Creek is limited by N (Inouye et al. 1987a, Tilman 1990), we have focused much effort on determining the influence of N on species abundance, composition, and diversity; the feedback effects of such changes on ecosystem functioning; and the mechanisms that control these effects. These mechanisms are potentially generalizable because NPP is a strong correlate of species composition, diversity and functioning in many ecosystems (e.g., Whittaker 1975, Grime 1979, Huston 1979, Vitousek 1982, Vitousek et al. 1982, Tilman 1988, Tilman and Pacala 1993, Chesson, in press). In addition, human activities have doubled the natural terrestrial rate of formation of fixed N (Vitousek 1994; Vitousek et al. 1997). Currently, atmospheric deposition of N ranges from about 0.5 to 2.5 g m<sup>-2</sup> yr<sup>-1</sup> in the US,



and from 0.5 to 6.0 g m<sup>-2</sup> y<sup>-1</sup> in Europe (Mathews 1994, Galloway et al. 1995). The doubled global food demand projected for year 2050 (Cohen and Fedoroff 1999) and trends in N fertilizer use (Fig. 16) projected to 2050 suggest that N deposition will be about 3 times higher by 2050 than today (Tilman et al., in prep). Although our N addition experiments were not designed to explicitly determine the effects of N deposition, they give insights into how N deposition will alter species composition, richness, and N and C dynamics (Wedin and Tilman 1996).

## **B. Description of Experiments and Methods**

***N Addition to Undisturbed Vegetation:*** This experiment (**E001**) is replicated in three successional fields and in a savanna prairie opening. Treatments are a control, addition of all nutrients except N, and addition of all nutrients plus N, with N added at 1 of 7 rates (Tilman 1987, [www.lter.umn.edu](http://www.lter.umn.edu)). Plots are annually sampled for aboveground biomass (sorted to species), litter mass, and extractable soil NH<sub>4</sub> and NO<sub>3</sub>, and periodically for belowground biomass, insect abundances, mycorrhizal fungal species densities, light penetration, small mammal densities, and microbial biomass. This experiment has provided insights into causes of successional dynamics (e.g., Tilman 1987, 1988, 1990), effects of N deposition on C and N storage (Wedin and Tilman 1996), causes of diversity differences along productivity gradients (Tilman 1990, 1993, 1996a), impacts of diversity on ecosystem stability (Tilman and Downing 1994, Tilman 1996a, 1999a, Tilman et al. 1998, Lehman and Tilman, in review), impacts of climatic variation on biodiversity (Tilman and El Haddi 1992, Tilman 1996a), and long-term dynamics after a major drought (Haddad and Tilman, in prep)

A second N addition experiment in oak savanna (**E095**; fire frequency, 2 of 3 yrs), begun in 1983, has 9 plots (20 x 50 m) receiving N at 0, 5, or 17 g m<sup>-2</sup> yr<sup>-1</sup>. It complements **E001** by separating out responses to N of woody vs. herbaceous species, including the long-term consequences of alteration in plant composition and diversity. It complements **E133** (fire frequency in savanna, below) by providing a different savanna N cycling gradient (in this case N deposition rather than long-term fire effects on N cycling). This experiment received increased attention in the late 1990s when we began documenting effects of N deposition on N cycling, soil water, NPP, and species composition and diversity, both beneath oak trees and in grassy openings between trees (Wrage and Reich, unpublished data; Reich et al. unpublished data).

***N Addition to Disturbed Vegetation:*** This experiment, **E002**, is identical to **E001** except that plots were initially disturbed via disking. After undergoing rapid successional changes, **E001** and **E002** converged in composition, plant abundances, and diversity (Inouye and Tilman 1988, 1995). As of 1993 we use **E002** for two new experiments. In each, we randomly chose 3 of 6 replicates of each treatment for a new manipulation and continued treatments in the other 3 replicates. In one experiment the new treatment was cessation of nutrient addition, designed to determine dynamics of recovery of productivity, composition and diversity after long-term N addition. In the other, we began annual spring burning in 3 plots per treatment.

***Gradient in N Availability across a Successional Chronosequence:*** Both total soil N (Knops and Tilman 2000; Fig. 3C, 17) and N mineralization rates (Pastor et al. 1982, 1984) increase during succession at Cedar Creek, providing an additional opportunity to examine effects of N on plants, arthropod and small mammal herbivores, and arthropod predators, parasitoids, and decomposers (Inouye et al. 1994, 1997, Siemann et al. 1999a, Pitt 1999, Lawson et al. 2000). We are exploring these relations in long-term observations in a series of over 2000 permanent plots in a successional chronosequence discussed in Set 5, below.

### C. Key Results

◆ N addition impacts ecosystem C and N stores in **E001** via effects on species composition and thus on litter C:N (Wedin and Tilman 1996). At higher N addition, diversity is lower, C4 grasses are less abundant, and litter and root C:N ratios are lower (Fig 18A-D). The N-dependent shift to low C:N species corresponds with decreased ecosystem retention of added N (Fig. 19A) and to lower C storage (Fig. 19B), likely because of immobilization and decomposition effects (Fig. 19C).

◆ The resistance of total plant biomass to drought was significantly greater at higher diversity in **E001** plots, even after controlling for numerous potentially confounding variables (Fig. 2A; Tilman and Downing 1994). For all non-drought years, interannual variation in total plant biomass (measured as CV) was greater at lower diversity (Fig. 20; Tilman 1996a, 1999a). Both results support the diversity-stability hypothesis.

◆ Addition of  $1 \text{ g m}^{-2} \text{ yr}^{-1}$  of N for 18 yr, comparable to regional wet+dry deposition, caused the loss of 27% of plant diversity (Figs. 21A). Greater rates of N addition led to greater species losses (Fig. 21B). However, the N-dependent loss of species was non-linear (Fig. 21C) and has not yet reached an asymptote for low rates of N addition, suggesting that effects of N deposition on species richness cannot be extrapolated from short-term but high-dose experiments.

◆ Since the 1988 drought, total plant biomass in the unfertilized control plots of this experiment has oscillated with a 2-3 y period (Fig. 22A). These oscillations cannot be explained by variation in climate or densities of herbivores (Haddad et al, in review), but might be caused by effects of litter on either immobilization of N or on dynamics of fungal diseases that overwinter in litter. Similar oscillations in an burned field have biomass lows in unburned years (Fig. 22B), supporting the hypothesized role of litter as a cause of these oscillations.

◆ In oak savanna, rates of soil net N mineralization were higher beneath trees than in grassy openings at all levels of N addition, and rates increased similarly with N addition in both vegetation patch types (Wrage and Reich, unpublished data).

◆ In 1999, the seventh field season after cessation of N fertilization in **E002**, there was no significant recovery in plant diversity or composition, suggesting that N deposition can have long-lasting effects. This experiment should continue to determine the trajectory of recovery.

◆ By 1999, burn treatments in **E002** led to marked differences in composition, diversity, and standing crop, with *Andropogon gerardi* (big bluestem) becoming dominant in high-N, burned plots, but *Agropyron repens* (quack grass) in high-N, unburned plots. *Schizachyrium scoparium* (little bluestem) remains dominant in burned and unburned low N plots.

**D. Past, Ongoing, and Future Work on Theory and Mechanisms:** Ongoing mechanistic studies include work testing the ability of the dispersal mechanisms and nutrient ecophysiology of the major plant species (Tilman and Cowan 1989, Tilman and Wedin 1991, Craine et al. 1999a, Craine et al., in review), when incorporated into resource competition theory (Tilman 1988, 1994a, 1997c; Tilman et al. 1994b, 1997c), to predict the species abundances, diversity and successional dynamics observed in our long-term N addition experiments and the chronosequence. This is aided by experimental studies of N and light competition (Tilman 1990, Wedin and Tilman 1993, Tilman and Wedin 1991). We are also using the N addition experiments and the successional chronosequence (Knops and Tilman 2000) for ongoing work on the effects of different plant species or functional groups on N mineralization and dynamics, and on C storage, via litter quality feedbacks (Wedin and Tilman 1990, 1996, Wedin et al. 1995).

## E. Future Work

- ◆ We will continue all sampling of experiments **E001** and **E002**, as before, to determine causes of biomass oscillations, to further study diversity-stability relations, to better understand the role of N in the assembly of plant and arthropod communities, the impacts of chronic N addition, the dynamics of recovery following cessation of N addition, and the interactions of fire and N addition.
- ◆ In the N addition experiment in savanna (**E095**), we will continue recently begun systematic sampling of aboveground and belowground biomass and NPP, soil net N mineralization rates, soil moisture, soil CO<sub>2</sub> flux, shoot and root decomposition, and N retention, and plant community composition and diversity to address hypotheses about patterns of change and mechanisms underlying those changes (see Fire Frequency experiment).
- ◆ We will continue to study N interactions in **E141** (BioCON), since N addition is one of three major treatments (described above)
- ◆ Work on microbial populations will greatly increase in 2000 with the initiation of the NSF Microbial Observatory grant, focusing mainly on the long-term N addition experiment (**E001**). This project, initiated by Dr. L. Kinkel, is not explicitly part of the LTER renewal, but is entirely dependent on LTER manipulations and the continued long-term collection of core data in **E001**.

### *Set 3. Effects of Fire Frequency*

**A. Introduction.** Although fire played an important role historically in the dynamics of many mixed tree-grass vegetation systems, the details are poorly understood, especially for oak savannas in central N. America prior to European settlement. The forest - grassland ecotone provides a number of puzzles about its stability, the role of disturbance, and internal vs. external controls on composition, diversity, productivity and nutrient cycling (Scholes and Archer 1997). Although we know an increasing amount about the influence of trees on grassy vegetation (e.g., Jackson et al. 1990, Belsky 1994, Haworth and McPherson 1994) via effects on light, water, and nutrient cycling, we know less about the dynamics of these ecosystems as a whole. In particular, although substantial effort has been directed at understanding controls on NPP and N cycling for forests (e.g., Pastor et al. 1984, Gower et al. 1992; Gholz et al. 1994) and grasslands (e.g. Risser et al. 1981; Knapp et al. 1993, 1998, Turner et al. 1997) generally and at Cedar Creek (Wedin & Tilman 1990, 1993; Reich et al. 1997a) this is not as true for savannas (Mitchell et al. 1999). Plant traits, disturbance, and climate exert joint control of ecosystem functioning (e.g., Pastor et al. 1984; Tilman 1988, Parton et al. 1987, 1988; Aerts 1990, 1992; Wedin & Tilman 1990), but studies of climate effects have usually been made at a single time across sites varying in climate, rather than examining across climate (i.e., interannually) at a single site.

**B. Description of Experimental Methods.** We are addressing the above issues as part of Theme 1, and within the context of fire and oak savannas, also addressing the other 3 themes. To do so we focus on a long-term prescribed burning experiment (**E015**, begun in 1964; expanded to **E133**; <http://www.lter.umn.edu/research/exper/e133/e133.html>) involving 29 landscape units (3 to 27 ha) which range widely in fire frequency. These semi-native oak woodlands may have experienced some selective logging and grazing, but were never plowed, and were protected from fire from 1938 to 1964. Fire treatments (prescribed spring ground fires) range from complete fire protection to near-annual burning (8 fires per decade), spanning the range of presettlement fire frequencies along the forest-prairie border. Permanent plots (50 x 75 m) were established in 12 burn unit plots in 1984, and in 17 more by 1995. Several other

ongoing fire experiments will also be continued, including **E012** (Effects of fire frequency on old field succession), **E143** (Accelerated savanna restoration), and **E002** (Effects of grassland fire and N).

### **C. Results to Date**

- ◆ Periodic fires (at medium to high frequency) gradually kill mature trees (Fig. 23) and suppress sapling recruitment, but responses differ by species (Peterson & Reich 2000a). As a result, there is a gradient of tree composition, density (Fig. 24) and biomass associated with fire frequency (Peterson & Reich 2000a, Reich et al. 2000). These long-term changes enable us to characterize the fire regimes required to sustain a presettlement landscape mosaic with savannas, and the prescribed fire regimes needed to restore and maintain oak savannas (Peterson & Reich 2000a).
- ◆ Fire, directly and indirectly by altering tree canopy cover, has had major effects on breeding bird composition and diversity (Davis et al. 2000ab) and on plant species composition (Fig. 25). Major plant functional groups diverged in presence and abundance due to within- and cross-plot variation in light, N and water availability (Fig. 26).
- ◆ Patterns of species diversity weakly supported the intermediate disturbance hypothesis (Peterson & Reich 2000b), with total vascular plant diversity highest at intermediate fire frequencies in communities dominated jointly by trees and grasses. However, individual functional groups did not follow that pattern. The data suggest that maintenance of spatial heterogeneity in woody cover and associated resources is likely the mechanism leading to higher plant diversity in savannas than grassland or forested plots.
- ◆ Fire has direct effects on ecosystem function and indirect effects via changes in the vegetation composition (Reich et al. 2000, Peterson et al. in review). Differences in traits between woody and herbaceous species influence C and N cycling because of how they change their acquisition and turnover rates at tissue-to-ecosystem scales. As a result, frequently burned, open savanna differs greatly from unburned, closed woodland in terms of NPP (Fig. 27, Reich et al. 2000), C storage (Fig. 7A, Tilman et al. 2000), and N cycling (Fig. 28, Reich et al. 2000). Belowground NPP as a proportion of total NPP is not higher in grass than tree-dominated communities, contrary to many hypotheses. Both fire and vegetation feedbacks play important roles. Net N mineralization rates beneath trees are greater than beneath adjacent grassy patches in the same fire treatment unit (Wrage et al., unpublished data) and even for a given fire regime, net N mineralization and ANPP are 3-fold greater in 80% tree-dominated than 80% grass-dominated communities (Reich et al. 2000).

**D. Past, Ongoing, and Future Mechanistic and Theory work:** Are savannas merely additive mixtures of grassland and forest patches in terms of their ecosystem function or compositional dynamics? Although empirical data address this, we are also beginning to use modeling as a means of integration. This involves both biogeochemistry modeling (PnET and Century) and modification of vegetation dynamics models to examine tree-grass compositional patterns. A variety of manipulative experiments enables tests of specific mechanisms. An example is a field study of competitive interactions under multiple resource combinations, which found that greater N availability led to increased competition for water by increasing herbaceous biomass, thereby leading to greater oak seedling mortality (Davis et al. 1998, 2000b). In contrast, without competition, a precipitation regime that simulated a 100-yr drought had minimal effects on young oaks, regardless of N supply rates.

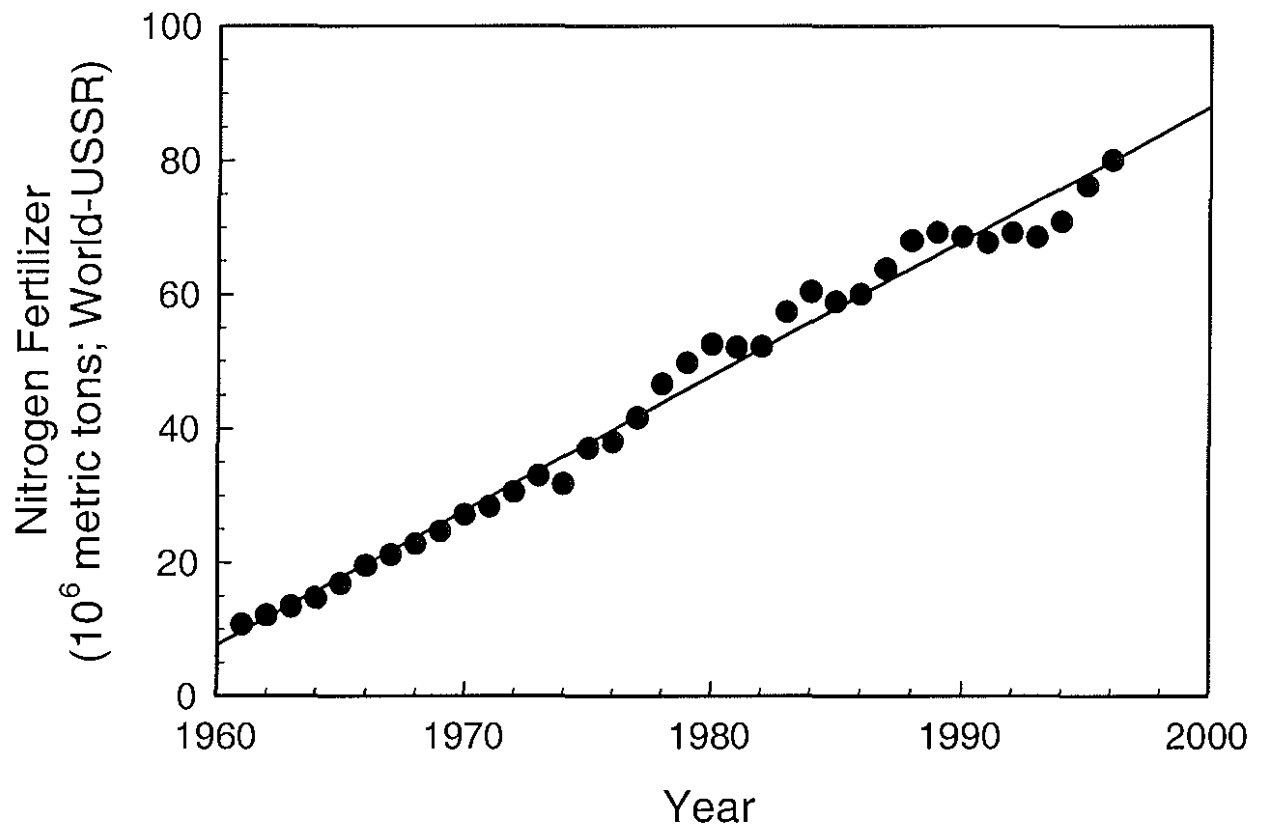


Figure 16. Trends in the global rate of nitrogen fertilization, based on FAO data, excluding the former USSR. Analysis of the dependence of this trend on time, global GDP, and global population led to the forecast that the global rate of application of nitrogen fertilizers would be 3.1 times larger in year 2050 than it is at present. (From Tilman, Fargione, Wolff, D'Antonio, Dobson, Howarth, Schindler, Schlesinger, Simberloff, and Swackhammer, in review.)

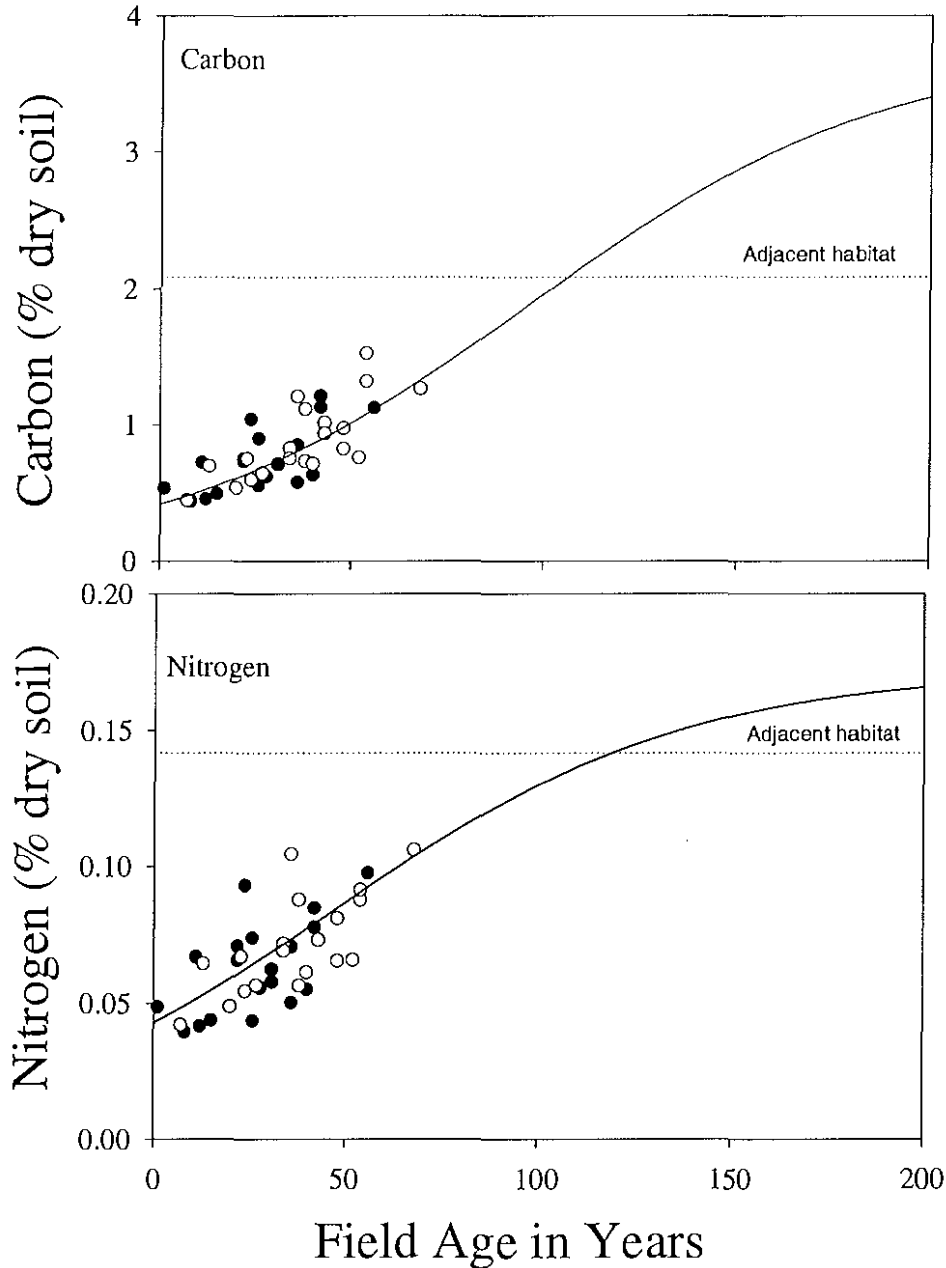


Figure 17. Modeled carbon and nitrogen accumulation and actual field averages of carbon and nitrogen versus field age based on the successional chronosequence, **E014** (from Knops & Tilman (2000) *Ecology*). The logistic curve are calculated from the changes within a plot from 1983 to 1995. Curves are drawn from a logistic curve with the following parameters for nitrogen,  $r = 0.0223$ ,  $K=0.1715$ ,  $N_0=0.0431$ ; for carbon,  $r = 0.0217$ ,  $K=3.754$ ,  $N_0=0.418$ . The  $N_0$  values were estimated from the average intercepts of the two sampling years versus field age. Open circles are 1995 data and closed circles are 1983 chronosequence data. The stippled line is the median of the adjacent undisturbed habitats for all fields.

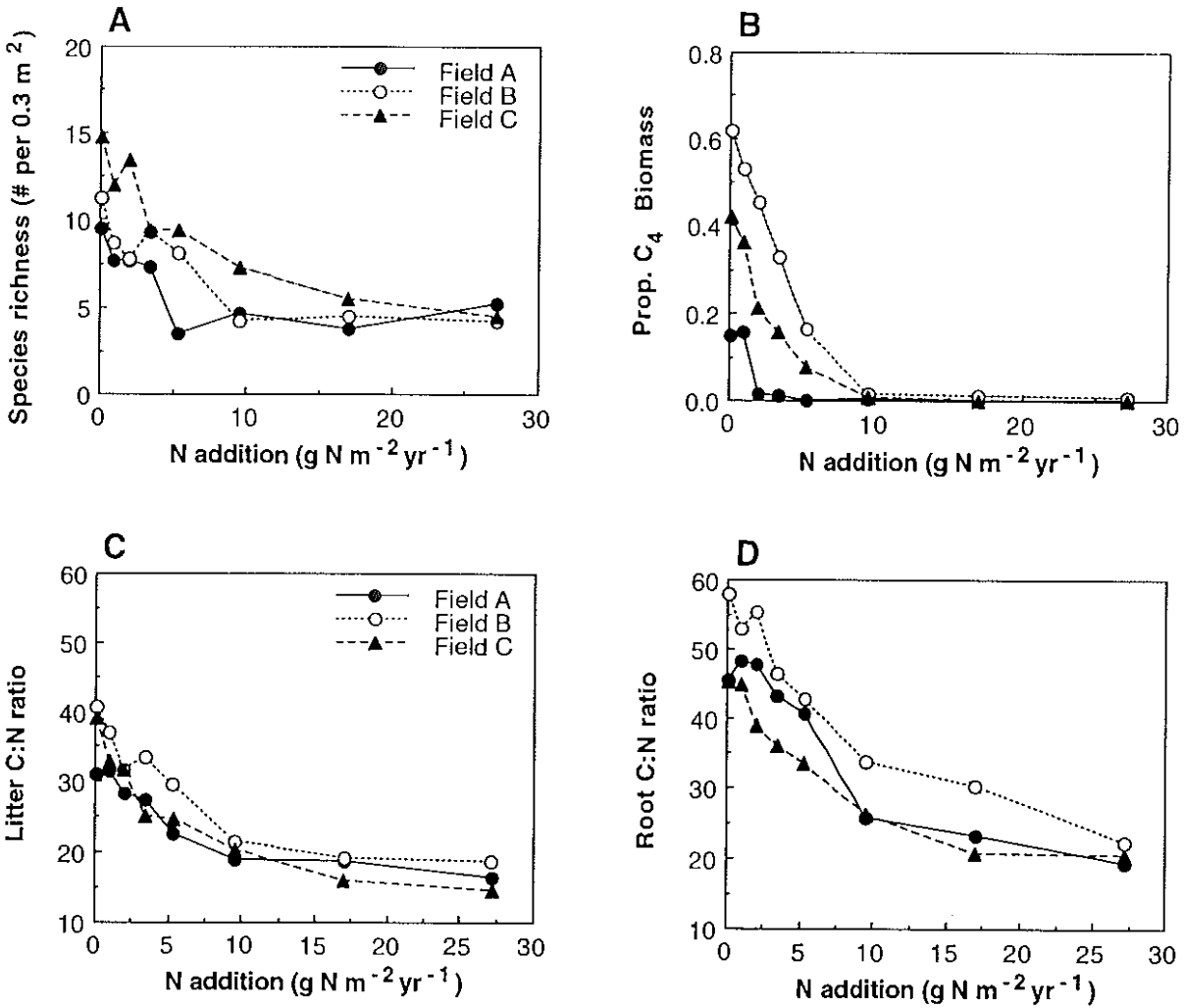


Figure 18. From Wedin and Tilman (1996) *Science* on ecosystem C and N and vegetation responses to 12 years of N addition in E001. Points represent treatment means (6 replicates per N addition level, 12 for controls) for each of three fields.

(A) Number of vascular plant species found in 0.3-m<sup>2</sup> vegetation samples.

(B) Biomass of grasses with the C<sub>4</sub> photosynthetic pathway as a proportion of aboveground live biomass at mid-growing season. One species, *Schizachyrium scoparium*, contributed >95% of the C<sub>4</sub> biomass in the plots.

Biomass C:N ratios for (C) litter, i.e. aboveground dead biomass (both recent and old) and (D) belowground root biomass, both alive and dead root fragments.

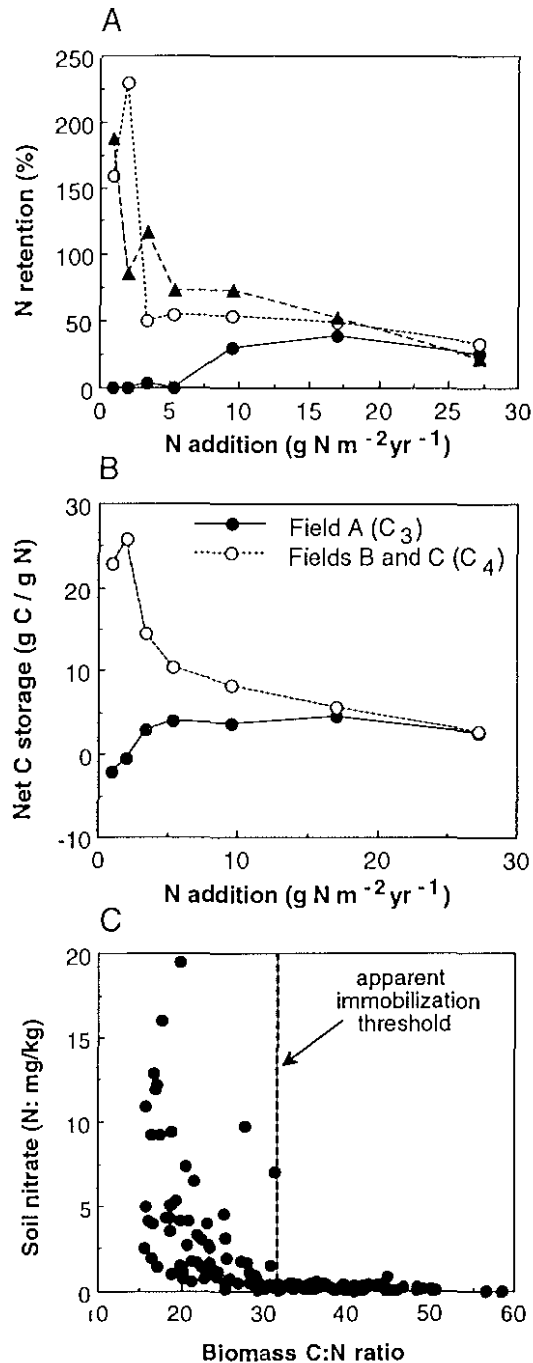


Figure 19. From Wedin and Tilman (1996) *Science*, based on **E001**, the N addition experiment. **(A)** Nitrogen dynamics after 12 years of N addition. Net N retention after 12 years estimated as the change in total system N (relative to controls) divided by the sum of experimental N additions. **(B)** Net C storage per unit experimentally added N after 12 years. Because C storage rates (g C/g N) did not differ significantly between Fields B and C (34), overall treatment means for the two C<sub>4</sub>-dominated fields are presented. **(C)** The relationship between soil NO<sub>3</sub><sup>-</sup> and the C:N ratio of plant biomass (aboveground dead biomass plus belowground biomass). Vertical line represents a biomass C:N ratio of 32.



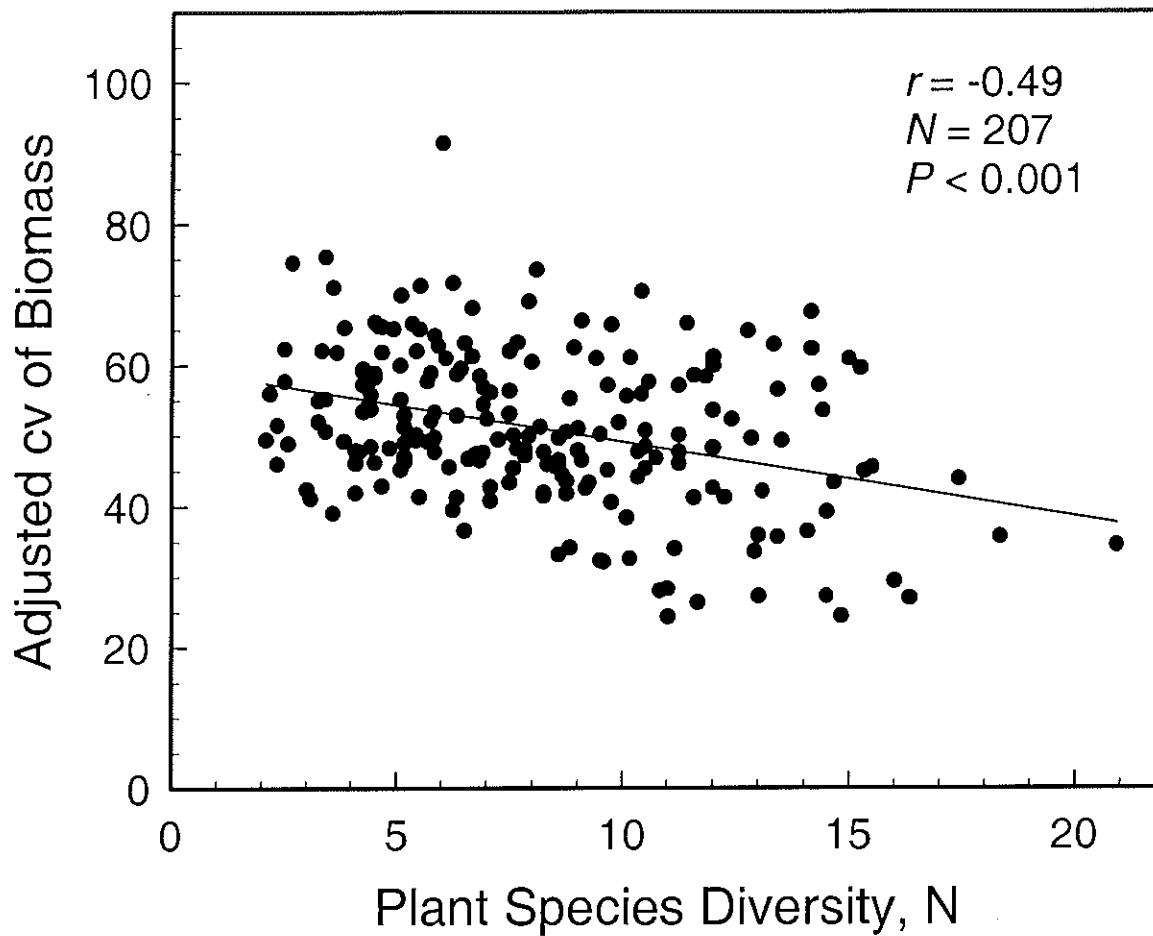


Figure 20. The dependence of the coefficient of variation (cv) of total community biomass on plant species diversity, based on the data for four Cedar Creek fields in **E001**. The cv measures the extent of year-to-year variation in total plant biomass within a plot (relative to mean biomass). The lower coefficients of variation of the more diverse plots mean that total community biomass is stabilized by diversity. As shown in Tilman (1996), abundances of individual species are destabilized by diversity. Coefficients of variation of each field were adjusted for differences in intercepts as determined by a GLM regression. (Tilman (1999) *Ecology*.)

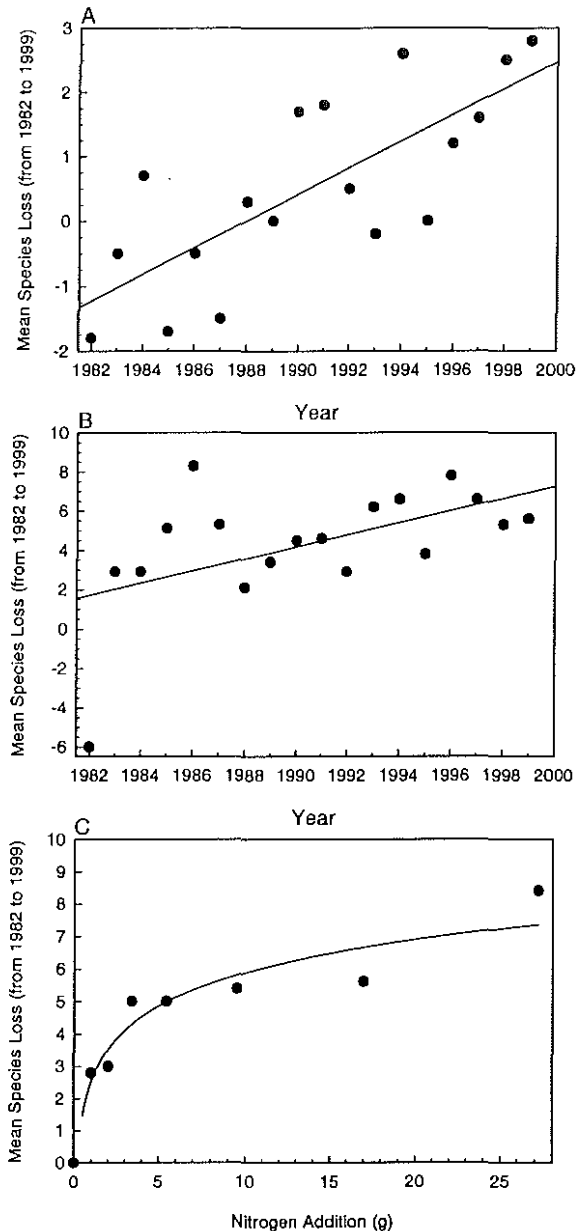


Figure 21. The effects of long-term nitrogen addition on plant diversity in **E001**.

(A) The effect of an N addition rate of  $1.0 \text{ g m}^{-2} \text{ yr}^{-1}$  on plant species richness in native savanna. By 1999, added N plots had lost about 3 plant species, relative to control plots, which is 27% of original plant species richness (regression:  $r=0.76$ ,  $N=18$ ,  $P<0.001$ ). Each point shows the difference (averaged across all replicates) between the observed number of plant species in the N addition plots compared to the plant species richness of the controls that received no added N.

(B) Similar results, except for plots in native savanna receiving  $17 \text{ g m}^{-2} \text{ yr}^{-1}$  of N.

(C) The mean number of plant species lost in 1999, after 18 years of N addition, graphed against the annual rate of N addition, for native savanna. The non-linear relation means that the short-term chronic N addition has a much larger impact than predicted by high rates of N addition. The rapid loss of species at higher N means that short-term, high dose experiments cannot predict the response to chronic, low-dose N addition.

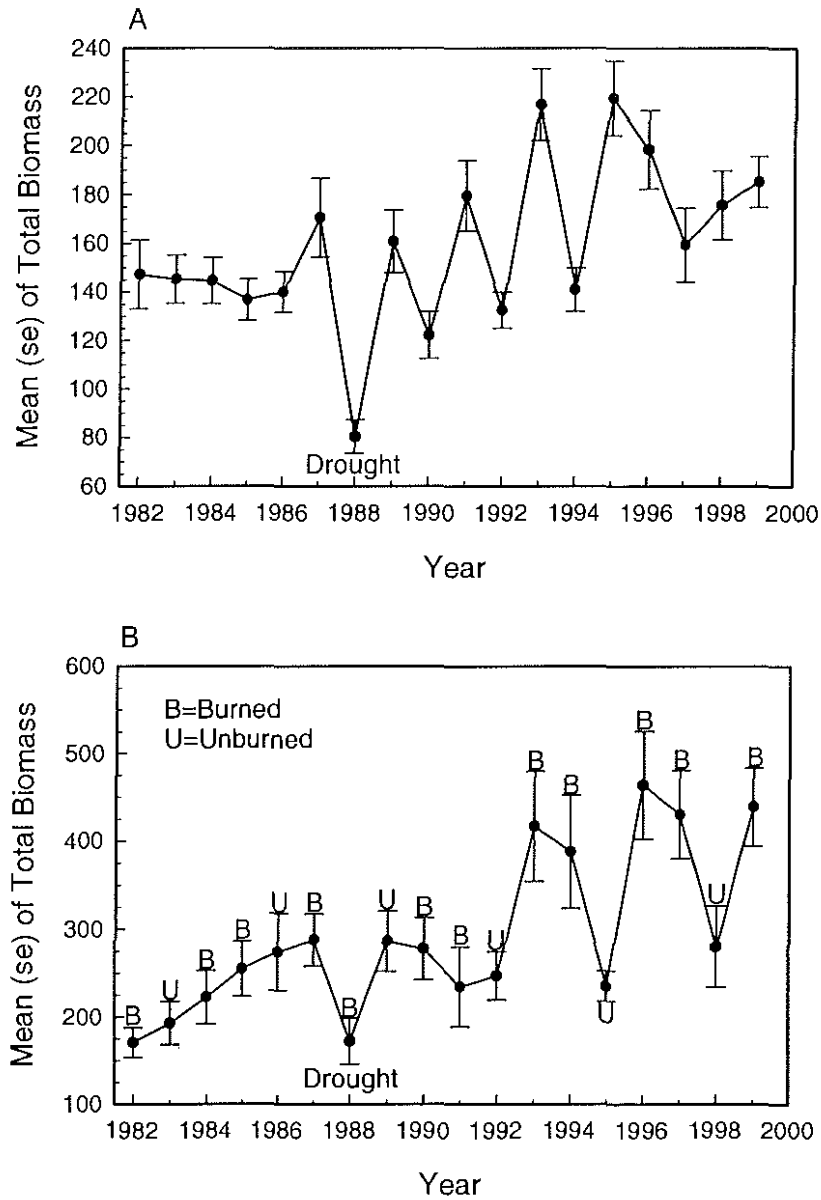
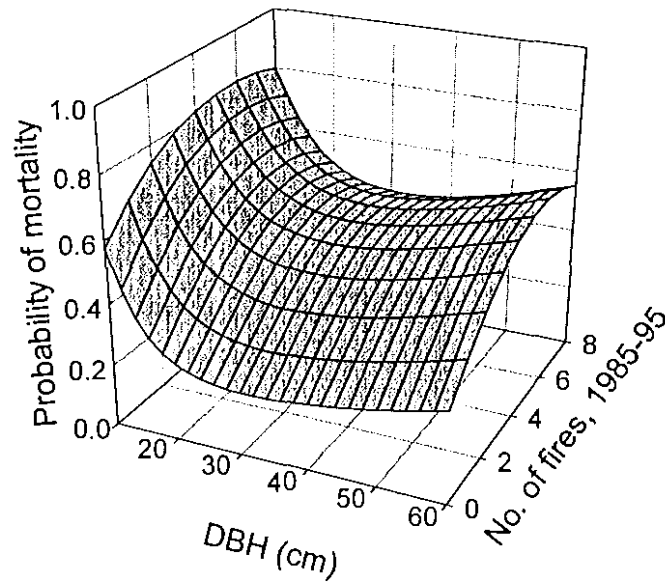


Figure 22. The dynamics of total plant biomass before and after drought in **E001** (from Haddad et al., in review).

**(A)** Mean and SE of total aboveground biomass in the unfertilized controls plots for three successional fields of **E001**. Note relative constancy before the drought and the 2 yr or 3 yr cycle after the drought. These fields are unburned.

**(B)** Similar dynamics for the periodically burned savanna plots. Note that, after the drought, low points correspond with years when plots were unburned.

A. Northern pin oak



B. Bur oak

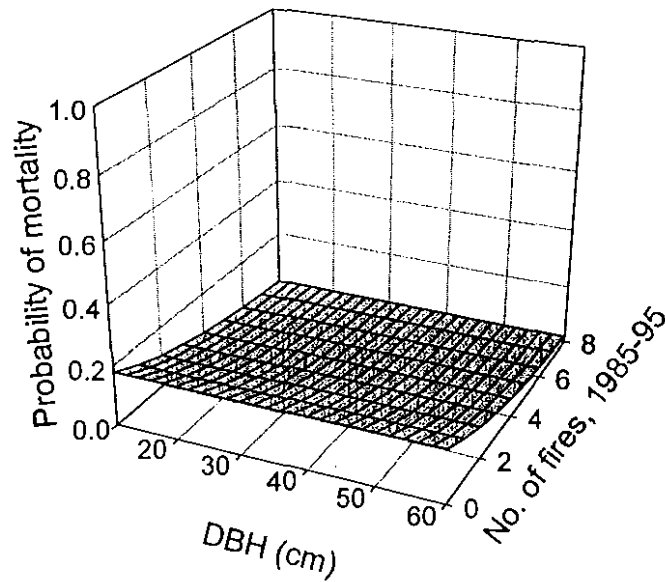


Figure 23. Probability of mortality of individual oak trees over an 11 year period as a function of tree diameter and the number of fires during that period. Separate response surfaces are presented for a) northern pin oak and b) bur oak. (Peterson and Reich 2000, based on E015 and E133.

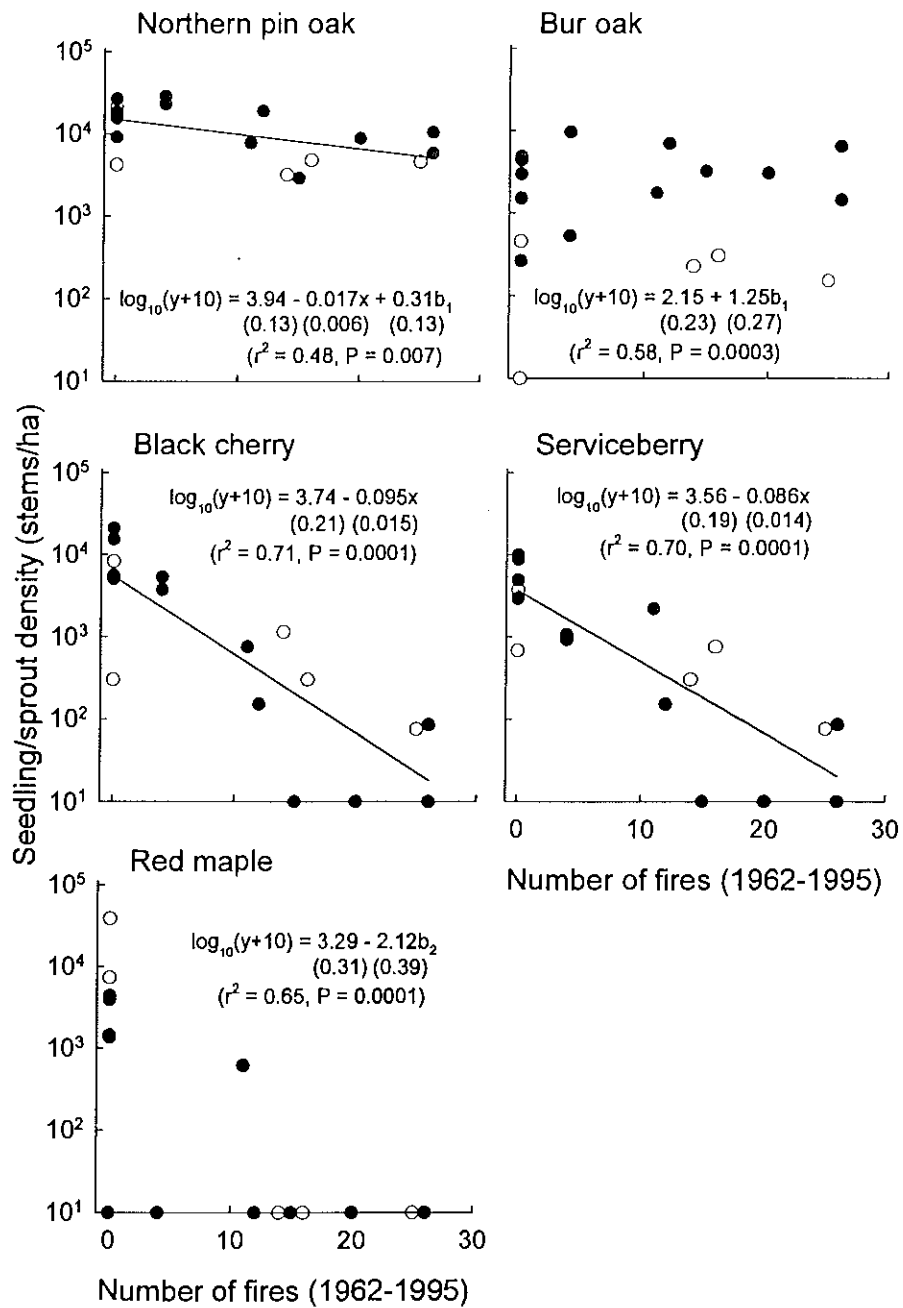


Figure 24. Seedling densities, by species, for 20 stands across a fire frequency gradient (E015, E133). Regression lines indicate significant responses to burn frequency or soil type predictors. Symbols signify Sarell (closed) and Zimmerman (open) soil series. (Peterson and Reich 2000.)

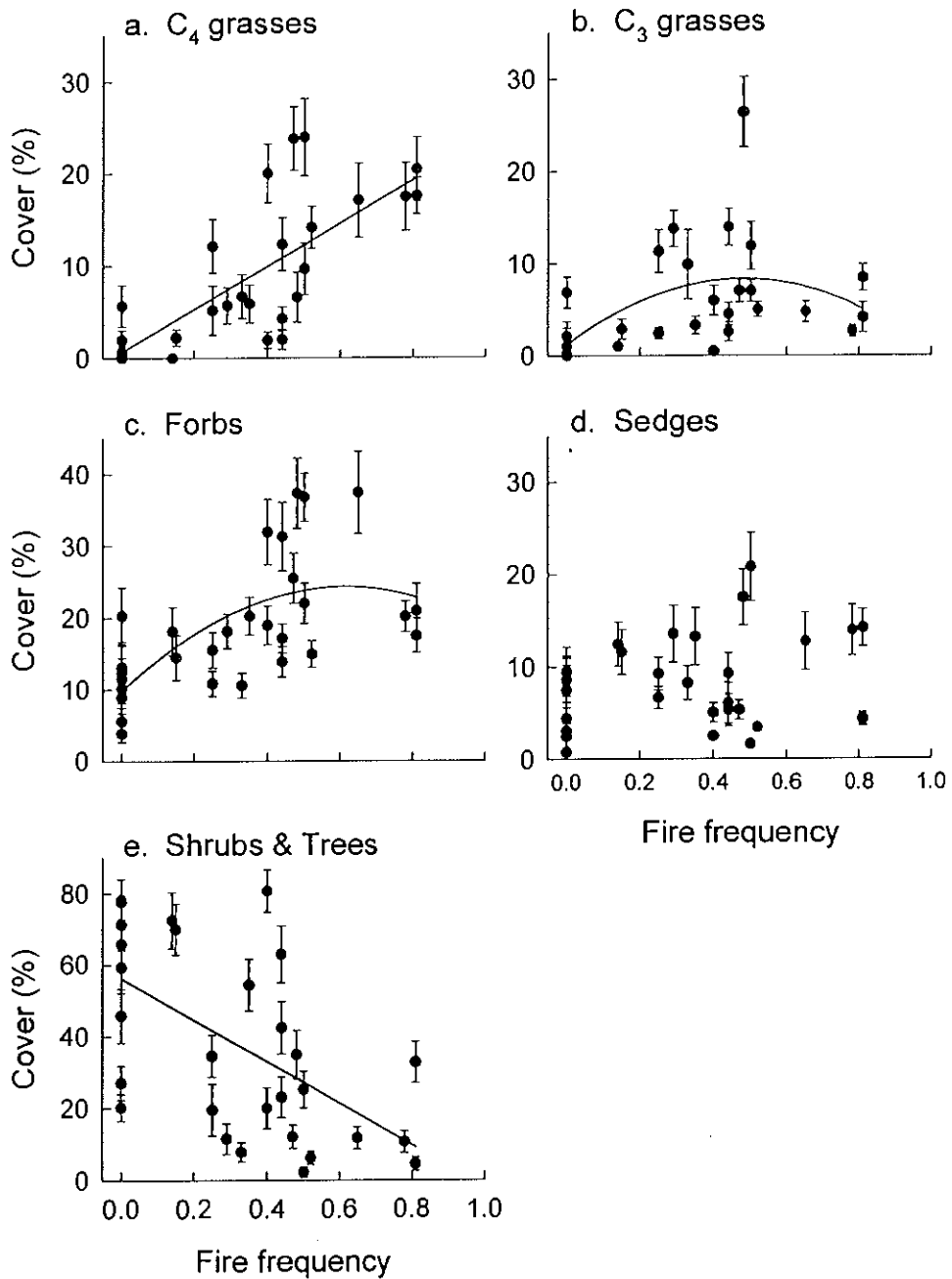


Figure 25. Fire frequency effects on understory plant cover, by functional group based on data from E015 and E133. Fitted curves indicate a significant linear or quadratic relationship between fire frequency and percent cover. Error bars indicate standard errors around the means. (Peterson et al. 2000.)

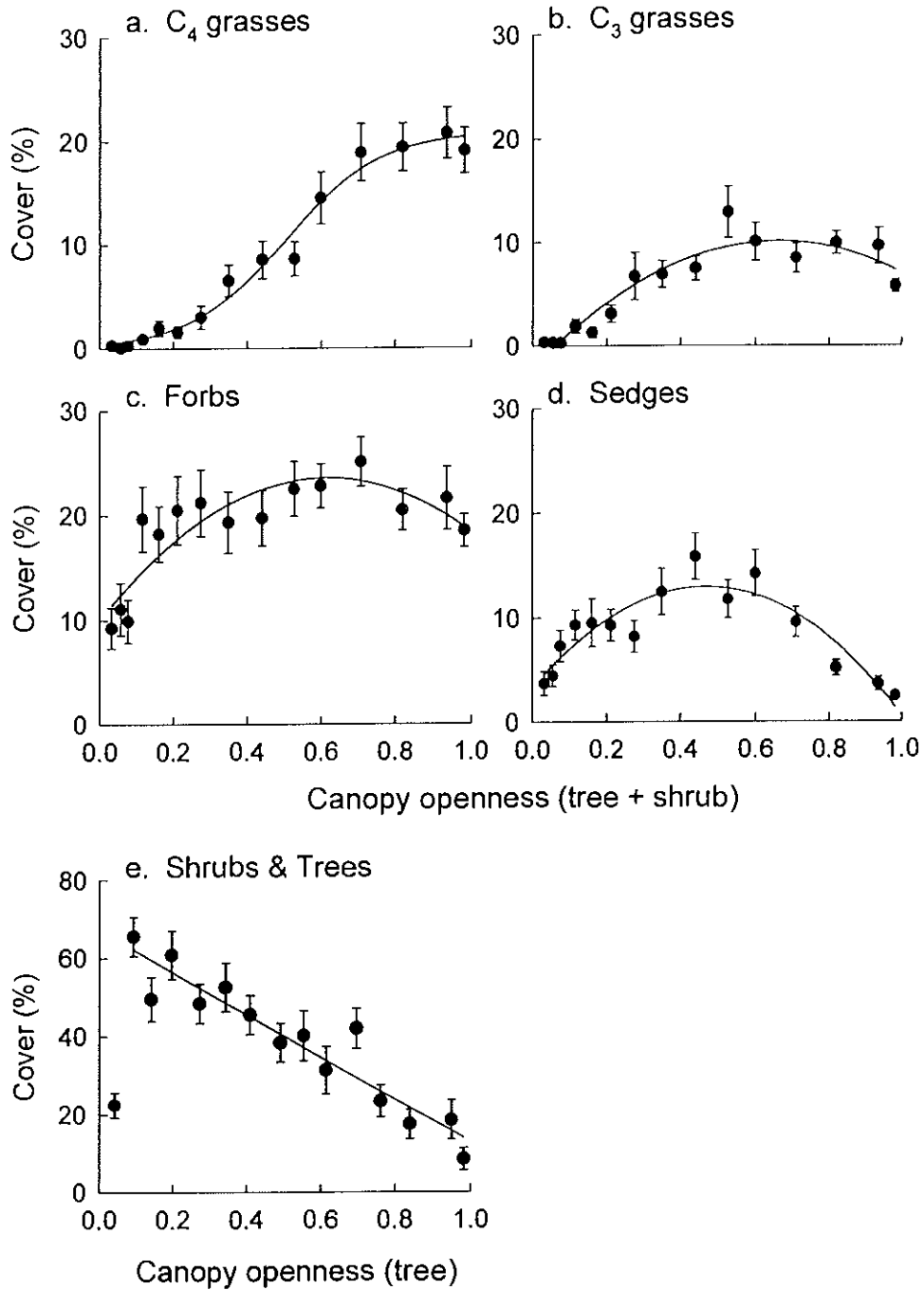


Figure 26. Variation in percent cover of plant functional groups along the canopy openness gradient of the savanna burning experiment, **E015** and **E133**. Tree/shrub canopy openness readings are used for herbaceous groups (a-d) and tree canopy openness readings are used for shrub and tree groups (e-f) Error bars indicate standard errors. (Peterson et al. 2000.)

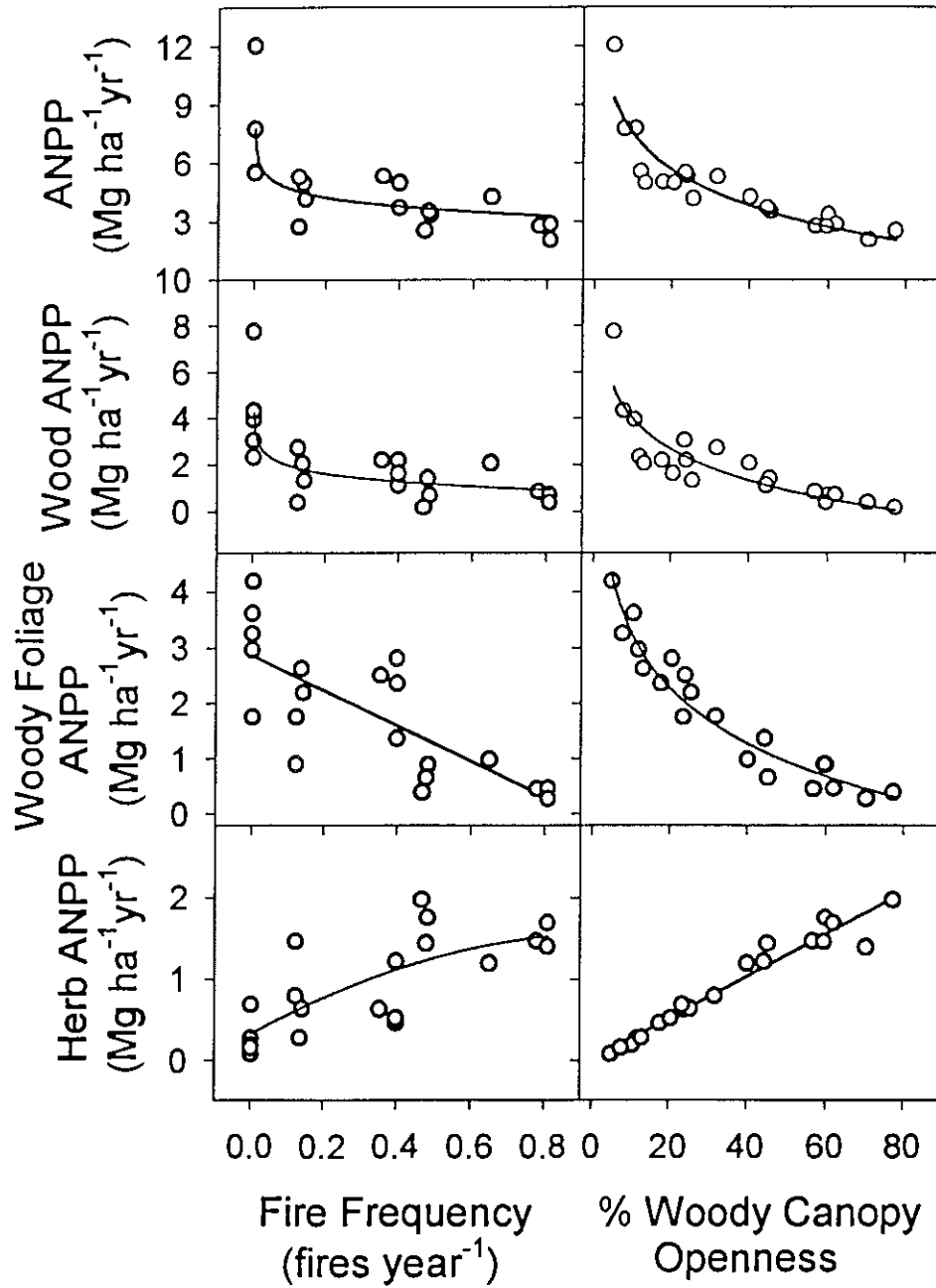


Figure 27. Total aboveground net primary production (ANPP, Mg ha<sup>-1</sup> yr<sup>-1</sup>) and its components, aboveground wood NPP, woody foliage NPP, and herbaceous ANPP, in relation to fire frequency ( $r^2 = 0.59, 0.57, 0.58$  and  $0.56$ , respectively) and percent woody canopy openness (%WCO) ( $r^2 = 0.83, 0.76, 0.94$  and  $0.95$ , respectively) for 20 woodland and savanna stands in E133. All relationships significant at  $p < 0.001$ . (Reich et al. 2000.)



**E. Future Research:** In 1999, we expanded our set of on-going measurements to more fully address all 4 Themes in E133. This sampling will continue, in some cases annually, for 2000-2006. We will examine C and N cycling to better understand the roles of disturbance (fire), plant traits (woody vs. herbaceous), resource supply (N) and climate (interannual variation). The annual studies will be made in 12 plots spanning the range of fire frequency. Composition will be characterized by annual censusing of vegetation. We will examine many aspects of C and N cycling, including aboveground litter N flux (Reich et al. 1997a, 2000), if possible fine root turnover rates (Eissenstat 1997; Eissenstat & Yanai 1997) and belowground litter N flux; decomposition rates of aboveground and belowground litter (Aber & Mellilo 1982, Melillo et al. 1982, Hobbie & Vitousek 2000); soil net N mineralization rate (Grigal & Homann 1994, Reich et al. 1997a, 2000), soil CO<sub>2</sub> flux (Craine et al. 1999b), aboveground NPP (Reich et al. 1997a, 2000), and three methods to assess belowground NPP- (1) N budget, (2) in-growth root cores, and (3) standing fine root biomass combined with fine root birth and mortality rates stratified by root order and diameter (Fahey et al. 1985, 1999, Vogt et al. 1989, 1998, Reich et al. 2000). Decomposition studies will include manipulations to determine effects of vegetation change on C and N cycling across the fire frequency gradient. Experiments will include in situ and reciprocal decomposition studies of both above- and belowground biomass; soil incubations; and reciprocal soil transplants. In addition to field mineralization studies (see above), in one year, C and N mineralization will be studied in laboratory incubations and with stable isotope techniques (e.g., Wedin et al. 1995). We will quantify N losses associated with fires compared to N immobilized in litter in short-term decomposition experiments, in an attempt to develop a complete N budget (including inputs and outputs) for these stands. Other research activities will complement these core measurements. These include: (1) an ongoing annual acorn predation and seedling establishment experiment; (2) a 1-year study of spatial heterogeneity in composition and function in two 4 ha savanna plots; (3) detailed measurements of composition and resource availability in all 24 subplots of the 29 oak savanna burn unit plots: these are made every 5 to 6 years and provide a more detailed basis for long-term changes than the 12 plots (8 subplots) to be examined annually; (4) a 1-year study of foliage and fine root ecophysiology in the core savanna plots, (5) collaboration on mycorrhizal research, and (6) use of stable isotope techniques to evaluate uptake and utilization of C, N and water. In total, these activities will enable us to concurrently explore root and foliage linkages to turnover, productivity, soil properties and C and N cycling at tissue-to-ecosystem scales, as influenced by interannual variation in climate, variation in fire frequency, and N availability and vegetation composition gradients.

#### *Set 4. Trophic Interactions*

**A. Introduction** The interactions among plants, herbivores, predators, and decomposers may be a critical determinant of population, community and ecosystem responses to disturbance (Theme 1). Trophic interactions can greatly influence abundances and diversity of plants and their herbivores (Theme 2) (Power 1992, Hunter and Price 1992, Hairston and Hairston 1993, Belovsky and Joern 1995, Polis and Strong 1996, Chase 1996, Hunter et al. 1997, Stiling and Rossi 1997). Trophic effects can “cascade” through food webs and influence the feedbacks of species and biodiversity on ecosystem processes (Theme 3), such as productivity and element cycling (Pastor et al. 1993, McNaughton et al. 1997, Ritchie et al. 1998, Maron and Jefferies 1999). This may depend heavily on whether herbivores or decomposers (e.g., microbes) consume a major fraction of annual production, and the relative availability of C and N for both herbivores and microbes. Furthermore, consumption of seeds and seedlings may limit plant colonization and

establishment (Louda et al. 1990, Hulme 1997, Reader 1993, Reader et al. 1994, Ostfeld et al. 1997) and thus plant diversity (Tilman and Pacala 1993, Crawley 1997, Hubbell 1997) and N budgets (Ritchie et al. 1998). Climatic variation and predator-prey interactions may induce annual fluctuations in the abundance of consumers and their impacts, which together may create pulses of recruitment of different species that lead to long-term lags in succession and the response of plant communities to environmental changes.

**B. Description of experiments and methods** Our long-term work on trophic interactions has established two sets of field experiments designed to address two principal questions: how predators influence arthropod abundance and diversity, and how herbivores modify plant productivity, species composition, and nutrient cycling.

A long-term core LTER experiment (**E061**), begun in 1989, has excluded vertebrate predators (birds and lizards) from unfertilized and fertilized ( $17 \text{ g N m}^{-2} \text{ yr}^{-1}$ )  $9 \times 9 \text{ m}$  plots within a single old field (Ritchie 2000). The abundance of grasshoppers and predators other than birds are sampled annually each year, as is plant biomass, plant species composition, and available soil ammonium and nitrate. A related experiment was established in 1995 in this field and three others to explore the separate effects of lizards and birds on all macroarthropods ( $>1 \text{ mg}$ )

Building on an experiment begun in 1983 with 3 deer exclosures and 3 controls placed along each of 3 successional ecotones (**E007**), we established six additional  $30 \times 30 \text{ m}$  deer fences and 6 paired control plots of similar size, across a fire frequency gradient in the oak savanna in 1995 (**E140**). A second small experiment (**E062**), begun in 1989, consists of ten  $2 \times 2 \text{ m}$  plots in oak savanna, half of which exclude deer with fencing and insects with carbaryl methylcarbamate insecticide (Ritchie et al. 1998). In each experiment, we measure percent cover of plant species, aboveground biomass of litter and different plant functional groups, belowground biomass and production, plant tissue N concentrations, and available and total soil N. These measurements allow us to assess the effects of deer exclusion on plant productivity and species composition, and their interaction with fire, at two different spatial scales (Theme 4).

**C. Results to Date** Our research highlights some of these effects and suggests that herbivores consume only a small fraction of primary productivity but nevertheless strongly influence plant productivity and species composition.

- ◆ The combined effects of white-tailed deer and insect herbivory reduces legume abundance five-fold and enhances aboveground productivity and N cycling (Ritchie and Tilman 1995, Ritchie et al. 1998, Figure 1A, D).
- ◆ Grasshoppers, an important herbivore group at Cedar Creek, consume 5-10% of available plant biomass when at peak densities. However, abundance varies annually by up to an order of magnitude (Fig. 29A), and is strongly influenced by climate variation and plant N concentration (Ritchie 2000).
- ◆ Predators of grasshoppers have variable effects (Figure 5) that are modified by strong indirect effects on each other. For example, birds reduce spider abundances, indirectly decreasing predation on grasshopper nymphs, but modify grasshopper behavior in a way that benefits and increases predation by lizards (*Eumeces septentrionalis*) (Pitt and Ritchie *in prep.*, Pitt *in prep.*).
- ◆ Abundances of granivorous rodents, which may affect recruitment of plant species, fluctuate annually in response to oak masting (Fig. 29B) and decline during succession (Fig. 29C).

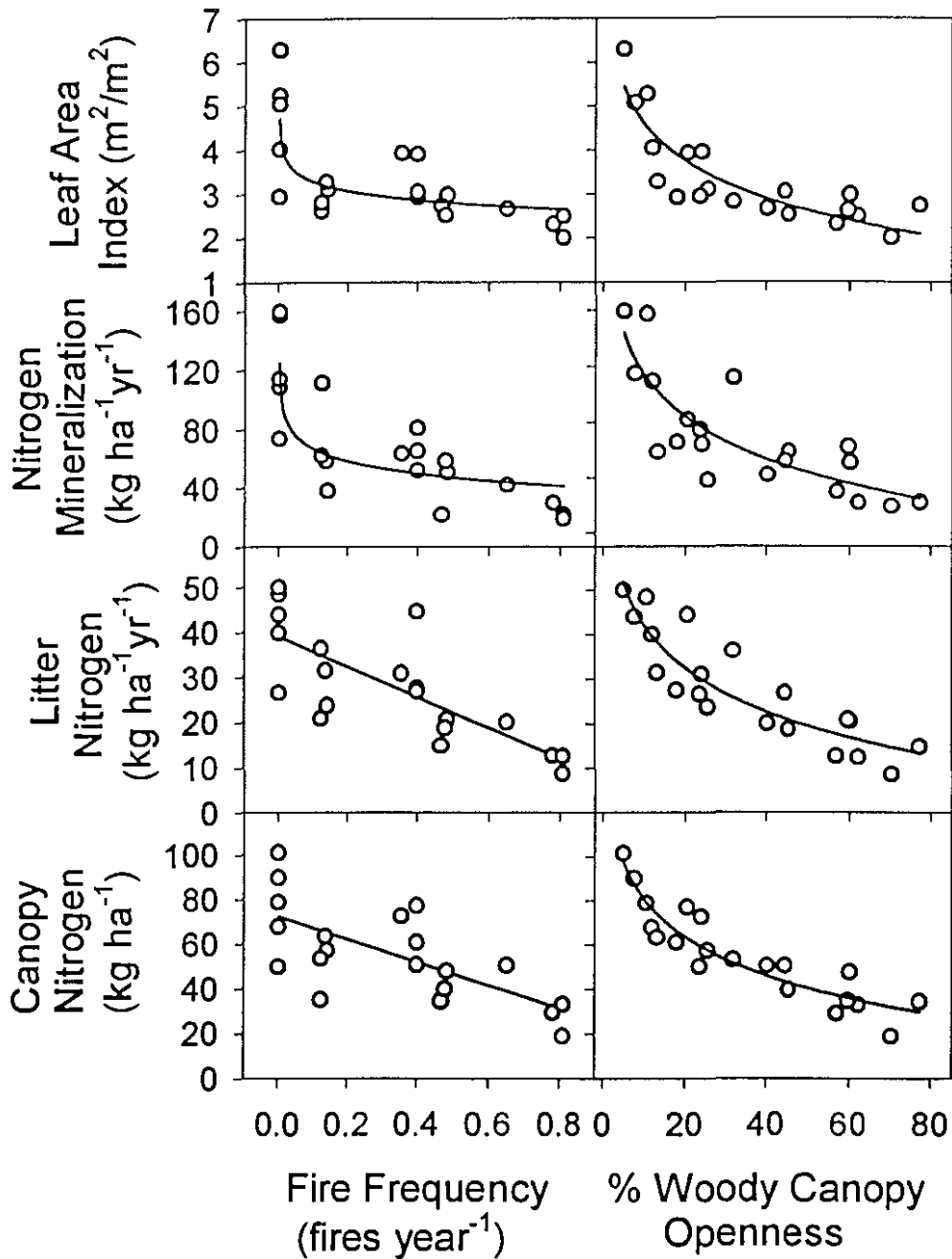


Figure 28. Total ecosystem LAI ( $\text{m}^2/\text{m}^2$ ), annual net N mineralization rate ( $\text{kg ha}^{-1} \text{yr}^{-1}$ ), total annual aboveground litter N ( $\text{kg ha}^{-1} \text{yr}^{-1}$ ), and total canopy N ( $\text{kg/ha}$ ), in relation to fire frequency ( $r^2 = 0.57, 0.65, 0.63$  and  $0.48$ , respectively) and percent woody canopy openness (%WCO) ( $r^2 = 0.77, 0.69, 0.80$  and  $0.86$ , respectively) for 20 woodland and savanna stands in E133. All relationships significant at  $p < 0.001$ . (Reich et al. 2000.)

**D. Mechanisms and Theory:** We performed a series of experiments to explore indirect effects of predators on grasshopper behavior. These indirect effects help explain the variable effects of predators on the dominant insect arthropods (Pitt and Ritchie *in prep.*, Pitt *in prep.*). Other studies have used “snapshots” of arthropod herbivore and predator abundance and diversity within a single year to assess the response of these trophic groups to factors associated with human impacts. Arthropod abundance and diversity depends on rates of N addition in E001 (Siemann 1998, Siemann et al. 1999b, Haddad et al. *in review*) and on plant species richness in Biodiversity II (Siemann et al. 1998, Knops et al. 1999, Haddad et al. *ms*).

**E. Future Research:** The effects of seed predators on plant dispersal have received little attention at Cedar Creek, despite the effects of recruitment limitation on succession and diversity. To assess the impact of seed predators on different plant species, we propose to measure seed predation rates in combination with annual monitoring of populations of seed predators such as small mammals. Seed predation of legumes, oaks, white pine, sumac, and dominant cool and warm-season grasses will be monitored annually within 12 fields within the chronosequence in two ways. First, small mammal and ant predation will be measured from weekly removal rates of seeds placed in 40 offer trays (50 x 50 cm) in each field. Each tray will either allow ants and exclude mice, allow mice and exclude ants, allow both, or exclude both, with 10 replicates of each treatment. The fates of acorns will be similarly monitored in oak savanna. Second,  $\geq 200$  mature seeds from  $\geq 10$  extant plants of each species will be collected at the end of summer in each field where they are present. Seeds will be dissected to determine the presence and species of depredated insects.

Soil microbes comprise a trophic group that plays critical roles in N fixation, N mineralization and litter decomposition (McKone and Biesboer 1986, Pastor et al. 1987a,b, Zak et al. 1990, Zak and Grigal 1991, Zak et al. 1994a,b), but is infrequently studied. In Section 2.C we propose measuring responses of the microbial decomposition trophic level in existing long-term experiments.

### *Set 5. Land Use and Succession*

**A. Introduction:** We are interested in the environmental constraints, organismal tradeoffs, and feedbacks that control the rate, pattern, and direction of succession (e.g., Huston and Smith 1987; Theme 2) because these give insights into the mechanisms controlling diversity, community assembly and ecosystem functioning (Theme 3). Moreover, successional patterns demonstrate the impacts and recovery from agricultural disturbance (Theme 1). The assembly of communities and the maintenance of diversity within them may relate to several potential mechanisms: (1) spatial heterogeneity in the physical environment (Tilman 1982, Tilman & Pacala 1993, Ritchie & Olff 1999); (2) temporal variability and non-equilibrium conditions (Levins 1979, Armstrong & McGehee 1980; Sommer 1984, 1985; Grover 1988, 1989; Huisman 1999); (3) multi-trophic level interactions and trophic complexity (Carpenter et al. 1985, Power 1990a,b, Oksanen et al. 1981, Fretwell 1977, Hairston & Hairston 1993); (4) neighborhood interactions and dispersal in spatial habitats (Skellam 1951, Levins & Culver 1971, Horn & MacArthur 1972, Levin 1976, 1992, Durrett & Levin 1994, Tilman 1993, 1994, 1997a); and (5) spatial interactions of competitively identical species (Hubbell & Foster 1986, Hubbell 1997). Theories based on these factors can also potentially explain successional dynamics. Recent work at Cedar Creek (Tilman 1997a, Ritchie & Olff 1999) and elsewhere (Brown & Nicoletto 1991, Levin 1992, Holling 1992, Hubbell 1997, Peterson et al. 1998) suggests that different mechanisms control community

assembly at different spatial scales of observation (Theme 4). Our periodic re-sampling of an old-field chronosequence is allowing us to test these ideas.

**B. Description, Design and Methods:** A key part of our study of disturbance, succession, and community assembly comes from long-term observations in 22 fields of different successional ages (E014), a periodically resampled chronosequence. In 1983 we established 100 permanent 0.5 m<sup>2</sup> plots along four parallel 80m long transects in each of 22 fields ranging in age from 1 to 56 years (Pierce 1954, Inouye et al, 1987c). All 2200 plots have been sampled every 5 or 6 years (1983, 1989, 1994, and 1997). All plants in a plot are identified to species and their cover estimated for all plots (Inouye et al. 1987a). Soil cores from each plot are collected, analyzed for total N and C, and archived for future analysis. Each field also is sampled annually for abundances of grasshoppers, the major herbivore (Huntly & Inouye 1988), small mammals (Huntly & Inouye 1987), and pocket gophers (*Geomys bursarius*, Inouye et al. 1987c). These abundance data are critical in assessing the role of trophic interactions in regulating species composition and diversity (see Section 2.B.D). A 0.1 x 3 m strip from a 5 x 5 m plot at the start of each transect in each field is annually clipped for aboveground biomass and sorted to species (E054). This provides annual information on long-term productivity patterns.

### C. Results to Date

- ◆ Our results suggest that the herbaceous phase of succession is largely driven by an interaction between competition for N at the neighborhood scale, and larger-scale processes, including dispersal and landscape patterns, that influence species presence (see Results of Prior Support). This causes the rate and pathway of succession to be stochastic (Foster & Tilman 2000).
- ◆ On average, agricultural disturbance had caused a 75% loss of soil N and 89% loss of soil C at the time of abandonment (Knops and Tilman, 2000). Within-plot accumulation rates of C and N, estimated via resampling soils of all chronosequence plots, were lower at higher C and N levels. A differential equation model based on this predicts that recovery to 95% of the pre-agricultural levels will require 180 years for N and 230 years for C (E014, Fig. 17; Knops & Tilman 2000).
- ◆ Compositional dissimilarity, species turnover, and rates of perennial and native cover turnover were all negatively correlated with field age, suggesting successional convergence and a decline in successional change as fields age (E054, E014; Fig. 30; Foster & Tilman, in review).
- ◆ The first chronosequence survey in 1983 accurately predicted many of the observed dynamic changes in species abundances but not in species richness (E014; Foster & Tilman, in review)
- ◆ Grasshopper and small mammal abundances fluctuated by an order of magnitude across years (Fig. 29A), and species composition shifted dramatically with field age (E014; Fig. 31).

**D. Related Mechanistic Studies and Theory:** These results suggest that succession emerges from a complex interaction of plant colonization of abandoned fields, of local competition for N, and of herbivory that limits the abundance and impacts of N-fixers (see Section 2.B.D). Because it is well documented and data rich, this chronosequence has been used for short term “snapshots” of successional patterns of 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 & Tilman 1990; Craine et al. 1999a), plant tissue C and N, and arthropod diversity and abundances (Siemann et al. 1996, 1999a). These snapshots have been instrumental in showing that succession is driven more by colonization limitation than by the resource ratio hypothesis (Tilman 1985) that initially

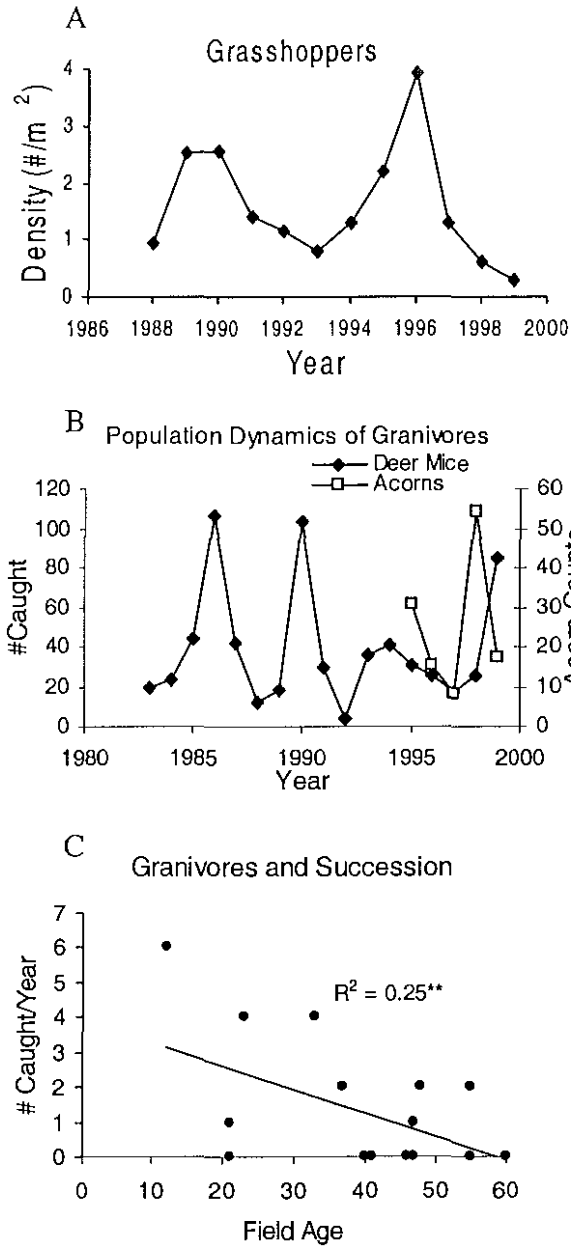


Figure 29. Dynamics of particular trophic groups at Cedar Creek and the influence of successional vegetation change, N addition, and plant species richness on consumer abundance and diversity.

(A) Based on **E014**. Grasshopper densities, averaged over all 22 fields in the old field chronosequence, fluctuated by an order of magnitude from 1988-1999. These fluctuations are best correlated with warm summers, which occurred in 1988 (drought year) and 1995.

(B) Abundance of deer mice in all 22 old fields of **E014** varied by over an order of magnitude with peak abundance lagging one year behind abundant oak mast crops.

(C) Granivorous rodents (primarily *Peromyscus maniculatus*) decline significantly with field age in **E014**, apparently in response to declines in seed availability associated with the dominance of C4 grasses, which produce much less seed per unit biomass, in later successional fields.

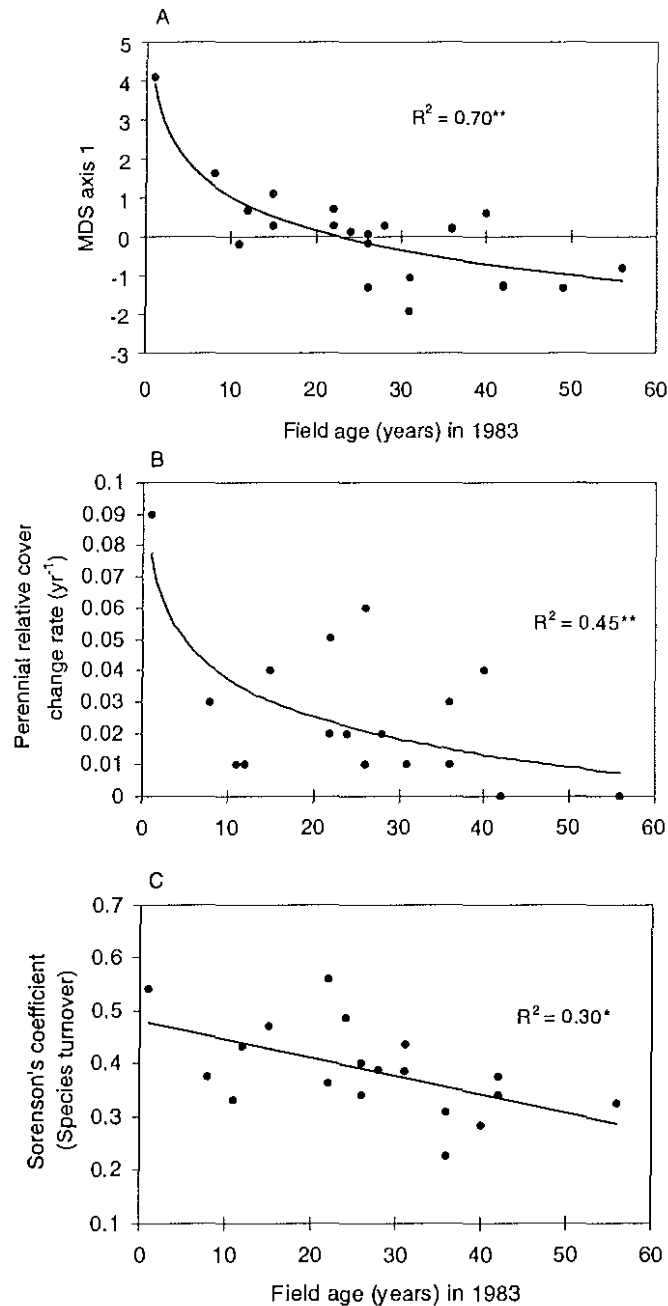


Figure 30. Patterns of succession inferred from re-sampling the 2200 plots of the old field chronosequence, **E014** (from Foster and Tilman (2000) *Plant Ecology*).

(A) Relationship between the first multi-dimensional scaling (MDS) axis of floristic composition and field age.

(B) Relationship between the rate of change in the cover of perennial plants (a measure of the rate of succession) and field age for the 22 fields of the old field chronosequence.

(C) A similar analysis, but using Sorenson's coefficient, which measures the turnover in species composition between the various survey dates. Note that this shows that species turnover is higher in young fields than in older fields, meaning that the rate of change in composition slows as fields age.

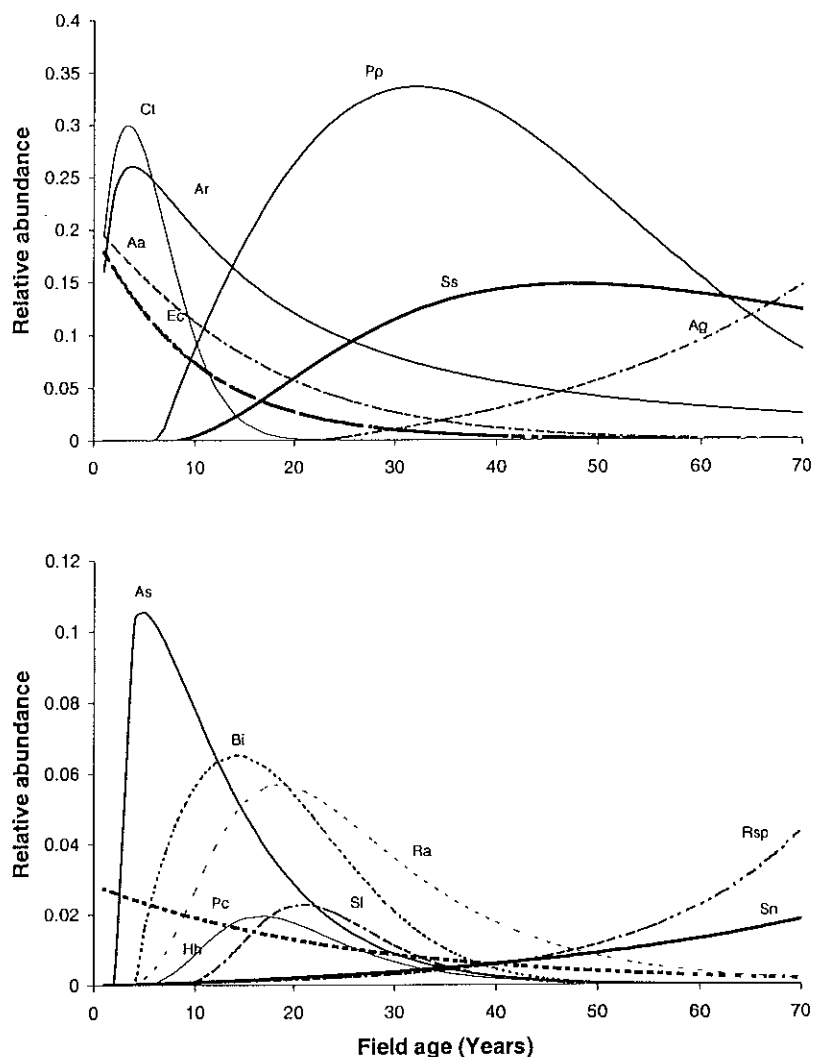


Figure 31. Each fitted curve shows the successional trends in the abundance of a species, with curves shown for the 15 species with the greatest abundance averaged across all sampling dates for all fields in the chronosequence, **E014**. Fitted curves use all data collected on all sampling dates, associating each data point with the then current successional age of a field. Note the difference in scale between the upper and lower graph. (Foster and Tilman, in review).

Aa = *Ambrosia artemisiifolia* ( $r^2 = 0.381$ ,  $P < 0.0001$ ), Ag = *Andropogon gerardi* ( $r^2 = 0.085$ ,  $P < 0.05$ , Ar = *Agropyron repens* ( $r^2 = 0.165$ ,  $P < 0.001$ ), As = *Agrostis scabra* ( $r^2 = 0.440$ ,  $P < 0.0001$ ), Bi = *Berteroa incana* ( $r^2 = 0.215$ ,  $P < 0.0001$ ), Ct = *Crepis tectorum* ( $r^2 = 0.591$ ,  $P < 0.0001$ ), Ec = *Erigeron canadensis* ( $r^2 = 0.504$ ,  $P < 0.0001$ ), Hh = *Hedeoma hispida* ( $r^2 = 0.299$ ,  $P < 0.0001$ ), Pc = *Polygonum convolvulus* ( $r^2 = 0.220$ ,  $P < 0.0001$ ), Pp = *Poa pratensis* ( $r^2 = 0.288$ ,  $P < 0.0001$ ), Ra = *Rumex acetosella* ( $r^2 = 0.171$ ,  $P < 0.001$ ), Rsp = *Rubus* species ( $r^2 = 0.163$ ,  $P < 0.0001$ ), , Sl = *Setaria lutescens* ( $r^2 = 0.134$ ,  $P < 0.01$ ), Sn = *Sorghastrum nutans* ( $r^2 = 0.064$ ,  $P < 0.05$ ), Ss = *Schizachyrium scoparium* ( $r^2 = 0.124$ ,  $P < 0.01$ ).



motivated this work. They continue to provide insights into mechanisms maintaining diversity and regulating C and N budgets following agricultural abandonment.

**E. Future Research:** We will resample soils and vegetation of the full chronosequence, **E014**, in 2002, giving us five sampling dates over a 19 year period. In order to examine the temporal patterns of C and N accumulation, especially at greater soil depths, we will pull deeper cores (to 60 cm depth), which has not been done since our original sampling in 1983. We will continue sampling plant biomass (sorted to species), insect abundances, and small mammal abundances annually.

At Cedar Creek, we are uniquely poised to explore how patterns in insect and plant diversity are influenced by habitat fragmentation and disturbance across 4 orders of magnitude in spatial scale [plot (1 m), transect (80 m), field (100-500 m, and all of Cedar Creek (12 km)], and 2.5 orders of magnitude in temporal scale (1-240 months). Plant diversity patterns will be discerned from the cover plots sampled in each field. To explore this question for insects, we will undertake an extensive insect fauna survey of 8 major orders of insects in each field in 2002, using monthly sweep and pitfall trap samples within the area proscribed by the transects in each field in **E014**. This is possible because of the expertise of our on-site entomologist, John Haarstad. Using the annual grasshopper data, we will also explore patterns of grasshopper diversity and community patterns across different temporal scales. This survey will measure size-diversity relationships at 4 different spatial scales, following Siemann et al. (1996). These data should provide unique insights into the causes of variation in insect and plant diversity.

To further explore species' effects on ecosystem function and succession, J. Knops and D. Wedin propose to examine the mechanism by which species impact ecosystem N cycling. This will use the 16 most abundant plant species of the chronosequence. They will perform a container experiment to determine if plant nutrient use (e.g. allocation patterns, photosynthetic N use efficiency, tissue longevity and stoichiometry) leads to positive feedbacks resulting in diverging productivity and N and C pools on initially identical soils. They will also determine species impacts on N input and losses and the consequence of such differential rates on primary productivity and ecosystem N and C pools. This will provide insights into the aspects of a species' biology that determine the long-term consequences of successional replacements on ecosystem C and N dynamics. This also will test if short term studies of species impacts on N and C can predict long-term successional patterns

### **Section 2.C. Proposed New Studies**

***Interactive Effects of N, Fire and Herbivory:*** We propose a new experiment, led by Ritchie and Knops, to examine interactions between several human-caused environmental changes relevant to Cedar Creek: fire suppression, N deposition, high herbivore densities, and altered species composition. We will focus on early-succession cool-season grasses and forbs, mid- to late-succession warm-season grasses, N-fixing legumes, and late-succession trees. Warm-season grasses increase with and encourage fire, resist herbivores, and inhibit woody plant invasion (Davis et al. 1998, Inouye et al. 1994). N deposition favors cool-season plants (Tilman 1987) that are fire-intolerant and palatable to herbivores. Legumes tolerate fire but decrease with herbivory and N deposition. Finally, woody plants are fire-intolerant and may be more susceptible to herbivory. The response of any ecosystem to the combined effects of fire, N, and herbivory will therefore depend on the ability of these critical plant species to invade and their magnitude of response to the different disturbance factors.

In an unburned old field co-dominated by native cool- and warm-season grasses and forbs, located in an area with historically low fire frequency and neighboring fragments of pre-settlement white pine or oak forests, we will conduct a complete factorial experiment that manipulates N (0 or 3 g m<sup>-2</sup> yr<sup>-1</sup>), fire (none or every 2<sup>nd</sup> year), and the addition, or lack thereof, of 4 critical plant species to 144 m<sup>2</sup> plots. Each set of plots, consisting of all 8 treatment combinations, will be nested inside 8 replicate fences (30 x 60 m) that exclude white-tailed deer, the dominant vertebrate herbivore, and inside 8 replicate unfenced areas of similar size. The 4 plant species that would be added to plots to overcome colonization limitation are a legume (*Lathyrus venosus*), white pine (*Pinus strobus*), bur oak (*Quercus macrocarpa*), and pin oak (*Quercus ellipsoidalis*). Species will be added by broadcasting seeds annually (200 *Lathyrus* and *Pinus*, 50 acorns for oaks), and by planting 8 seedlings of each species in year 1. We will measure treatment effects on composition and diversity of plants and major consumers (insects, small mammals, lizards) annually and on above- and belowground plant biomass, C and N, extractable soil N, and total soil C and N in Years 1 and 5.

***N Deposition in Grassland and Forest:*** Increased N deposition resulting from human activity will potentially alter the biogeochemistry of C, N, base cations, and aluminum (Aber et al. 1989, Schulze 1989, Aber et al. 1993, Aber et al. 1998, Likens et al. 1998, Townsend et al. 1996, Nadelhoffer et al. 1999). Deforestation may weaken links between C and N cycling since grasslands lack significant production of high C:N tissues (i.e., wood) and thus have a low capacity for N-induced C storage (Asner et al. 1997). Furthermore, litter and soil, rather than plant biomass, are strong sinks for N deposition (Nadelhoffer et al. 1998, 1999), although the effect of N on soil processes is uncertain (Berg and Matzner 1997, Aber et al. 1998).

We propose a new N addition experiment, led by Hobbie, in grassland and adjacent oak forest to expand on existing Cedar Creek work. Existing N-addition experiments apply N with other plant nutrients (P, K, Mg, etc). This experiment will add N alone, will be the first large-scale N addition to forest at Cedar Creek and will provide direct comparison of long-term N addition in forest and grassland. We will establish 8 replicate 400 m<sup>2</sup> plots in closed-canopy oak forest and 8 replicate 144 m<sup>2</sup> plots in adjacent old-field grassland for each of three N addition treatments (0, 3, and 10 g N m<sup>-1</sup> y<sup>-1</sup> as NH<sub>4</sub>NO<sub>3</sub>), giving 48 plots. The lower N addition rate is less than is the threshold of ca. 5 g N m<sup>-1</sup> y<sup>-1</sup> above which major species compositional shifts occur (Wedin and Tilman 1996). The higher N addition rate will overcome any N limitation by plants or microbes, and may be indicative of N deposition rates in parts of North America within 50 years. The grassland plots will be the same as the unburned, unfenced, unplanted plots just described for the experiment on the interaction of N, fire and herbivory, but with an added high-N treatment. The forest plots will be in forest adjacent to this field. Periodic measurements in all plots will include: species composition, aboveground NPP, belowground production and biomass, rates of N cycling, decomposition, and N leaching losses. Results will be compared to those of the Harvard Forest LTER chronic N addition experiments (Aber et al. 1993).

***Invasion Ecology:*** The invasion of habitats by non-native species is a global phenomenon with serious consequences for ecological, economic, and social systems (Vitousek et al. 1996; Williamson 1999; Dukes & Mooney 1999; Ewel et al. 1991). Many hypotheses have been proposed to explain the invasibility of communities including disturbance (Crawley 1987, Elton 1958, Hobbs 1989, Orians 1984, Rejmánek 1989), successional stage (Rejmánek 1989), chance (Crawley 1989), herbivory (D'Antonio 1993), absence of mutualists (Crawley 1987; Marler et al.

1999), and species richness of the invaded community (Elton 1958, Case 1990, Lodge 1993, Tilman 1997a, 1999a). We hypothesize (Tilman 1999a; Davis, Grime and Thompson, in review) that the effects on plant invasibility of factors including diversity, plant species composition, disturbance, and herbivory may come via their effects on resource levels, and the resulting effects of resources on potential invaders. Clearly, a propagule of a potentially invading plant species can become established only if it can survive and reproduce on the resources left unconsumed in a habitat. Many PI's will work on these issues, with C. Brown, a post-doctoral researcher, leading a plant species invasion experiment nested within a subset of the Biodiversity II plots. This would focus on neighborhood mechanisms that control establishment of new species in existing communities that differ in diversity and composition (and thus in soil N and water, and light). We would introduce seeds and transplants of 16 species (4 species each from C3 grasses, C4 grasses, forbs and legumes) into several 30 cm x 100 cm subplots within each of 130 plots of Biodiversity II. We would measure responses of all added plant species and levels of limiting resources, and ecophysiological traits and resource use in separate monocultures of the 16 species.

***Microbial Responses to Plant Diversity and Composition:*** Plants are resources or suppliers of organic material to belowground decomposers (primarily microbes). Because plant biodiversity affects NPP and resource quality, decomposer trophic levels should respond to changes in plant diversity as manipulated in Biodiversity I. Preliminary results obtained using DAPI epifluorescent enumeration (Porter and Feig 1980), sole source C use profiles (Ecology plates, Biolog Corp., Garland and Mills 1994), and microbial biomass (Islam and Weil 1998a, 1998b) show complex microbial responses to variation in plant diversity. Final analyses await the completion of the samples.

DAPI enumeration and estimates of total microbial biomass do not provide insights into microbial diversity nor do Biolog data, though they correlate well with microbial functioning (Garland and Mills 1994, Zak et al. 1994b, Guckert et al. 1996), and necessarily correlate with microbial diversity (Smalla et al. 1998). Here we propose using new methods in microbiology to assess microbial diversity responses to manipulations of plant diversity (Yokoyama 1993, Allsopp et al. 1995, Colwell et al. 1995, Tiedje 1995, Kennedy and Gewin 1997, Wall and Moore 1999). To deal with the large number of samples in Cedar Creek research (>1000/y) we will use MoBio Soil DNA isolation kits, a widely used, cost effective method for extracting microbial DNA from soil samples. Currently we are working on collaborations with James Borneman (U. C. Riverside) and possibly Brendan Bohanan (Stanford U.). We plan to do such work in a variety of the long-term core LTER projects, starting with the BioCON experiment (E141), which manipulates plant species richness, CO<sub>2</sub>, N deposition, and the interactions among these factors. We are especially interested in how microbial processes and diversity associate with rates of C and N cycling. In addition, we are looking at the effects of plant diversity on mycorrhizal fungi (R. Burrows and F. Pflieger), and on the abundance and dynamics of plant foliar fungal pathogens (C. Mitchell, in prep.; Knops et al., 1999).

## **Section 2.D. Regional and Cross-Site Research**

We have, underway, a variety of empirical (local Cedar Creek, regionalization, and LTER intersite), synthetic, and theoretical studies to better understand the nature of variation among species in their traits (Reich et al. 1997b, 1998ab, 1999a, 2000, Reich 2000; Ackerly & Reich 1999; Craine et al. 1999a, unpublished data; Westoby et al. 2000; Tjoelker et al. unpublished

data) and the causes and consequences of this variation at plant, patch, ecosystem and landscape scales (Aber et al. 1995, 1996; Reich et al. 1999b; Ollinger et al. 1997, *ms*; Reich 1998a, 2000; Peterson et al. 1999; Frelich & Reich 1999). These are all components of Theme 4. We have found strong evolutionary and physico-chemical constraints on the combination of traits possible in any given tissue or plant, enabling us to develop scaling relations that hold broadly across ecosystems and biomes (Reich et al. 1997b, 1999a), and to better understand convergent evolution (Ackerly & Reich 1999, Ackerly et al. *ms*). We will continue this work by gathering more ecophysiological data on Cedar Creek species, and by synthesizing and integrating these data with existing data and new data from other sites, regionally, nationally and globally.

These findings of fundamental trait relationships have been incorporated into ecosystem-scale models validated against direct data measurements at LTER sites, including stream flow (Aber et al. 1995), eddy covariance (Aber et al. 1996), and ANPP (Reich et al. 1999b) and used to explore spatial scaling issues and hypotheses about ecosystem responses to global change (part of Theme 1) (Aber et al. 1995, Ollinger et al. 1997, *ms*; Reich et al. 1999b). At Cedar Creek, we are modeling biogeochemical processes in the diverse set of local vegetation types, including agricultural, wetland, swamp and other types in addition to the old fields, savannas and forests more intensively studied heretofore at Cedar Creek. Such activities will be expanded regionally to provide simulations of key fluxes at that scale under a variety of global change scenarios (Themes 1 and 4). Additionally, the modeling work at Cedar Creek complements an ongoing multi-site NASA project (BigFoot; Cohen, Gower, Reich, Turner, Running, PIs) where spatially distributed C flux models will be developed and validated at several sites (including at least two LTER sites) against eddy covariance measurements and ground measurements of NPP, and then implemented over 25 km<sup>2</sup> landscapes to assess satellite-based simulations of C flux from the new Earth Observing System spectral sensors. We hope to make Cedar Creek a site for these landscape scale studies by encouraging the development of eddy covariance studies at Cedar Creek. However, no funds are available from the current proposal for these purposes.

Another cross-site activity, led by Mark Ritchie, is the experimental comparison of herbivory across North American sites. This experiment tests alternative hypotheses about how primary productivity influences the effects of herbivores on plant standing crop, composition and diversity, on soil disturbance, and on spatial heterogeneity (Huston 1979, Milchunas et al. 1988, Milchunas and Lauenroth 1993). Further, we are testing whether large (> 100 kg) and intermediate-sized (1-100 kg) herbivores have different effects on these responses, and how effects depend on productivity (Ritchie 1998a, Ritchie and Olf 1998, Olf and Ritchie 1998). Specifically, we established an herbivore enclosure experiment at each of 7 sites across North America [Utah (3 sites), Colorado, South Dakota, Kansas, and Minnesota] that range in primary productivity from 60 - 600 g/m<sup>2</sup>. Each site has 3 unfenced plots (controls), 3 plots with fence to exclude only large herbivores, and 3 plots with fence to exclude all mammalian herbivores > 10 g. In each plot, plant species composition, peak standing crop of litter and live grasses, forbs, and legumes, and current annual growth of woody plants are sampled. The spatial heterogeneity in plant productivity and functional group composition is also measured. Early results in this ongoing study suggest that large and intermediate-sized herbivores have opposite and balancing effects on plant species richness, and that large herbivores reduce plant diversity at low-intermediate productivity but increase plant diversity at high productivity.

J. Knops and W. Koenig have an ongoing cross-site research project surveying acorn densities in Cedar Creek savanna and in 14 California oak woodland and savanna sites (Koenig & Knops 1999). Standard methods (Koenig et al 1994) allow consistent and comparable assays

of acorn crops for determination of spatial and temporal patterns and correlations between sites (Koenig et al. 1996, Koenig & Knops 1998). The Cedar Creek data also document seed production in relation to oak establishment and may give insights into interactions between acorn productivity, small mammal, insect and deer abundances, as observed in the Eastern US (Jones et al. 1998).

Other cross-site activities include studies of plant invasions and diversity in Cedar Creek and Californian savanna (J. Reichman and D. Tilman); of tree-grass ecotone dynamics at Cedar Creek and in Nebraska (J. Knops and D. Wedin); of ecophysiological and community responses to elevated CO<sub>2</sub> at Cedar Creek and at other FACE sites in desert (Neveda), conifer forest (N. Carolina) and hardwood forest (Wisconsin) (P. Reich et al.); and of Cedar Creek forests with regional (e.g., Reich et al. 1997a) and global forests (Reich and Bolstad 2000).

### **Section 2.E. A Synthetic Summary**

Cedar Creek's program of integrative research blends long-term observations, theory, and long-term experiments to develop a predictive understanding of ecosystem response to environmental change. Not surprisingly, this strategy has steered Cedar Creek into becoming a research center that addresses key issues surrounding the dynamics and functioning of human-dominated ecosystems (Fig. 32). Changes in fire frequency, in plant community composition due to biodiversity loss or invasions, changes in trophic structure, in edaphic factors such as soil C, N, and moisture, in atmospheric CO<sub>2</sub>, and in land use have all been, and remain, central foci of Cedar Creek's research. Alterations of these very same elements of environmental change represent the primary characteristics of human-dominated terrestrial ecosystems. Cedar Creek's new directions, consisting of an intensification of research on N-deposition, invasions, alterations of trophic structure, C cycling, and microbial processes are a natural outgrowth of its past and its current emphasis on environmental change.

This program is designed to serve broadly both the scientific community as well as public interests. Its investigators consist of senior and junior researchers, each holding expertise in specific areas of physiological, population, community, and ecosystems ecology, each focusing on different trophic groups (plants, consumers, and decomposers), and each emphasizing observational, experimental, or theoretical approaches. The investigators' interests, however, overlap broadly, creating the mutually reinforcing network of collaborative research projects described in this proposal (Fig 33). This multidisciplinary approach creates efficient use of data and resources leading to the ability of Cedar Creek to tackle complex issues that could not be readily addressed by other means. It permits identifying resource-based, physiological, microbial, ecosystem, and population mechanisms that govern ecosystem response to environmental change. It provides data, insights, theories, and results of interest to many ecological disciplines including population, community, ecosystems, restoration, conservation, plant, animal, and microbial ecology as well as global change biology. Through active publication in a diverse array of scientific journals, presentation in scientific and public forums, workshops, postdoctoral and graduate training, undergraduate internships, outreach, web site sharing of information, and multi-institutional exchanges between Washington, Nebraska, Utah, California, and Minnesota, Cedar Creek's findings reach increasingly larger academic and public audiences. The new directions that augment Cedar Creek's on-going focus on the causes and consequences of environmental change will provide valuable insights into fundamental and applied issues in community and ecosystems ecology.

# Core Long-Term Studies of the Cedar Creek LTER

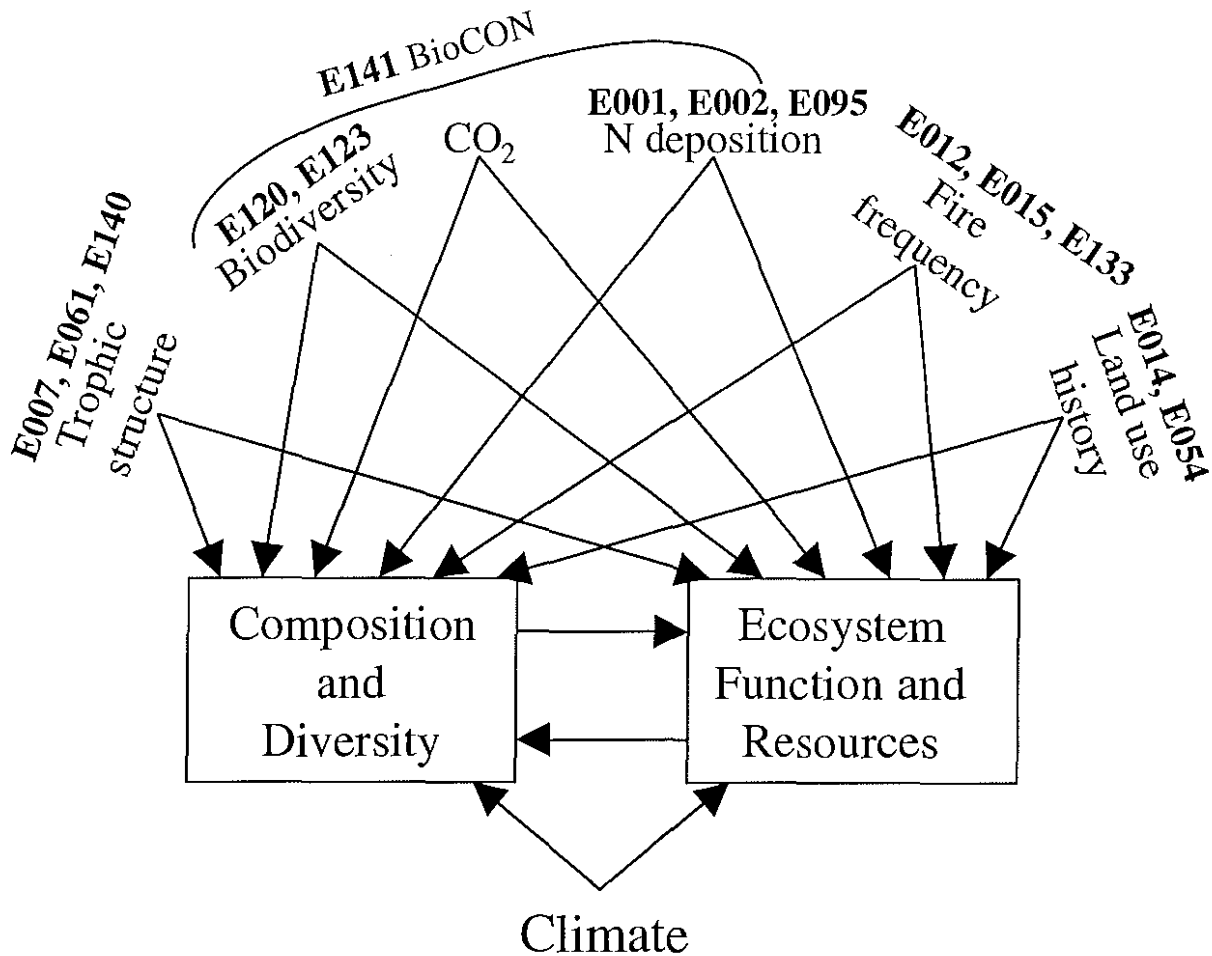


Figure 32. The major topics addressed by the core long-term studies of the Cedar Creek LTER. Each of the core studies addresses how more or more factors (e.g., trophic structure or N deposition, etc.) impacts community composition and diversity, and various aspects of ecosystem functioning. The numbers listed, such as **E141** or **E001**, refer to the experiment number assigned to each LTER study. The 15 studies listed in this figure are the core long-term studies of the LTER.

### Section 3. Literature Cited

(cited papers resulting from the 1994-2000 Cedar Creek LTER are in Section 1.B)

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## Section 4. Site Management

**A. Background.** The Cedar Creek LTER project and the Cedar Creek Natural History Area (CCNHA) field site have developed in tandem. New scientific protocols for sampling and recording observations and new software tools and data management methods developed by LTER researchers are now in demand for non-LTER projects. Summer staff has increased from relatively few when LTER started here in 1982 to over 100 faculty, post-doctoral researchers, graduate students, undergraduates, and technicians on a typical summer day now. Housing, facilities, and equipment have been expanded and adapted to meet this growth. In parallel, management methods and organization of both LTER projects and the field site have been expanded and adapted as well.

**B. CCNHA Management.** David Tilman, the Director of CCNHA, reports administratively to the Dean of the College of Biological Sciences, as previously. Clarence Lehman is a new PI on this grant proposal and in addition has assumed duties in July 1999 as Associate Program Director of CCNHA, reporting to the Director of CCNHA. As Associate Director he oversees all site-related issues, including the allocation and use of all facilities, equipment, and housing, review and approval of all experiments, long-range site planning, and all site-related personnel, such as the resident supervisor, resident entomologist, and summer interns. He provides day-to-day coordination and guidance for all research performed at CCNHA, including the Cedar Creek LTER. He oversees all University budgets related to CCNHA. As an LTER PI, he coordinates the LTER subaccounts established for all PI's, and he organizes and coordinates regular meetings of the LTER PI's.

Many CCNHA and LTER management procedures are being formalized and decentralized, so that decisions are delegated to the level at which they apply. For example, (1) Review of proposals for research at CCNHA is now coordinated on site (by C. Lehman). (2) Allocation of central facilities and shared summer employees is coordinated by discussions among all PI's. (3) Initial interviews for summer interns and hiring recommendations are now made by the team leaders responsible for supervising them. (4) Reporting structure for the analytical chemistry laboratory has been moved to CCNHA (C. Lehman), with time allocated back to individual projects, both LTER and non-LTER. Similar changes will be made for other shared personnel or facilities as needed.

**C. LTER Funding and Research Decisions.** Our group of LTER PI's is the largest it ever has been. Though there are overlaps, the LTER PI's have differing research interests that, in total, span the LTER goals (Figure 33). Our management plan is to establish frequent meetings in which there is open discussion of all issues, scientific and budgetary. Our evolving structure is designed to support this communication and to maintain high scientific productivity from the LTER. To do this, PIs meet periodically to discuss scientific and administrative issues. Meetings, chaired by D. Tilman, include an annual late winter three-day LTER Retreat (often out-of-town to allow better focus), monthly meetings of all PI's during the field season, weekly meetings of PI's and staff during the field season, and monthly meetings of the five resident PI's (M.D., S.H., C.L., P.R., D.T.) during the off-season. Before the meeting of the resident PIs, we poll the off-site PI's on issues. Meetings are designed to have an informal format to encourage wide-ranging discussion.

At the Retreat we systematically review all existing research projects, discuss results, and raise potential new research initiatives. From this discussion come our priorities and a plan on how best to combine the interests and abilities of members of the LTER team to meet LTER goals. From

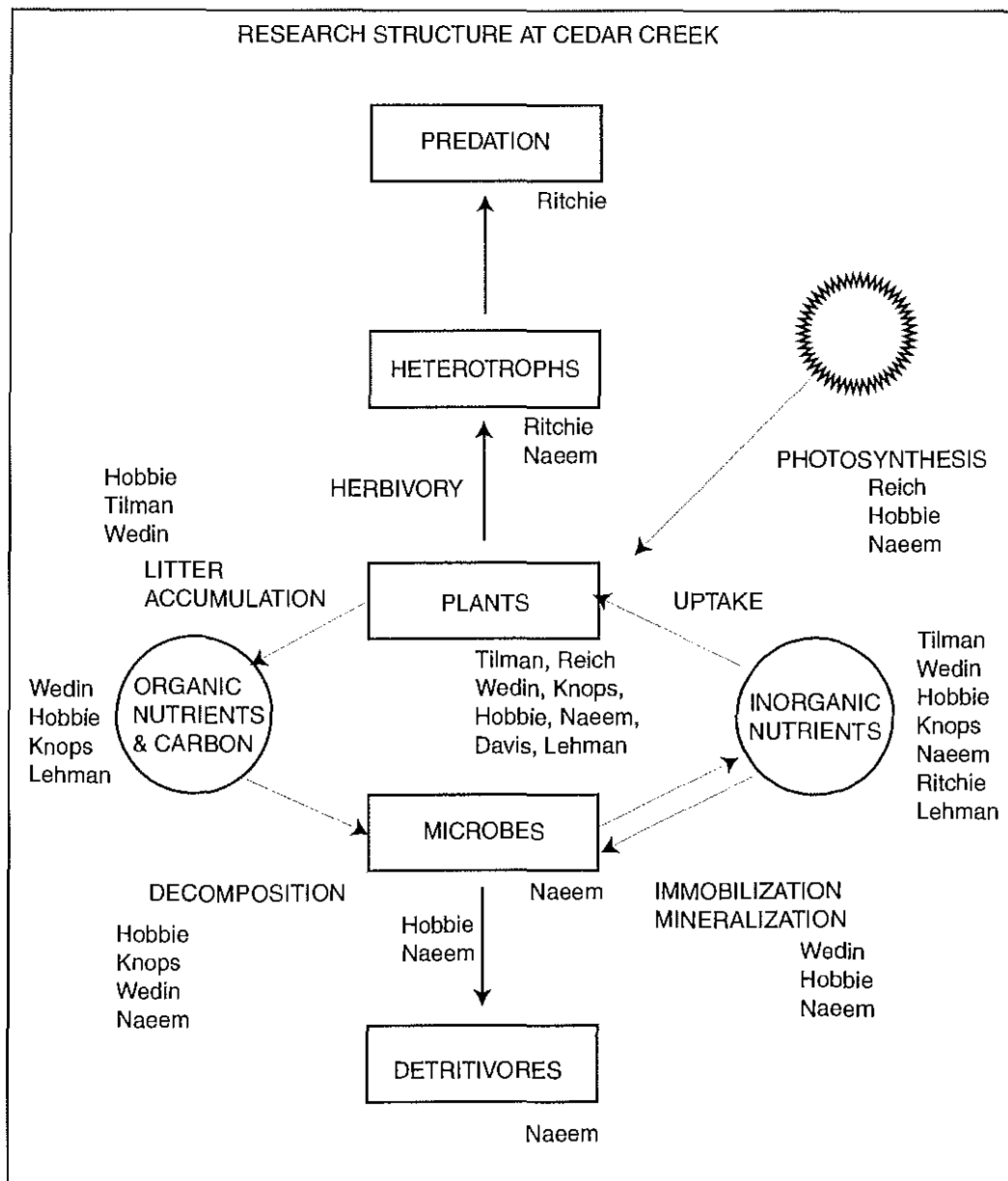


Figure 33. Framework of structure of Cedar Creek research and principle investigators. This figure illustrates the fundamental components of a community and its ecosystem processes and the areas of study by each of the principle investigators. In understanding how communities and ecosystems respond to environmental change, such as biodiversity loss, invasion, N deposition, CO<sub>2</sub> enrichment, or alteration of trophic structure, the investigators focus on population to ecosystem processes to identify mechanisms. Approaches include observational, experimental, and theoretical approaches.

that plan, in turn, budget allocations follow. Any initiative started through the above process must be approved by the field site, which follows the same procedure for both LTER and non-LTER projects. (This procedure includes a written proposal which is distributed to two or three peer reviewers who examine the project for compliance with field site rules and conventions, for non-interference with existing and future experiments at the field site, and for scientific merit.) Because of existing commitments of LTER funds to the established long-term projects that are the focus of our work, major new initiatives most often must be supported by a combination of LTER funds and funds from a new grant. For smaller initiatives, LTER funds may be reallocated among sub-accounts, or personnel or services may be reallocated, as appropriate, to be used by the initiative's research sub-team. Such resource allocations are made by consensus typically before the start of a field season, and are always subject to the constraint that we retain our commitment to the long-term research that is the core of our project.

**D. Participation of Other Scientists.** Just as plant diversity increases primary productivity, we feel that intellectual diversity can increase scientific productivity. Thus, we openly encourage non-project scientists to join in Cedar Creek LTER research. Such interactions can be particularly fruitful when the other scientists have skills and/or ideas that differ from those of the Cedar Creek LTER PIs. For instance, Phil Grime of Sheffield, UK, has markedly different views on plant community ecology and on the reasons why plant diversity might effect ecosystem functioning than David Tilman (e.g., Grime 1997). In conjunction with his Ph. D. student Graham Burt-Smith, he is working on Biodiversity-I to test his ideas on the role of plant traits as determinants of community composition and of ecosystem responses to diversity. Similarly, F. S. Chapin and his Ph. D. student, Joe Craine, add ecophysiological skills related to root dynamics.

Ongoing work by non-LTER researchers includes studies of bacterial genetic and phenotypic diversity, by Linda Kinkel and Deborah Samac, Plant Pathology, U of MN (NSF, \$782,082 for a Microbial Observatory); biological stoichiometry, by James Cotner and Robert Sterner, Ecology, U of MN (NSF, \$849,944 subcontract to U. of MN); impacts of insect herbivory, by Walt Carson, U of Pittsburg (NSF, \$373,910); spatial dynamics of rust infections, by C. Barnes and J. Groth, Plant Pathology, U of MN (Agric. Exper. Stn, \$8000); above and below-ground plant dynamics, by Joseph Craine, U. C. Berkeley (NSF and NASA, \$66,000 total); mycorrhizal functioning under elevated CO<sub>2</sub> and N, by Nancy Johnson, Northern Arizona University (NSF, \$500,000); predictions of community structure and dynamics, Graham Burt-Smith and J. P. Grime (Nat. Environ. Research Council, UK); and a variety of projects by NSF and/or University of Minnesota grants to graduate students for study at Cedar Creek.

In addition to the above, this is the 60th anniversary of CCNHA's founding. We are preparing a comprehensive plan for the field site's next 30 years. Its development is involving all researchers who have been associated with Cedar Creek in the past and all those who have potential for doing so in the future. This process is generating a diverse set of ideas that connect new and past projects, and is expected to further involve non-LTER researchers in Cedar Creek work.

**E. Summary.** Our management style is an evolving response to the changing needs of our LTER, which has grown and diversified greatly in the past 6 years. It has a wide range of interests, and naturally forms diverse arrays of sub-teams to suggest and tackle specific questions. We have learned that our management structure necessarily involves flexibility and change, and that the most critical element is regular, open discussion by all PI's.



## Section 5. Data and Information Management

Cedar Creek data are managed according to two principles: (a) data quality and availability must be assured for the long-term, and (b) data organization must promote research and analysis. LTER data management personnel are involved in all core LTER projects from their beginnings, helping with plot placement, suggesting numbering schemes to reduce data-gathering errors, performing treatment randomization, and maintaining detailed design notes. Data management personnel prepare the procedures and forms for standardized data collection, such as for plant percent cover, biomass, and soil nutrients. Field data collected from all palmtop computers pass through a common downloading, backup, and processing program on our central computer. All numerical analyses of output from autoanalyzers and other chemistry equipment are performed by software procedures designed to assure data quality. This approach, started for core LTER projects and now adopted by non-LTER projects at the site, means that most data collected at Cedar Creek is automatically contributed to the site's archival database. Derived data, of course, still must be contributed to the database. Derived data are retrieved from researchers through email solicitations, phone calls, and personal visits by the Data Manager.

**A. Data Storage.** After data are collected, validated, and edited, they are stored as tables in a simple non-proprietary Ascii format (Fig. 34). This format is designed so that (1) documentation (i.e., meta-data) can be incorporated directly, (2) the data can be printed, read, and directly understood without using special programs, and (3) it can be readily imported into proprietary computer applications such as spread sheets, data bases, and statistical packages. A simple non-proprietary format is one of the most reliable ways to keep data accessible for long periods, during which time computers and the recording media continually change.

Each round of data collection (e.g., all the soil total nitrogen measurements taken in the first sampling of Experiment 121 in 1999) is assigned a unique serial number, which it retains for all time. If any modifications are needed to the data stored under that accession number, notes defining which lines and columns have been changed, and their previous contents, are stored at the end of the data to allow any version of the original data to be reconstructed automatically. This is similar in concept to a software source code control system (such as Unix SCCS).

We have a large collection of soil and plant tissue samples archived for the distant future (over 30,000 samples to date) that are tracked in the database through files of the format described above. (Fig. 35; also [www.lter.unn.edu/samples](http://www.lter.unn.edu/samples)). We also use the database to record map coordinates for sampling locations within experimental plots.

**B. Data acquisition.** Whenever possible, data are acquired directly from machines that produce them; data collected on paper are the exception. Automatically collected data include:

1. *Analytical balances.* Scales are connected to computers by communications lines. Attached to each scale (*Mettler*) is a bar-code reader (*Riverside*). Before samples to be weighed are collected in the field, bar-coded labels are printed (e.g., Fig. 36) and placed directly on sample containers. At the weighing machine, the only action necessary is to place the sample on the scale and point the bar-code reader at the label. This technology has virtually eliminated the minor errors that had to be corrected in the past when a weighed sample was incorrectly identified. The software for this was developed at Cedar Creek.

2. *Field observations.* Palm-top computers (*HP200LX*) are used for most data entry in the field. These are personal computers small enough to fit in a pocket. The software is a specialized spread-sheet-like package developed at Cedar Creek that makes it easy to search for scientific names, enter numeric values, display notes for species identification, and so forth.

Title: Productivity on a fertilization gradient  
 Project: E001  
 Datasets: biomass, species richness  
 Accession: 1001681

Label Exp: Experiment number.  
 Label Year: Year of collection.  
 Label Field: Field code (A, B, C, D).  
 Label Plot: Plot number.  
 Label Trt: Treatment code, representing grams of nitrogen added per square meter per year. (1=0gN, 2=1.0gN, 3=2.0gN, 4=3.4gN, 5=5.4gN, 6=9.5gN, 7=7.0gN, 8=7.2gN, 9=0gN. Treatments 1-8 have the trace metals P, K, Ca, Mg, and S added; treatment 9 has nothing added at all).  
 Label Prod: Aboveground productivity, dry biomass (g/m2/yr).  
 Label SR: Species richness (total number of species present).  
 Label Shannon: Shannon index of species diversity.

Exp	Year	Field	Plot	Trt	Prod	SR	Shannon	<== Labels
001	1982	A	01	9	61.3	13	1.998	
001	1982	A	05	9	436.5	9	0.803	
001	1982	A	12	1	105.5	19	1.858	
001	1982	A	20	9	84.3	9	1.473	
001	1982	B	01	1	94.0	7	0.634	
001	1982	B	06	9	164.1	8	0.739	
001	1982	B	11	1	66.8	11	1.566	
001	1982	B	12	9	132.8	8	0.340	
.	.	.	.	.	.	.	.	
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.	.	.	.	.	.	.	.	

**Figure 34**

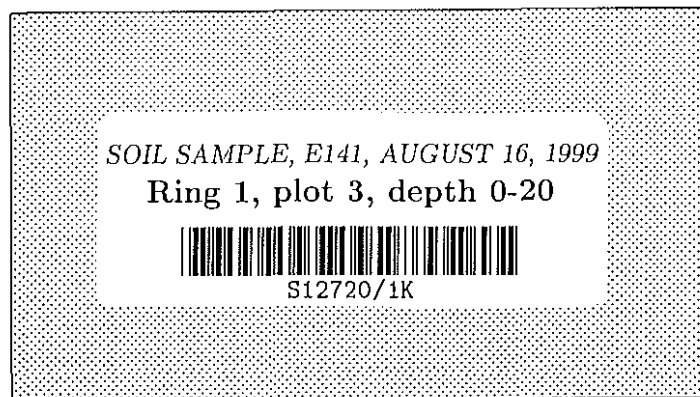
Showing the format of data recorded in the Cedar Creek data archives. Archival data are stored in a simple ASCII format that will not become obsolete with changing computer generations, yet can be readily imported into proprietary database or statistical packages.

## Summary of Cedar Creek Archival Samples

<i>Description</i>	<i>Proj.</i>	<i>Soil Samples</i>	<i>Biomass Samples</i>	<i>Litter Samples</i>	<i>Total</i>
Biodiversity-I	E123	1,764	1,054	1,505	4,323
Biodiversity-II	E120	1,238	2,390	42	3,670
BioCON	E141	4,412	1,572	762	6,746
Functional group simplification	E116	100	-	-	100
Herbivory and plant diversity	E140	144	-	-	144
Legume competition	E070	168	448	-	616
Monoculture plots	E111	-	1,295	-	1,295
Nitrogen and disturbance	E052	208	-	-	208
N addition to undisturbed vegetation	E001	1,270	1,815	716	3,801
Nitrogen gradient	E055	826	84	167	1,077
Nitrogen supply and disturbance	E004	255	893	-	1,148
Oak canopy and resource heterogeneity	E135	-	-	243	243
Productivity in old-field chronosequence	E054	-	231	-	231
Survey in old-field chronosequence	E014	6,304	-	-	6,304
Primary productivity and gophers	E138	162	-	-	162
Fire frequency in savanna	E133	-	-	258	258
Secondary succession	E064	2,580	-	-	2,580
Tree competition	E069	152	478	-	630
<b>Totals</b>		<b>19,583</b>	<b>10,260</b>	<b>3,693</b>	<b>33,536</b>

**Figure 35.**

To date, over 30,000 samples of soil, biomass, and litter have been archived for reference in the distant future. These samples are distributed among projects as shown above. Archiving of a sample involves placing it in a suitable archival container (e.g., a glass screw-top vial for soils), labeling each container with a laser-printed label that identifies the sample, organizing all containers for a sampling period in numerical order in drawers or boxes, and labeling the boxes as to their contents. All data for individual samples are included in printed form in the boxes and in electronic form on the web ([www.lter.umn.edu/samples](http://www.lter.umn.edu/samples)). Many early samples were collected before this archival system was established. They are not represented in the figure above, but are being placed in the archival system as time permits.



**Figure 36**

Sample barcoded label used for automated weighing of Cedar Creek samples. These labels, printed on an ordinary laser printer, have virtually eliminated simple weighing errors.

3. *Light readings.* Ratios of below- to above-canopy light penetration are taken with recording light meters (*Decagon*), annotated with plot number or other code for location while they are taken, then downloaded over communication lines.

4. *Weather station.* Climatological data such as temperature, rainfall, and wind speed are monitored by a permanent weather station (*Campbell*) at Cedar Creek. The weather station periodically downloads its data to a computer at the field site, where it is automatically formatted and placed on the world-wide web. Data are summarized hourly.

**C. Web Site.** We have a substantial web site comprising over 7000 web pages and 5000 images ([www.lter.umn.edu](http://www.lter.umn.edu)). All major projects are described there. Components of the web site include (a) descriptions of major projects, (b) data, (c) weather records, (d) lists of archives, (e) flora and fauna, (f) plant identification pictures, (g) bibliography, (h) research opportunities, (i) site personnel, and (j) other material. Our most recent addition is a large section (over 1500 web pages and 1500 images) describing the insects of Cedar Creek ([www.lter.umn.edu/insects](http://www.lter.umn.edu/insects)), which is our most diverse and well-sampled community.

**D. Data access.** Data often result from multi-year research efforts, and the original investigators who have invested such effort naturally have first priority to the data. To respect this priority yet promote broad use, our data are organized into three classes:

1. *Available directly on the web.* In this class are meteorological data, information on flora and fauna, and information on the layout and design of experiments.

2. *Available on the web after registration.* In this class are treatment summaries of biomass, percent cover, soil nutrients, light penetration, and other variables for major experiments. Access to data is immediate and automatic once the researcher agrees to the code of ethics by providing a name and address on a web form.

3. *Available through the original investigator.* All major experiments are documented on the world wide web with the name of the original investigator. Researchers desiring access to non-summary data that are in the process of publishing must contact the LTER investigator. Experience has shown that for non-LTER users, some data are best shared in collaborative work with original investigators, thus minimizing the chance that data would be misinterpreted or used out of context.

We emphasize that this is a dynamic policy in a rapidly changing technological field. Our data policy has adjusted to new situations as they arose (e.g., the web), and may need further adjustment in the future. The LTER grant pays only a portion of the cost of data collection and management at Cedar Creek, and investigators must feel that they have reasonable priority and control if we are to convince them to submit data collected with other funding to be part of the LTER data set. Our data policy will comply with developing NSF and federal policy, and with codes of ethics developed by scientific societies to address the use of data gathered by others.

Weather data are updated on the web daily. Other data are updated on the web during the winter following the summer field season in which they were gathered. Data for core LTER experiments has always been available electronically use within weeks of its collection. The Cedar Creek field site would now like to apply similar standards to data collected by non-LTER projects and to maintain a Cedar Creek data archive patterned after the LTER standards.

**E. Data archiving.** We consider the proper archiving of LTER data to be among our greatest responsibilities. The data we collect is valuable now, but will likely become increasingly valuable in the future. The Rothamsted England site is a case in point; experiments there have been running for over a century, and the original data, including archived samples, have complemented present data in modern research studies (see Leigh and Johnston, *Long-term Experiments in Agricultural and Ecological Sciences*, 1993). That was possible because the original data and

archived samples were preserved and curated for over 150 years. Unfortunately, modern magnetic computer media have a much short life, primarily because any given storage format (e.g. 8" floppy disks) becomes obsolete, and within a few decades no machines exist to read that format. Any lapses in field-site funding during the next century that prevent all data from being copied to new media would result in loss of data. As long as we have funding, we will maintain the data in the most modern digital form, with multi-site backup. However, as an ultimate archival backup, we also employ a novel algorithm named *PERMI*, developed for the Cedar Creek LTER. It applies to printed paper records the same kind of error-checking codes presently used on computer media like magnetic disks. If a page printed with *PERMI* is later scanned, these error-checking codes allow the computer to detect any scanning errors and rescan erroneous parts of the page automatically, thereby achieving the same accuracy in printed text as commonly expected from magnetic computer media. As we transcribe certain old Cedar Creek records from hand-written form to electronic media, we are taking care to print archival copies using *PERMI*. Should the electronic form ever be lost, a computer scanner can retrieve data from the paper copies with complete reliability. In addition to normal electronic storage, the full set of data and metadata associated with each of the core LTER studies discussed in this grant is recorded on pages printed with *PERMI*. These printed pages, housed both at Cedar Creek and on the central campus of the University of Minnesota, will remain readable and scannable as long as our alphabet is intact and paper copies can survive. (See our web site at [www.lter.umn.edu/tools/utility/perm1.pdf](http://www.lter.umn.edu/tools/utility/perm1.pdf) for a complete technical description of the *PERMI* algorithm.)

**F. Computing equipment.** We have two main computer sites: (1) Campus equipment includes a Sun Sparc 10 multiprocessor attached to the local network and the Internet. This machine handles email, serves the main web site, and is the main data repository. It also handles data analysis, statistical analyses using SAS, and numerical simulation. Additional campus computer equipment includes approximately one dozen personal computers, several laser printers, inkjet printers, a slide scanner, a document scanner, and a slide maker. (2) Field site equipment includes a Sun Ultra 450 multiprocessor with 50GB of secondary storage. This machine serves email locally, serves the local web site, and is an auxiliary data repository and backup machine for computation and data analysis. It is connected to other machines at the site by a local Ethernet and to the world by T1 communications lines. Additional computer equipment on the site includes approximately two dozen personal computers, four attached to analytical balances with bar-code readers, one dozen palmtop computers, several laser printers, inkjet printers, a document scanner, and a digital-imaging microscope connected to a computer for macrophotography.

**G. Data backup.** The full set of all LTER core data, metadata, and all related data, are stored on hard disks both on campus and 35 miles away at Cedar Creek, and on tape at the homes of D. Tilman and C. Lehman. In addition, our system is backed up using three different methods, each independent of the others to reduce the chance that all methods fail at once. (1) Each night files modified during the previous day are automatically copied to a backup tape using the standard backup method of the operating system (Unix *ufsdump*). Biweekly a composite tape of the entire system is created and taken off site. (2) Later each night an independent software system called *Mirrim* automatically collects all files modified during the day on campus into a single collective file and transmits that file to the Cedar Creek computer. The collected files are retained as long as disk space permits (typically six months). (3) Each year new printed copies of the basic data are produced, using the *PERMI* algorithm described above. This provides ultimate archival backup.

## Section 6. Public Communication and Education

We believe that scientists are obliged to communicate their findings not just with other scientists but, when relevant, with the public. The only logical reason for public support of research is that research ultimately helps society. However, if research that is relevant to societal issues is not communicated with the public, it will be of limited utility to the public, and public support for research would likely diminish.

These thoughts motivate the Cedar Creek approach to public communication and education. When results of our research seem relevant to issues of public interest, which is often the case for research related to environmental issues, we try to communicate the results with the public and, as appropriate, with local and national public officials. Although such activities can be time-consuming, we consider them an obligation we took on by accepting public research funds. Such activities have been undertaken by many different Cedar Creek LTER researchers.

We participate in three modes of public communication and education. The first is by responding to the media when reporters for newspapers, magazines, radio or television contact us about our research. We have found that this occurs most frequently for papers published in *Nature* or *Science* because science reporters read these journals, and the journals send science reporters press releases about selected articles. Second, we give public talks on our research. Third, we give talks to, or testify before, various state and national governmental organizations.

**Newspapers:** In particular, during the course of the current LTER grant (1994-2000), our public communication and education efforts have included interviews for 34 newspaper articles. The "Science Times" section of the *New York Times* has published 8 articles, most a half page to a full page in length, on Cedar Creek LTER research, and it has been covered by the *Boston Globe*, the *Milwaukee Journal Sentinel*, the *Washington Post*, the *London Times*, the *Des Moines Register*, the *London Daily Telegraph*, the *Minneapolis Star Tribune*, the *St. Paul Pioneer Press*, and by other newspapers that picked up stories supplied by the Associated Press and by Reuters.

**Magazines:** There also have been 55 magazine articles related to Cedar Creek LTER research, with coverage ranging from *Good Housekeeping*, and *U. S. News and World Report*, to *Smithsonian*, *Discover Magazine*, and *National Wildlife*, to *The Economist*, *Science* and *Nature*, to *Garbage*, *Earth*, and *Mother Jones*, to the *Congressional Record*.

**Radio:** We have participated a total of 29 radio interviews and talk shows including the Earth Day version of National Public Radio's *Science Friday with Ira Flato*; a morning drive-time talk show on KPSA radio of Berkeley, CA; the BBC's *Science Update* and its *World Service Radio* programs; the Australian Broadcasting Corporation's *Earth Beat* program; Chicago's WBEZ public radio; Minnesota Public Radio; the Voice of America; the Canadian Broadcasting Corporation's *Radio Active* program; Monitor Radio; and Associated Press Radio.

**Governmental Testimony and Service:** We have also given presentations or formal testimony to state and federal legislative bodies and governmental officials on 11 occasions, including the Minnesota legislature's Environment and Natural Resources Committees, the Minneapolis Park Board, the White House Office of Science and Technology Policy, the U.S. House Agriculture Committee, the U.S. Senate Natural Resources Committee, and the U.S. Senate Committee on Agriculture, Forestry and Nutrition. In addition, D. Tilman served on the President's Committee of Advisors on Science and Technology (PCAST) Subcommittee on Biodiversity.

**Documentary/TV:** Cedar Creek research has been featured in TV/video coverage six times, including the made-for-TV documentary *The Web of Life*, two other documentaries that have been filmed but not yet produced, a short clip in *Bill Nye the Science Guy*, and a self-produced slide show and video titled, *Isanti County: A Rural Landscape At A Crossroads*.

**Public Talks and Seminars:** Finally, Cedar Creek researchers have given many public talks on our research and its relevance to society, including talks at elementary and high schools, at various conservation organizations, at museums and at a botanical garden, to the Board of Directors of a major foundation, and to a business group, and given both general audience talks and research seminars at many universities.

### **Some Highlights of Media Coverage of Cedar Creek LTER Work**

Article by William Stevens, of *The New York Times*, entitled "Study Bolsters Value of Species Diversity" page B7 of the Tuesday, February 1, 1994, Science Times section of *The New York Times*. Based on D. Tilman and J.A. Downing. 1994. *Nature* 367:363-365.

Article by Linda J. Brown, of *Good Housekeeping*, entitled "There is strength in numbers" appearing in the July 1994 *Good Housekeeping*, page 96. Based on D. Tilman and J.A. Downing. 1994. *Nature* 367:363-365.

Public TV production entitled "Web of Life" produced by WQED TV, first airing on public television in April 1995.

Article by William K. Stevens entitled "Extinction of the fittest may be the legacy of lost habitats" page B8 of the September 27, 1994, *The New York Times*. Based on Tilman et al. 1994. *Nature* 371:65-66.

Article by Roger Highfield entitled "Your number's up: the maths of extinction" featuring an interview with Robert May, and appearing in the October 26, 1994, *Daily Telegraph* in London, England. It is based on Tilman, May, Lehman and Nowak 1994. *Nature* 371:65-66.

Article by Carol Yoon, of *The New York Times*, entitled "Ecosystem's Productivity Rises with Diversity of its Species," appearing Tuesday, March 5, 1996, Page B8. Based on Tilman, Wedin and Knops. 1996. *Nature* 379: 718-720.

Article by William Stevens, *The New York Times*, entitled "Too Much of a Good Thing Makes Benign Nitrogen a Triple Threat," appearing in "Science Times," Tuesday, December 10, 1996, Page B5. Based on Wedin and Tilman. 1996. *Science* 274: 1720-1723.

Article by Jane Brody, *New York Times* "Science Times" entitled, "A delicate creature yields its secrets," highlighting work of John Haarstad. Tuesday, August 12, 1997, Page B7.

Article by William Stevens, *The New York Times*, entitled, "Ecologist measures nature's mosaic, one plot at a time," appearing Tuesday, October 6, 1998, Pages B11 and B15.

Article by Paul Raeburn, *Popular Science*, entitled "Science answers the most critical questions for the 21<sup>st</sup> century," pages 48-50, January 2000.