

## COVER SHEET FOR PROPOSAL TO THE NATIONAL SCIENCE FOUNDATION

PROGRAM ANNOUNCEMENT/SOLICITATION NO./CLOSING DATE/if not in response to a program announcement/solicitation enter NSF 04-23					<b>FOR NSF USE ONLY</b>	
<b>PD 05-7381</b>					<b>NSF PROPOSAL NUMBER</b>	
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<b>DEB - ECOSYSTEM SCIENCE CLUSTER</b>						
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IS AWARDEE ORGANIZATION (Check All That Apply) (See GPG II.C For Definitions) <input type="checkbox"/> SMALL BUSINESS <input type="checkbox"/> MINORITY BUSINESS <input type="checkbox"/> IF THIS IS A PRELIMINARY PROPOSAL THEN CHECK HERE <input type="checkbox"/> FOR-PROFIT ORGANIZATION <input type="checkbox"/> WOMAN-OWNED BUSINESS						
TITLE OF PROPOSED PROJECT <b>Biodiversity, Environmental Change and Ecosystem Functioning at the Prairie-Forest Boarder</b>						
REQUESTED AMOUNT \$ <b>4,920,000</b>		PROPOSED DURATION (1-60 MONTHS) <b>72</b> months		REQUESTED STARTING DATE <b>10/01/06</b>		SHOW RELATED PRELIMINARY PROPOSAL NO. IF APPLICABLE
CHECK APPROPRIATE BOX(ES) IF THIS PROPOSAL INCLUDES ANY OF THE ITEMS LISTED BELOW						
<input type="checkbox"/> BEGINNING INVESTIGATOR (GPG I.A) <input type="checkbox"/> HUMAN SUBJECTS (GPG II.D.6) Exemption Subsection _____ or IRB App. Date _____						
<input type="checkbox"/> DISCLOSURE OF LOBBYING ACTIVITIES (GPG II.C) <input type="checkbox"/> INTERNATIONAL COOPERATIVE ACTIVITIES: COUNTRY/COUNTRIES INVOLVED (GPG II.C.2.j)						
<input type="checkbox"/> PROPRIETARY & PRIVILEGED INFORMATION (GPG I.B, II.C.1.d) <input type="checkbox"/> HIGH RESOLUTION GRAPHICS/OTHER GRAPHICS WHERE EXACT COLOR REPRESENTATION IS REQUIRED FOR PROPER INTERPRETATION (GPG I.G.1)						
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<input type="checkbox"/> SMALL GRANT FOR EXPLOR. RESEARCH (SGER) (GPG II.D.1)						
<input type="checkbox"/> VERTEBRATE ANIMALS (GPG II.D.5) IACUC App. Date _____						
PI/PD DEPARTMENT <b>Dept. of Ecology, Evolution &amp; Behavior</b>			PI/PD POSTAL ADDRESS <b>100 Ecology Building 1987 Upper Buford Circle Saint Paul, MN 55108 United States</b>			
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CO-PI/PD						

## Project Summary

### Intellectual Merits:

The Cedar Creek Long-Term Ecological Research project, which has eleven co-investigators, would use long-term experimentation, observation and theory to examine (1) the impacts of human-driven changes—especially loss of biodiversity, climatic variation, N deposition, land cover and use change, changes in fire frequency, elevated CO<sub>2</sub>, and exotic species—on community dynamics and ecosystem structure and function; (2) how the traits and evolutionary heritages of species influence community assembly, ecosystem dynamics, biogeochemistry and the invasiveness of exotic species; (3) how predators, pathogens and diseases influence species and ecosystem dynamics; (4) the causes of multispecies coexistence; and (5) how the quantity and economic value of services produced by ecosystems depends on ecosystem species composition, diversity and management. These questions would be pursued in a coordinated series of large-scale, long-term field experiments, related long-term observational studies, and theoretical analyses.

The overriding goal of this research is to provide deeper understanding of the processes and principles that govern the dynamics and functioning of communities and ecosystems. This research centers on the interplay among experimental results, observational data, and the predictions of theory. Each constrains, modifies and inspires the other, providing deeper understanding of the dynamics and functioning of the grassland, savanna, and forested ecosystems of the region. The research combines studies of numerous species on several trophic levels with studies of ecosystem processes and of the feedbacks between species and the ecosystem processes. It combines and synthesizes the often disparate approaches of ecophysiology, population, community and ecosystem ecology. The new and continuing work proposed would build on the rich knowledge base that has accumulated at the site.

### Broader Impacts:

This project achieves broader impacts because results of the proposed studies would improve understanding of the long-term societal implications of human impacts on ecosystems. For instance, the research would help elucidate both the factors that control biodiversity and the effects of the loss of biodiversity on ecosystem services such as the removal by ecosystems of atmospheric carbon dioxide and the long-term sequestration of this carbon in soil. In addition, results would be communicated to the media and government organizations; K-12 teachers, K-12 students, journalists and the general public would be taught about scientific research and recent results; undergraduates would gain research experiences; and graduate students and post-doctoral researchers would receive advanced research training.

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Appendix (List below. ) <b>(Include only if allowed by a specific program announcement/ solicitation or if approved in advance by the appropriate NSF Assistant Director or designee)</b>	_____	_____
Appendix Items:		

\*Proposers may select any numbering mechanism for the proposal. The entire proposal however, must be paginated. Complete both columns only if the proposal is numbered consecutively.

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## Section 1. A. RESULTS OF PRIOR NSF LTER SUPPORT

NSF/DEB-0080382, Long-Term Ecological Research (LTER; 2000-2006) *Biodiversity, Disturbance and Ecosystem Functioning at the Prairie-Forest Border*, G. David Tilman, Peter B. Reich and Sarah E. Hobbie, co-PI's. \$700,000 per year.

From its inception in 1982, the Cedar Creek LTER (which we abbreviate CDR) has combined and synthesized ecophysiological, population, community and ecosystem perspectives using the interplay among experiments, theory and long-term observations. During the past six years, research in the grasslands and woodlands of Cedar Creek Natural History Area (CCNHA) has added to mechanistic understanding of (1) the causes and consequences of biodiversity, (2) the population, community and ecosystem impacts of human-driven environmental changes, especially elevated CO<sub>2</sub>, elevated nitrogen (N) deposition, changes in plant biodiversity, altered disturbance regimes, and changes in trophic structure, and (3) the underlying processes, mechanisms, interactions and feedbacks that control the dynamics, structure and functioning of CCNHA communities. The results of this research are presented in numerous publications (*Supplementary Documentation: Table 1: Publications of the Cedar Creek LTER*), and summarized below.

We believe that scientists are obliged to communicate their findings, when relevant, with the public. In partnership with the Science Museum of Minnesota we helped design, plant and interpret an outdoor "Prairie Maze". Our Schoolyard LTER program and related CDR outreach activities, funded by several NSF grants and by a private foundation, have provided K-12 teachers and students with a deeper knowledge of the scientific process and of the causes and consequences of human-driven environmental change. Newspapers, magazines, and public radio and television have reported on aspects of our research that are relevant to environmental issues. Politicians and other policy makers have visited CCNHA to learn about our research, and we have testified to legislative bodies. In addition, our LTER has trained new scholars, including numerous undergraduates, MS and PhD students, and post-doctoral researchers.

Our research has addressed six fundamental questions expanded upon below:

1. How and why do plant species numbers and identities influence the productivity, nutrient use, stability, C and N dynamics and trophic structure of prairie grassland ecosystems?
2. How and why do elevated levels of CO<sub>2</sub> and N and changes in biodiversity impact community diversity and composition, and processes from physiological to ecosystem scales?
3. What determines the differential susceptibilities of ecosystems to the establishment and spread of novel species, the differential successes/failures of such potential invaders, and the process of community assembly and species coexistence?
4. What forces control the dynamics of ecosystems at the woodland-grassland border?
5. How and why do underlying processes, including litter decomposition, plant resource competition and plant-herbivore interactions influence composition and ecosystem functioning?
6. To what extent do our findings at CCNHA generalize to other ecosystems, including other LTER sites?

We summarize our work on these issues and our process-oriented studies below.

## 1. Biodiversity and Ecosystem Functioning

Our biodiversity experiments and related theory (Lehman and Tilman 2000, Tilman and Lehman 2002) have explored how, why and under what conditions plant species numbers and composition may have population, community and ecosystem effects. Early results of our biodiversity experiments showed that greater plant species numbers led to greater plant standing crop (Tilman et al. 1996, 1997). These seeming effects of diversity on productivity and stability contributed to considerable controversy regarding the underlying mechanisms and the implications for environmental policy (e.g., Huston 1997, Grime 1997, Garnier et al. 1997, Aarssen 1997, Hodgson et al. 1998, Wardle et al. 2000, Kaiser 2000, Guterman 2000). Results of the past 6 years have helped clarify and resolve portions of this debate, as have two synthesis books co-edited by members of the Cedar Creek team (Kinzig, Pacala and Tilman 2002; Loreau, Naeem and Inchausti 2002) and a synthesis paper (Loreau et al. 2001). We found that effects of plant diversity on productivity became progressively stronger during the experiment, with 16 species plots having 2.7 times the biomass of monocultures (Tilman et al. 2001b; Fig 1). Diversity effects resulted more from niche complementarity than from sampling effects (Tilman et al. 2001b; Fig 2; Hille Ris Lambers et al. 2004), though sampling effects did occur during the early years of the experiment (Pacala and Tilman 2002). Recent analyses that used our full 10-year data set have shown that steadily increasing net effects of diversity on plant biomass were increasingly attributable to complementarity rather than to selection (*sensu* Loreau and Hector 2001; Fargione et al. in preparation; Fig 3).

Species composition and plant species numbers had almost equally strong effects on plant biomass (Tilman et al. 2001b; Tilman et al. 2002). Greater plant species numbers had no effects on litter decomposition and N turnover (Knops et al. 2001) but did lead to lower extractable soil NO<sub>3</sub> (Tilman et al. 2002). Higher plant species numbers also led to lower incidence of foliar fungal diseases (Mitchell et al. 2002), greater insect diversity (Haddad et al. 2001) and significant shifts in soil microbial communities and the processes that they control (Fig 4; Zak et al. 2003), best explained as resulting from effects of plant diversity on plant biomass.

As to stability, decadal ecosystem temporal stability was significantly greater at higher plant diversity (Fig 5), and tended to increase as plots matured (Tilman et al., submitted). Ecosystem stability was also positively dependent on root mass, a measure of perenniating biomass, and negatively dependent on legume presence. Ecosystem stability increased with diversity, despite lower stability of individual species, because of both sampling and overyielding effects, but not from covariance effects.

## 2. Interactive Effects of CO<sub>2</sub>, Nitrogen and Biodiversity on Grassland Ecosystems

A second major long-term experiment (BioCON) examines the interactive effects of increased atmospheric CO<sub>2</sub>, enriched N supply, and variation in the number and identity of plant species and functional groups, all important components of environmental change, on plant community dynamics and the pools and fluxes of plant and soil C and N. This research has addressed integrated questions from ecophysiological, multi-trophic, stoichiometric, community and ecosystem perspectives. Species identity, functional group membership, richness, CO<sub>2</sub>, and N all influence plant tissue C:N ratio, which in turn influences the photosynthetic, biomass accumulation, and biogeochemical responses to CO<sub>2</sub> and N treatments. Down-regulation of photosynthesis in response to elevated CO<sub>2</sub> was marked in all species, but species and functional groups differed in photosynthetic down-regulation with variable CO<sub>2</sub> and N supply (Lee et al. 2001, Ellsworth et al. 2004). Additionally, stoichiometry of species was a good predictor of responsiveness to CO<sub>2</sub>; species with higher %N under ambient conditions had proportionally greater responses to CO<sub>2</sub> (Reich et al. 2001c). Stoichiometry-dominated relationships between plants, soil microbes and N cycling led to gradual but progressive N limitation of the elevated

CO<sub>2</sub> fertilization effect (Fig 6; Reich et al. 2006a). This effect of N on CO<sub>2</sub> response was only detectable because of the long-term nature of the experiment. If such N limitation of rising CO<sub>2</sub> effects are widespread it will have important consequences for the capacity of the terrestrial biome to serve as a C sink (Hungate et al. 2004).

Reduced species and functional group diversity constrained the plant biomass accumulation response to CO<sub>2</sub> or N (Figs 7, 8; Reich et al. 2001a, 2004). In addition, N fixation by legumes varied among species and with CO<sub>2</sub> and N supply (Lee et al. 2003ab, West et al. 2005). In mixtures this influenced tissue %N and photosynthetic performance of non-fixing neighbors (Lee et al. 2003ab). Changes in foliar chemistry due to CO<sub>2</sub>, N and competitive gradients (Novotny et al. submitted) also influenced the incidence and severity of plant disease and insect herbivory (Mitchell et al. 2003; Strengbom and Reich submitted; Strengbom et al. submitted). Finally, the quantity and chemical quality of tissues and likely root exudates, as they vary among species and CO<sub>2</sub> and N treatments, regulate the composition of the belowground community (Wolf et al. 2003; Chung et al. submitted) as well as litter and SOM dynamics (e.g., Dijkstra et al. 2004, 2005, 2006b; West et al. submitted), and the total belowground C flux (Craine et al. 2001ab).

### 3. Controls of Invasion and Community Assembly

Elton (1958) hypothesized that resident biodiversity decreased the chance of invasion by exotic species. Our biodiversity experiment allows us to test Elton's hypothesis and to seek the underlying causal mechanisms. Early results showed that higher plant species numbers were associated with lower rates of establishment and biomass of invaders (Knops et al. 1999). Subsequent work showed that higher resident diversity increased neighborhood crowding and the number of interspecific interactions, decreased light availability and decreased soil NO<sub>3</sub>, thus creating a more highly competitive environment that inhibited the establishment and growth of invaders (Naeem et al. 2000; Kennedy et al. 2002; Figs 9, 10). To further test these ideas, 27 plant species of four functional groups were seeded into subplots of our small biodiversity experiment. Invader biomass and species richness were much lower in higher diversity plots (Fargione et al. 2003; Fig 11). In addition, established species most strongly inhibited introduced species from their own functional group (Fig 12). Similarly, in a different experiment, species that invaded into neighborhoods with higher *Schizachyrium* densities had different phenology (grew during the cool season) and rooting depth (were more deeply rooted) than established *Schizachyrium* individuals (Fargione and Tilman 2005b). In another study nested in the big biodiversity experiment, both sampling effects (Huston 1997, Aarssen 1997, Tilman et al. 1997) and niche complementarity contributed to the lower rate of exotic invasion into higher diversity plots (Fargione and Tilman 2005a). Moreover, the biomass of invaders into unweeded subplots in the biodiversity experiment was greater for plots with higher soil NO<sub>3</sub> and lower root mass (Fargione and Tilman 2005b; Fig 13).

Finally, we developed a new theory of community assembly and community structure, which we call stochastic niche tradeoff theory (Tilman 2004; Figs 14, 15). This theory offers potential resolutions to many of the differences between Hubbell's (2001) neutral theory and classic niche theory, possibilities that we will be testing in our proposed research.

### 4. Controls of the Woodland-Grassland Border

The ecoregions of the world, such as CCNHA, that are located in ecotones between forest and grassland biomes are likely to be dramatically impacted by human-induced changes in land use, climate, atmospheric chemistry, the fire cycle, and species invasions (Foley et al. 2005). We have explored these issues with both short- and long-term experiments and observations of tree-grass interactions across a range of ecosystem types. In one of these, we use an experiment initiated in 1964 to determine how variation in fire frequency and feedback effects of altered

species abundances influence plant community composition and structure, productivity and nutrient cycling. Variation in fire frequency results in a gradient of vegetation structure from closed-canopy oak forest (in unburned sites) to open oak savanna in frequently burned sites (Figs 16, 17; Peterson and Reich 2001, Reich et al. 2001b, Peterson et al. submitted ab). Increased fire frequency also decreases NPP and slows rates of N cycling (Fig 18; Reich et al. 2001b) by promoting losses of N through volatilization and by reducing litter %N, thereby increasing N immobilization and reducing net N mineralization rates (Fig 19; Dijkstra et al. 2006a). The decline in litter N with increasing fire results both from within-species (i.e., oak) shifts (Reich et al. 2001b; DL Hernandez, unpublished) as well as from a shift from oak to C4 grass dominance. Reduced litter %N within oaks and in C4 grasses relative to oaks is more important than changes in the abiotic environment in slowing decomposition and soil N cycling in frequently burned sites (Norris et al. unpublished data). We are currently determining effects of fire frequency on P cycling.

Fire, species effects, and resources also influence trophic dynamics and interactions in woodland-grassland systems. Despite important effects of fire-mediated declines in plant %N for decomposition processes, insect herbivores can be insensitive to declining foliar N with greater fire, but rather respond to changes in C chemistry associated with the fire-induced increase in light availability. For example, the lace bug (*Corythuca arcuata*, an oak specialist) is 7 times more abundant in frequently burned than in unburned sites and shows higher survivorship when grown on leaves from burned sites under controlled laboratory (Fig 20; Kay et al. submitted). Variation in N supply due to fire, N deposition, or species effects on the N cycle also influences the mycorrhizal community (Avis et al. 2003, Dickie et al. in preparation). In turn, oak tree effects on resource competition (shade) and facilitation (ectomycorrhizal colonization) influence spatial patterns of oak ecophysiology and establishment success in savanna openings or old fields (Fig 21; Dickie et al. 2004, 2005, in preparation; Dickie and Reich 2005). Interannual climate variation and tree competition and facilitation also determine the white pine colonization in old fields (Dovciak et al. 2005). Finally, the mosaic of woodland-grassland communities at CCNHA and in the nearby region influences bird community composition and diversity at a variety of spatial scales (Chapman and Reich submitted).

## 5. Additional Process and Mechanistic Studies

**Nitrogen:** All of the studies summarized above have shown that N plays a central role in structuring our ecosystems. To better understand N feedback effects, we performed a 5-year decomposition study that compared effects of externally supplied N and substrate N on early versus late stages of decomposition. We decomposed eight substrates varying in initial %N with and without increased inorganic N fertilizer for five years. We replicated the experiment in eight different sites representative of a variety of old-field and forest habitats. As expected, litter N was strongly and positively related to first-year decomposition at all sites (Fig 22). However, addition of N as fertilizer increased initial decomposition at only two of the eight sites (Fig 23; Hobbie 2005) and after five years decreased decomposition at three of eight sites (Hobbie, in preparation). Within a site, the effects of added N were independent of substrate lignin concentration. Thus, the effects of fertilizer N (where they occurred) switched from being positive in the early stages of decomposition to being negative in the later stages of decay. However, negative late-stage effects were not a result of N inhibition of lignin degradation.

**Herbivory:** Thirteen years of deer enclosure in native savanna markedly increased densities of the legume *Lathyrus venosus* and doubled annual aboveground primary production (Knops et al. 2000). In addition, Dipteran and Lepidopteran larvae, also major seed predators at CCNHA, cause many competitively dominant grasses to suffer heavy pre-dispersal seed loss, leading to recruitment limitation (Kitijima and Tilman, in preparation).

**Competition:** Recent results of a 12-year competition experiment among some of the dominant perennials of the Great Plains has shown that competitive displacement is slow, and that

displacement or coexistence was generally well-predicted by plant traits, especially the use by each species in long-term monocultures of soil NO<sub>3</sub> and their light interception (Fig 24).

## 6. Cross-Site Research and Synthesis

We have performed a variety of collaborative and cross-site studies and participated in and/or provided CDR data for LTER cross-site working groups. For instance, we currently are part of LTER (Pennings et al. 2005) and international (ARC-NZ Vegetation Function Network) cross-site groups working on productivity, plant functional traits, plant species diversity, and vegetation dynamics. We contributed samples and data for cross-site studies of effects of N on mycorrhizal fungi (Johnson et al. 2003b, 2005), of CO<sub>2</sub> on plant <sup>15</sup>N (Bassirirad et al. 2003) and of CO<sub>2</sub> on the biochemistry of photosynthetic down-regulation (Ellsworth et al. 2004). Data from our experiments are available on our web site ([www.lter.umn.edu](http://www.lter.umn.edu)) and have been used by non-CDR researchers in a variety of studies (*Supplemental Documentation*: Table 2). For instance, data from our long-term N addition experiment have been used to study diversity - productivity relationships (Gough et al. 2000, Gross et al. 2000, Suding et al. 2005). CDR data were also used in an LTER cross-site study of primary productivity (Knapp and Smith 2001) to evaluate alternative ways to quantify diversity (Wilsey et al. 2005). Finally, insights from CDR research helped guide and inspire a variety of synthetic activities, including an evaluation of global environmental impacts of agriculture (Tilman et al. 2001a), paths toward greater agricultural sustainability (Tilman et al. 2002), and economic and ecological relationships between stability, productivity and diversity (Tilman and Polasky 2005, Tilman, Polasky and Lehman 2005).

Harpole and Tilman collaborated with E. Seabloom and J. Reichman to establish a cross-site experiment in an exotic-dominated California grassland that showed that similar processes were influencing exotic abundance in California (Seabloom et al. 2003) and CCNHA grasslands. In a different study, we used data on grassland species abundances at CCNHA and the Konza LTER to test Hubbell's (2001) neutral theory. Changes in abundances in response to N addition and disturbance were not neutral, but were attributable to plant traits (Harpole and Tilman 2006). In a cross-site experiment, Knops, Ritchie and Milchunas determined the effects of primary productivity and herbivory by animals of different body sizes on plant species richness and nutrient cycling along a 10-fold productivity gradient for 7 grassland sites in North America and Europe. Assemblages with larger herbivores had higher plant diversity at higher productivity, while those with just small herbivores did not (Bakker et al. submitted; Fig 26).

Reich initiated and led an international network to develop a comprehensive global plant physiological data base (GLOPNET) to test hypotheses about the nature of design alternatives in leaves (Fig 25; Reich and Oleksyn 2004, Wright et al. 2004, 2005ab;). Data were obtained from CCNHA, other LTER sites and hundreds of other sites around the world. This and related synthetic cross-site studies (1) assessed trait variation within and among species and scaling relationships (e.g., Tjoelker et al. 2001a, Cornellissen et al. 2003, Reich et al. 2003b, Reich and Oleksyn 2004, Reich 2005; Wright et al. 2001, 2003, 2004, 2005ab; Niklas et al. 2005, Shipley et al. 2006), (2) examined causes and consequences of this variation at plant, ecosystem, and biogeographic scales (Fig 27; e.g., Wythers et al. 2003, Reich and Oleksyn 2004, Reich et al. 2006b), including responses to global change (Bassirirad et al. 2003, Ollinger et al. 2002; Wythers et al. 2005, Ellsworth et al. 2004), and (3) incorporated trait relationships into ecosystem models validated at LTER sites and used to explore ecosystem responses to global change (Ollinger et al. 2002, Wythers et al. 2003, 2005). One study refuted the theory that scaling of metabolism to body size applied in plants as in animals because of similar constraints by vascular network scaling (West et al. 1999, Gillooly et al. 2003) and instead showed that whole-plant respiration rate scaled proportionally with total N across a wide set of taxa, environments, and plant sizes (Fig 28; Reich et al. 2006b).



## **Section 2: Biodiversity, Environmental Change and Ecosystem Functioning at the Prairie-Forest Border**

### **A. CONCEPTUAL FRAMEWORK**

#### **Research Philosophy**

As articulated in our original 1982 LTER proposal, the overarching goal of the Cedar Creek LTER (CDR) is to gain deeper understanding of the processes and principles that govern the dynamics and functioning of communities and ecosystems through the synthesis and integration of experimental results, observational data, and the predictions of theory. Each constrains, modifies and inspires the other, helping us discover, test among, and better understand the dynamics and functioning of the grassland and savanna ecosystems of Cedar Creek Natural History Area (CCNHA). An example of this interplay comes from our work on biodiversity. The apparent stabilizing effects of plant diversity on biomass stability that we observed during a major drought (Tilman and Downing 1994) led us to start a biodiversity experiment in which we are testing hypotheses about diversity effects and the underlying mechanisms (e.g., Tilman et al. 1996, 1997, 2001b, 2002, Kennedy et al. 2002, Tilman 1999, Lehman and Tilman 2000). This soon led to a second experiment, BioCON, that seeks to understand the interactions and feedback effects that determine ecosystem responses to three major drivers of environmental change, loss of biodiversity, elevated atmospheric CO<sub>2</sub>, and elevated nitrogen (N) deposition (e.g., Reich et al. 2001a, 2004, 2006a).

This interplay between results and concepts, and its interface with the work of many others within the discipline, have led to our current focus on the mechanistic and synthetic understanding of the impacts and long-term implications of human actions for the dynamics and functioning of populations and ecosystems. Humans are becoming an ever stronger force driving rapid ecological changes, ranging from evolutionary changes (Palumbi 2001), to loss of biodiversity (e.g., Manne et al. 1999, Pimm and Raven 2000) and invasions by exotic species (Mack et al. 2000) to the biogeochemical doubling of terrestrial N inputs (Vitousek 1994, Galloway et al. 2003) and elevated greenhouse gases and climate change (e.g., Sellers et al. 1999, Alroy et al. 2000, Stenseth et al. 2002), to subsequent changes in ecosystem services (Daily 1997). These forces, their effects and the underlying ecological processes, mechanisms and feedbacks that lead to these effects are the foci of our proposed research.

#### **Context**

Our research is performed within the context of our 22 km<sup>2</sup> site, CCNHA, and the surrounding region. CDR is unique among LTER sites because of its location on the climatically, edaphically, and disturbance controlled boundary between North America's prairie and forest (Fig 29). The prairie and oak savanna vegetation that characterizes this "tension zone" between forest and prairie is sensitive to climatic variation (Tilman and El Haddi 1992), edaphic factors, especially soil N availability (Tilman 1988; Hairston and Grigal 1991), fire frequency (White 1983, Tester 1989, Peterson and Reich 2001, Reich et al. 2001b) and herbivores (Huntly and Inouye 1988, Ritchie et al. 1998, Ritchie 2000). CCNHA contains large tracts of native oak savanna, prairie openings and successional grasslands, oak forest, and smaller stands of basswood-sugar maple and pine. This diverse mosaic of upland ecosystems has been shaped by the soil parent materials, by a variety of 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. One m<sup>2</sup> of savanna contains 10-40 plant species, and one hectare about 200 plant species. About 4000 insect species are in our on-site collection, which, like our herbarium, is accessible on-line at [www.lter.umn.edu](http://www.lter.umn.edu). The species-rich

successional grasslands and savannas of CCNHA have been, and remain, the central focus of our LTER program, but we also do propose new work that incorporates the region surrounding CCNHA. Our research explores the various physical factors (climate and its variation, soil N, fire, and various disturbances), human-driven changes (elevated CO<sub>2</sub>, climate change, N deposition, fire suppression, loss of species diversity, exotic invasive species), species interactions, and feedback effects that have shaped these ecosystems, including their species diversity, species composition, productivity, nutrient dynamics and stability.

### **Research Team**

In response to past reviewer concerns that our site has had a limited number of investigators and needed greater intellectual diversity, we are adding eight new researchers (six of whom are junior faculty) to the CDR research team and two current members, M. Ritchie and S. Naeem, will not be on the new team. Specifically, we are adding expertise in microbial ecology, evolutionary ecology, biogeochemistry, and ecological economics. L. Kinkel, a microbial ecologist, studies microbial plant pathogens, and soil bacteria, especially Streptomyces. S. Polasky, an economist, works on the valuation of ecosystem services and on full-cost accounting of biomass-based fuels. J. Cavender-Bares is an evolutionary ecologist who brings a long-term phylogenetic perspective to our team. H. Muller-Landau adds expertise on the effects of natural enemies, and cross-site research on the causes of biodiversity in temperate grasslands and Panamanian rainforest. J. Powers is an ecosystem ecologist interested in effects of climate change on C and N dynamics and microbial communities. J. King is a biogeochemist who works on trace gas fluxes, land use change and suburbanization. R. Montgomery is an ecophysiological who will pursue tree-shrub-herb interactions, plant adaptation and physiological responses to climate change. J. McFadden brings expertise in C, energy and water flux in urban landscapes. Other researchers are continuing their long-term CDR collaborations, including M. Davis, T. Lee, C. Lehman, N. Johnson, D. Ellsworth, D. Zak, and N. Haddad. In combination with long-term members J. Knops, S. Hobbie, P. Reich, and D. Tilman, the CDR team has the diversity of skills and interests needed to pursue the research goals articulated in this proposal.

### **Research Themes**

CDR continues to evolve by elaborating on our initial themes and developing new themes inspired by our results and their relevance to the work of others. We began by focusing on the effects N competition and disturbance on plant succession and on the causes of species coexistence. Next we focused on the community and ecosystem consequences of biodiversity and on the interactive effects of biodiversity, elevated N deposition, and elevated CO<sub>2</sub> on communities and ecosystems. We now wish to synthesize these two endeavors, because we believe that each can give insight into the other. For instance, we propose testing the simple hypothesis that the same mechanisms that explain coexistence and high biodiversity should also explain the effects of composition and diversity on productivity; and that the same mechanisms that explain why ecosystem processes change in response to shifts in environmental drivers should give insight into how and why species abundances also change. We also propose to expand our research to include two other major drivers of environmental change, climate change and land use change in the region surrounding CCNHA. As before, we will pursue these questions across ecophysiological, population, community and ecosystem scales using a combination of observations, experiments and theory. The six major themes of our research are:

***Theme 1:*** *What underlying mechanisms and feedback effects determine the impacts of human-driven changes — especially loss of biodiversity, climatic variation, N deposition, land cover and use change, changes in fire frequency, elevated CO<sub>2</sub>, and exotic species — on invasion dynamics, biotic interactions, and community and ecosystem functioning?*

***Theme 2:*** *How do the traits and evolutionary heritages of species and environmental conditions combine to determine the pattern and dynamics of community assembly and the*

*species composition, ecosystem dynamics, biogeochemistry, and biodiversity of sites ranging across scales from square meters to landscapes?*

**Theme 3:** *How do changes in one level of a trophic web influence other levels, and how do these changes, in turn, feedback on the initial level? For example, how does climate change influence plant species abundances, and how does this influence soil microorganisms, decomposition and nutrient cycling, soil pathogens, and thus plant dynamics?*

**Theme 4:** *What traits of established species, communities and ecosystems and what traits of novel species (be they native or exotic) determine the establishment and abundances of exotic species, and their impacts on resident species?*

**Theme 5:** *Do the same constraints and tradeoffs that explain multispecies coexistence also explain effects of diversity and composition on ecosystem processes, and vice versa?*

**Theme 6:** *What general principles determine the quality and quantity of the services produced by ecosystems, and how can these services be valued, including economically?*

We propose to pursue these themes in three interrelated sets of long-term experiments and observational studies, and in associated shorter-term mechanistic, process-oriented studies. The experiments of Set 1 focus on determining the consequences of human-caused environmental drivers, specifically elevated N deposition, loss of biodiversity and changes in species composition, climate warming, and elevated CO<sub>2</sub>. In Set 2, the nature of grassland-woodland dynamics as influenced by disturbance and resource variation (including fire, invasion, N addition and others) are explored in two on-going long-term and one new experiment, and in multi-scale analyses. Top-down effects of pathogens, seed predators and herbivores on population, community and ecosystem properties are explored in the two new and two on-going experiments of Set 3. Our work in each set is complemented by process-oriented studies that help elucidate underlying mechanisms. It is also complemented by cross-site studies and syntheses that expand our work beyond the geographical boundaries of CCNHA. We will continue to do theory-based synthetic activities, such as further developing and testing recent stochastic niche theory (Tilman 2004), and will complement these with a new effort at synthesis based on trait-based theory and results. In addition, we will seek a synthesis of ecological and economic approaches to ecosystem services, their valuation, and their implications for society.

## **B. CORE LONG-TERM STUDIES AT CEDAR CREEK**

### **Set 1. Consequences of Human-Caused Environmental Drivers**

The studies in this set are designed to seek, through a synthesis of experiments, observations and theory, a mechanistic and generalizable understanding of the functioning of our grassland and woodland ecosystems and how they will be impacted by major human-caused changes. Land management is greatly simplifying ecosystems, reducing their biodiversity (Foley et al. 2005). Modern transport has reduced biogeographic barriers to dispersal, allowing large numbers of novel species to become established in new realms (Lonsdale 1999, Mack et al. 2000). Agriculture, energy use and land use change are changing nutrient and CO<sub>2</sub> availability, temperature and precipitation, all of which may influence the species composition, diversity, dynamics and functioning of communities and ecosystems (e.g., Vitousek 1994, Vitousek et al. 1997ab, Carpenter et al. 1998, Schlesinger 1997, Cohen and Federov 1999). There are, as yet, few rigorous experiments to determine the long-term effects of changes in these drivers, and especially the interactive effects of multiple drivers.

We are using four complementary and interrelated experiments to determine the separate and interactive effects of loss of biodiversity, climate change, elevated CO<sub>2</sub> and elevated N

deposition on the grassland ecosystems of CCNHA. The first of these is a biodiversity experiment in which we directly control the number of perennial grassland plant species. The second is a new experiment, nested within the biodiversity experiment, in which we will have either ambient or elevated temperature, and ambient or elevated precipitation. The third is our 'BioCON' experiment in which CO<sub>2</sub> (via FACE rings), N deposition and biodiversity are experimentally manipulated using a split-plot design (and which includes several long-term nested studies). The fourth is our oldest CDR experiment, in which we impose various rates of N addition on 369 permanent plots, some of which are now undergoing cessation of N addition, prescribed burning, or herbivory treatments.

## ***I. Biodiversity (Experiment E120; <http://cedarcreek.umn.edu/research/exper/e120/>)***

### **Introduction**

This experiment (often called the "Big" Biodiversity Experiment; the "small" experiment is no longer maintained) determines effects of plant species numbers and functional traits on community and ecosystem dynamics and functioning. It manipulates the number of plant species in 168 plots, each 9 m x 9 m, by imposing plant species numbers of 1, 2, 4, 8, or 16 perennial grassland species. The species planted in a plot were randomly chosen from a pool of 18 species (4 species, each, of C4 grasses, C3 grasses, legumes, non-legume forbs; 2 species of woody plants). Its high replication (about 35 plots at each level of diversity) and large plots allow observation of responses of herbivorous, parasitoid and predator insects and allow additional treatments to be nested within plots. Planted in 1994, it has been annually sampled since 1996 for plant aboveground biomass and plant species abundances and for insect diversity and species abundances. Root mass, soil nitrate, light interception, biomass of invading plant species, and C and N levels in soils, roots, and aboveground biomass have been determined periodically. In addition, soil microbial processes and abundances of mycorrhizal fungi, soil bacteria and other fungi, N mineralization rates, patterns of N uptake by various species, and invading plant species, have been periodically measured in subprojects in the Biodiversity Experiment.

### **Key Results**

Many results are summarized in *Results of Prior NSF LTER Support*. We highlight:

- Plant biomass production increased with diversity (Fig 1) because of complementary interactions among species and not because of selection (sampling) effects (Figs 2, 3; Tilman et al. 2001b, Pacala and Tilman 2002, Hille Ris Lambers et al. 2004; Fargione et al. in prep.).
- Foliar fungal disease incidence decreased at higher diversity because of greater distance between individuals of a species, and resultant lower rates of disease spread (Mitchell et al. 2002).
- Greater plant diversity led to greater diversity of herbivorous insects, and this effect continued up the food web to predator and parasitoid insects (Haddad et al. 2001).
- Fewer novel plant species invaded higher diversity treatments because of their lower soil NO<sub>3</sub> levels, greater neighborhood crowding and competition, and greater chance that functionally similar species would occur in a given neighborhood (Figs 9 – 13; Naeem et al. 2000, Kennedy et al. 2002, Fargione et al. 2003, Fargione and Tilman 2005a, 2005b).
- Greater plant species numbers led to greater ecosystem stability (lower year-to-year variation in total plant biomass) but to lower species stability (greater year-to-year variation in abundances of individual species), with the stabilizing effect of diversity mainly attributable to statistical averaging effects and overyielding effects (Fig 5; Tilman et al, submitted).
- Data gathered this past field season shows that soil total C has now become an increasing function of plant species numbers (Fig 30).
- Our results have helped resolve a debate about why plant diversity affects ecosystem functioning. Such resolution was accomplished by a Paris symposium in which we made CDR biodiversity data available so others could test their alternative hypotheses; by a paper by 12 ecologists with divergent views that explored areas of agreement and articulated areas in need of

further testing (Loreau et al. 2001); and by our analyses of alternative hypotheses using results of the CDR biodiversity experiment (Tilman et al. 2001b).

### **Future Research**

Major questions about why biodiversity affects population, community and ecosystem properties and dynamics remain unanswered:

- *Why Does Higher Diversity Lead to Stability?* We have found strong support for the diversity-stability hypothesis. During the coming six years, we will gather annual data on plant species abundances, total plant biomass, and their relationships to climatic and arthropod variation to test among alternative hypotheses of why ecosystem stability depends on diversity.
- *How do arthropod communities depend on plant diversity and composition, and what feedback effects do arthropods have on plant communities?* The arthropod communities that had assembled in the first years of the biodiversity experiment had diversities and compositions that depended on the diversity and composition of the plant community (Haddad et al. 2001). Preliminary analyses of subsequent arthropod dynamics (based on annual samples, sorted to species and counted) show increases in arthropod diversity and shifts in the ratios of herbivores to parasitoids and herbivores to predators, relationships that we will explore in detail. We are especially interested in food chain structure and stability, and possible feedback effects of arthropods on plant dynamics, such as via seed predation and resultant recruitment limitation of species abundances. These questions will also be explored by new experimental treatments nested within a subset of the plots (see *Set 3: Enemies and Biodiversity*).
- *How do Biodiversity and Composition Influence Carbon Sequestration and Other Ecosystem Services and How Sustainable Will These Services Be?* We will focus on four ecosystem services (Daily 1997) potentially produced at different rates in response to plant biodiversity – C sequestration, quality of ground water, restoration of soil fertility, and provisioning of pollinators and predator/parasitoids of value to agriculture – by gathering data on these and relevant underlying processes. For instance, preliminary analysis of results from the 10<sup>th</sup> year of this experiment, 2005, suggested that annual belowground C sequestration was equal to about 1/3 of C in annual aboveground biomass. Soil N levels, and resultant soil fertility, also increased with diversity (Fig 31). Soil NO<sub>3</sub> is about 60% lower in high diversity plots than in monocultures, which suggests the possibility that higher plant diversity might lead to lower leaching losses and higher ground water quality. We propose exploring these possibilities, and potential agricultural impacts of arthropods, in our work on ecosystem services (see: *D. Synthetic Research*)
- *Biofuels and Ecosystem Services:* Another grant (Polasky et al.) will use CDR data on biomass energy (Ragauskas et al. 2006) produced with prairie plantings of various compositions and diversities to explore use of prairie biomass for heating and electric generation (pelletized biomass) and for cellulose-based ethanol as a transportation biofuel. We will build on recent analyses (Farrell et al. 2006) to perform full-cost accounting of net energy balance and of full life cycle environmental benefits/costs in an approach that explicitly considers and economically values ecosystem services.
- *How Generalizable are the Results of the CDR Biodiversity Experiment?* We are collaborating with a “sister” biodiversity experiment, the Jena Biodiversity Experiment, a large-scale well-replicated grassland biodiversity experiment established a few years ago by the Max Plank Institute for Biogeochemistry in Jena, Germany. We have agreed to share data, exchange scholars, and, through comparative analyses, determine which of the results of biodiversity experiments are site-specific and which are general.

## **II. Biodiversity and Climate (“BAC”)**

### **Introduction**

Climate changes forecast for our region by GCM’s and shifts in biodiversity and composition each have the potential to alter ecosystem functioning; their interactive effects are unknown. The new “BAC” experiment is designed to determine the direct and interactive effects of plant species numbers, plant community composition, temperature, and precipitation on

productivity, C and N dynamics, stability, and plant, microbe, and insect species abundances in CDR grassland ecosystems.

The experiment will use a subset of 42 plots from the Biodiversity experiment: 14 monoculture plots (one randomly chosen replicate for each of the 14 non-woody species that became well established in monoculture), 14 plots planted to 4 species (randomly chosen from 4-species plots planted with combination of these 14 species), and 14 plots planted to 16 species (randomly chosen from all 16 species plots containing these 14 species). Plant species are from 4 different functional groups (4 species, each, of C3 grasses, C4 grasses, legumes and non-legume forbs) that are likely to respond differently to changes in temperature and water availability. Treatments, to be applied to 4 subplots (3 m x 4 m each) within each of these 42 plots, will create conditions that are (a) warmer than ambient, (b) warmer and watered, (c) ambient temperature but watered, and (d) un-warmed and un-watered, i.e., a full factorial of ambient or elevated temperature and of ambient or elevated precipitation. Temperature will be increased using infrared heat lamps (DeValpine and Harte 2001, Kimball 2005), and increased precipitation using automatic sprinklers; both methods were tested and refined in 2005. Current LTER funds and other funds will establish the experiment during the summer of 2006.

### **Future Research**

This experiment focuses on the following questions: (1) How do temperature, water availability, and biodiversity impact species abundances and ecosystem functioning? (2) Does plant species composition shift in response to climate, do such shifts impact ecosystem functioning, and are ecosystem processes stabilized by higher species or functional diversity? (3) How do climate and biodiversity affect belowground C cycling, and how is this mediated by responses of soil microorganisms to climate shifts (e.g., Fang et al. 2005, Fierer et al. 2005) and shifts in plant species composition? (4) How do climate change, species composition and biodiversity interact to determine the patterns of invasion by novel species, and what underlying mechanisms explain these patterns?

To address these questions, the 168 subplots will be annually sampled for aboveground biomass, sorted to species. Seed of 24 novel species will be added to a 0.5 x m 0.5 m portion of each 3 m x 4 m treatment subplot. Soil and biomass C and N will be measured every three years. We will measure microbial community composition and biomass (via PLFA/FAME analyses), stable and labile soil C fractions, and extracellular enzyme activities in BAC. We expect that plots with different compositions and diversities will vary in both the quality and quantity of detrital carbon inputs to the soil, allowing us to evaluate the importance of substrate versus microbial communities in mediating responses of C cycling to temperature and precipitation.

### ***III. BioCON – Effects of CO<sub>2</sub>, N and Biodiversity (E141; <http://www.lter.umn.edu/biocon/>)***

#### **Introduction**

The simultaneous changes in three important aspects of global environmental change, coupled with a lack of understanding of their interactions (Vitousek 1994), led us to develop the long-term BioCON field experiment, which addresses the interactions among multiple terrestrial ecosystem components in response to elevated CO<sub>2</sub>, added nitrogen (N), and varying plant diversity, including both shifts in richness and in composition (e.g., Reich et al. 2001ac, 2004). This experiment simultaneously provides information relevant to society about the mechanisms by which these important ecological elements interact, while addressing basic scientific questions about coupled biogeochemical cycles, biodiversity, and many other issues.

BioCON focuses on 5 key questions and a host of related sub-questions: (1) Do CO<sub>2</sub> and N interact at physiological, whole plant, multi-trophic, community and/or biogeochemical scales, on short- and long-term time horizons? (2) Does plant diversity (species and/or functional group) influence responses to CO<sub>2</sub> or N, or their interaction? (3) Does the composition of the plant

community (including long-term shifts in composition in response to CO<sub>2</sub> and N over time) influence responses to CO<sub>2</sub> or N, or their interaction? (4) Are there linear or non-linear changes with time in effects of treatments on plant, community or ecosystem metrics? (5) What mechanisms (physiological, biotic interaction, biogeochemical, etc.) explain the patterns observed in addressing questions 1-4. In other words, how does the integration of plant, consumer, mutualist, and decomposer interactions at multiple temporal scales lead to the responses observed at tissue to ecosystem scales across various time scales?

The main BioCON experiment (E141) directly controls plant diversity (1, 4, 9 or 16 perennial grassland species randomly chosen from a pool of 16 species, planted as seed in 1997), soil N availability (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. 560 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. It includes 296 individual plots, each 2 x 2 m, in six 20-m diameter 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. Additional fully factorial experiments (many plots serve multiple experiments) include tests of species composition (in monoculture) x CO<sub>2</sub> x N (n=128 plots, Reich *et al.* 2001c), of functional group composition x CO<sub>2</sub> x N (n=176, Reich *et al.* 2004), of species richness x CO<sub>2</sub> x N at a standard functional group richness (n=176), and of functional group richness x CO<sub>2</sub> x N controlling for species richness (n=123).

*Sampling methods:* Photosynthesis, biomass, community composition, plant abundance, soil CO<sub>2</sub> flux, soil moisture, soil decomposer and mutualist communities and their activities, plant and soil N dynamics, reproductive output, and other metrics are measured using well developed protocols (see BioCON citations in proposal and in reference list).

## Key Results

- Low species diversity constrained plant biomass accumulation in response to CO<sub>2</sub> or N or their combination (Fig 7; Reich *et al.* 2001a). Additionally, in a complementary experiment we found the impacts of diversity on biomass, and on the biomass response to CO<sub>2</sub> and N, are independently caused by both species and functional group richness (Reich *et al.* 2004).
- At any level of species richness, increasing functional group richness leads to higher biomass, while at any level of functional group richness, increasing species richness leads to higher biomass (Fig 8). The effects of increasing species richness within functional groups occurred in all functional groups, and as well, the effects of increasing functional group richness were seen in all functional group combinations (Fig 32).
- Species and functional groups differ in long-term acclimation (i.e., down-regulation) of photosynthesis to variable CO<sub>2</sub> and N supply (Lee *et al.* 2001, unpublished data; Ellsworth *et al.* 2004), with a direct stoichiometric feedback of CO<sub>2</sub> on tissue N leading to lower potential photosynthetic capacity at any given CO<sub>2</sub> concentration.
- Diversity, CO<sub>2</sub>, and N all influence plant tissue stoichiometry, in particular the C:N ratio (Dijkstra *et al.* 2005; Reich *et al.* 2006a; Novotny *et al.* submitted), which in turn influences the photosynthetic, biomass accumulation, and biogeochemical responses to CO<sub>2</sub> and N treatments.
- Legume N<sub>2</sub>-fixation increases with elevated CO<sub>2</sub> and decreases with increasing soil N, but more so for some species than others (Lee *et al.* 2003ab, West *et al.* 2005). The effect of elevated CO<sub>2</sub> on *Lupinus* N<sub>2</sub>-fixation in mixtures enhances tissue %N and photosynthetic performance of non-fixing neighbors (Figs 33, 34; Lee *et al.* 2003a, unpublished data).
- Changes in foliar chemistry caused by CO<sub>2</sub>, N and competitive gradients (Novotny *et al.* submitted) influence the incidence and severity of plant disease and insect herbivory (Fig 35; Mitchell *et al.* 2003, Strengbom and Reich submitted, Strengbom *et al.* submitted). However, both the nature of the foliar chemical responses and their impacts on disease severity and herbivory are idiosyncratic.
- Elevated CO<sub>2</sub>, enriched N, and plant composition and richness influence mycorrhizal and soil decomposer communities (Fig 36, 37; Wolf *et al.* 2003, Dijkstra *et al.* 2005, Chung *et al.*

submitted). Additionally, these treatments influence soil C flux, and litter and SOM decomposition, turnover, and mineralization (e.g., Craine et al. 2001bc, Dijkstra *et al.* 2004, 2005, 2006a; West *et al.* submitted a), largely reflecting CO<sub>2</sub> and N effects on, and species difference in, the chemistry of organic inputs to soils. For example, plant species producing lignin-rich litter increased stabilization of soil C older than 5 years, but only in combination with elevated N inputs (Fig 38), suggesting that N deposition will increase soil C sequestration in those ecosystems where vegetation composition and/or elevated atmospheric CO<sub>2</sub> causes high litter lignin inputs to soils.

- Stoichiometry-dominated relationships between plants, soil microbes and N cycling led to a gradual progressive N limitation of the elevated CO<sub>2</sub> fertilization effect (Reich *et al.* 2006a). This was observed for soil N availability, total plant N pools, and total plant biomass, with soil and plant N dynamics apparently driving the biomass patterns (Fig 6). These results support the idea of N limitation of the CO<sub>2</sub> fertilization effect, which has significant implications for the global terrestrial C sink (Hungate et al. 2004).

### **Future Research**

We propose to continue and expand a wide variety of studies within BioCON that address the five key issues listed above. LTER funds are essential for continuing this research, but it requires substantially more support than LTER can provide. In particular, we will seek to characterize temporal dynamics in plant and ecosystem physiology, community composition, and biotic interactions, including plant-plant interactions, mutualisms, disease, and biogeochemistry, that reflect changes with time in treatment effects on key response variables. Discovering whether there are temporal dynamics to the interactions of plant diversity, CO<sub>2</sub> and N and testing hypotheses about the causes and generality of the mechanisms that may drive such interactions are at the core of what makes the BioCON experiment of long-term value.

We will address the role of plant functional (i.e., ecophysiological) diversity in influencing the responses of species in mixtures and monocultures, using a developing plant trait data base in conjunction with the suite of measures mentioned above. We are also using a mechanistic ecosystem model (G'Day, McMurtrie et al. 2000, Corbeels et al. 2005, Pepper et al. 2005) (currently adapted for BioCON as part of ongoing collaboration with R. McMurtrie and B. Medlyn) to assess whether trait-driven differences in photosynthesis, canopy dynamics, and biogeochemistry lead to predicted biomass accumulation patterns that match the observed time course of the progressive N limitation of CO<sub>2</sub> fertilization as it continues to unfold over time.

### ***IV. Nitrogen Addition (E001, E002; <http://cedarcreek.umn.edu/research/exper/e001/>)***

#### **Introduction**

Biologically available nitrogen, a major limiting resource in terrestrial ecosystems, is being released by human actions at high rates (e.g., Galloway et al. 1995, Howarth et al. 1996, Smil 1997, Vitousek et al. 1997, Holland et al. 1999). To determine the effects of N supply, and of resultant shifts in competitive interactions, plant-herbivore interactions, and C and N cycling on CCNHA ecosystems, in 1982 we established closely-related N addition experiments. An N addition experiment (**E001**) consisting of 207 4 m x 4 m plots is located 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). Plots have been annually sampled for aboveground biomass (sorted to species) and litter, and periodically for extractable soil NH<sub>4</sub> and NO<sub>3</sub>, belowground biomass, insect abundances, mycorrhizal fungi, small mammals, and microbial biomass. In addition, three closely related experiments, each with 54 plots, had received the N treatments above starting in 1982, but now differ as noted below:

*N Cessation:* An N cessation experiment was begun in 1993 to determine the dynamics of recovery after cessation of N addition. In 1993, N addition was halted to 3 randomly chosen plots per treatment, but has been continued in the other 3 replicates of each N treatment.



*N and Fire*: Similarly, to determine how the effects of N addition depended on litter accumulation and other factors related to fire suppression, 3 randomly chosen replicates of each N treatment have been burned and 3 have been unburned each spring beginning in 1993.

*N and Deer Herbivory*: Deer, a major mammalian herbivore at CCNHA, can significantly impact CDR grasslands (see Set 3, below). In autumn of 2004, 3 randomly chosen replicates per N treatment were randomly assigned to be fenced to exclude deer and the other three were left open to deer herbivory.

Finally, a complementary experiment (**E145**) of N addition to replicated plots in 8 different upland grassland and forested sites was established in 1999 to examine the influence of inorganic N addition alone on decomposition processes and litter and soil microbial communities.

### **Key Results**

- Chronic but low level N addition led to significant losses of plant species numbers even for rates of N addition as low as 10 kg/ha (Clark and Tilman, submitted; Fig 39), with the greatest loss of diversity per unit of added N at the lowest rate of N addition. After N cessation, plant species numbers recovered to control levels, but only after a period of cessation (13 years) comparable to the period of elevated N addition (10 years; Fig 40).
- Shifts in species abundances in response to N addition did not support predictions of Hubbell's (2001) neutral theory (Harpole and Tilman 2006). Cavender-Bares (in preparation) used these data to test for the role that the phylogenetic histories of plant species might play in their distributions and abundances along experimental productivity gradients. Data from this experiment have also been extensively shared with and used by non-CDR researchers, and been included in a variety of publications (Gough et al. 2000; Gross et al. 2000; Knapp and Smith 2001; Johnson *et al.* 2003ab, 2005; Pennings et al. 2005; Suding et al. 2005).
- Substrate and fertilizer N had contrasting effects on both initial and long-term (5 y) litter decomposition (Hobbie 2005, unpublished).

### **Future Research**

These experiments continue to provide important information on issues related to the impacts of N deposition on plants, soil microbes, pathogens, herbivores, parasitoids, and predators, and on a wide variety of ecosystem processes, such as those summarized above, and will be maintained. However, because recent analyses show few, if any, changes in the past five years, we propose sampling the 'classic' N addition plots for aboveground plant biomass only about every 4<sup>th</sup> year, but we will sample the N and Deer, the N and Fire and the N Cessation experiments every second year.

In addition, we will be characterizing the response of the belowground community (using PLFA and microbial enzyme assays) and litter (Hobbie 2005) and soil C pools and dynamics to long-term N addition. Preliminary results indicate site-specific and surprising effects; for example, cellulose- and lignin-degrading enzyme activities respond idiosyncratically to N addition in magnitude and direction among different sites. These and studies should help resolve uncertainties about long-term N effects on microbially mediated litter and soil processes (Carreiro et al. 2000, Saiya-Cork et al. 2002, Frey et al. 2004, Knorr et al. 2005).

## **Set 2. Woodland-Grassland Ecology, Interaction, and Dynamics**

### **Introduction**

Past work at CCNHA has demonstrated an overriding influence of fire in maintaining prairie openings and oak savanna at the prairie-forest border, with lack of burning leading to oak canopy closure and frequent fire maintaining open oak savanna (Peterson and Reich 2001, Reich et al. 2001b). These shifts in vegetation structure are associated with changes in productivity and biogeochemistry (Reich et al. 2001b, Dijkstra et al. 2006a). In the absence of fire, mesic grasslands of the tallgrass prairie region are also experiencing compositional increased

abundances of woody shrubs and trees (Briggs et al. 2005), including several important invaders. On the sandy outwash plains of Minnesota, recent decades have been characterized by invasion of successional old fields by white pine (*Pinus strobus*) (Figs 41-43; Dovciak et al. 2005). Invasion of grasslands by woody species has potential consequences for ecosystem processes, as woody species often have different productivity (Reich et al. 2001b), detrital chemistry (Dijkstra et al. 2006a), soil C stocks (Jackson et al. 2002), nutrient dynamics (Dijkstra et al. 2006a), and mycorrhizal and other soil microbial associations (Dickie et al. 2005). Yet, our knowledge of the biology and ecology of woody and herbaceous species remains largely housed in different silos of scientific communities, despite the enormous range and area of their co-existence on the planet. Our past and future work at CCNHA examines the similarities and differences in these two important functional groups and how these influence their biotic interactions, and the dynamics, structure and function of the communities and ecosystems they form. Although of basic interest, such work is increasingly relevant given that changes in fire regimes, climate, atmospheric chemistry, land use, and biotic invasion all influence the outcomes of tree-grass interactions and the dynamics of vegetation at ecotones such as the prairie-forest border in Minnesota.

This work addresses aspects of all six Themes. We focus on two long-term studies as well as short-term manipulations nested within or separate from those experiments. First, we study a prescribed burning experiment (<http://www.lter.umn.edu/research/exper/e133/e133.html>; **E015**, begun in 1964; expanded to **E133**) of 29 landscape units (3 to 27 ha) that range widely in fire frequency, but were protected from fire from 1938 to 1964. Fire treatments (prescribed spring ground fires) range from complete fire protection to near-annual burning, spanning the range of pre-settlement 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. We also use historical records, including pre-settlement surveys and air photos from several decades during the 20<sup>th</sup> century to evaluate oak woodland changes at a landscape scale centered around CCNHA.

Second, we study an old-field chronosequence (Inouye et al. 1987; **E014**; <http://cedarcreek.umn.edu/research/exper/e014/>) established in 1983 and consisting of 100 permanent plots in each of >20 successional fields with time since abandonment spanning 7 decades. We have sampled these plots every 5 or 6 years for herbaceous species composition and cover and soil C and N. In addition, 4 permanent plots per field are sampled annually for aboveground biomasses of plant species, and each field is sampled four times per growing season for arthropods, which are sorted to species and counted (e.g., Siemann et al. 1999). Many of the fields in this chronosequence are currently being invaded by pine. Each of these fields has been divided in half, and one half randomly chosen for periodic prescribed burning (a fire about every other year). We anticipate that the burned half will continue succession to prairie grassland and the unburned will rapidly become white pine stands if seed sources are nearby, or will otherwise undergo extremely slow succession to oaks.

## Key Results

- Variation in fire frequency results in a gradient of vegetation composition, diversity, and structure from closed-canopy oak forest (in unburned sites) to open oak savanna in frequently burned sites (Peterson and Reich 2001, Reich et al. 2001b, Peterson et al. submitted a, b; Figs 16, 17). Increased fire frequency also decreases NPP and slows rates of N cycling (Reich et al. 2001b; Fig 18). This occurs because of a compositional change from oak to C4 grass dominance (Reich et al. 2001b, M. Norris unpublished), and also because fire promotes N losses through volatilization and reduces intraspecific litter N concentrations, thereby increasing N immobilization and reducing net N mineralization rates (Fig 19; Dijkstra et al. 2006a, DL Hernandez unpublished).
- Variation in N supply due to fire, N deposition, or species effects on the N cycle also influences the composition of the mycorrhizal community (Avis et al. 2003, Dickie et al. in preparation). However, some herbivores appear more sensitive to fire-induced changes in microclimate and foliar C chemistry than to N *per se* (Fig 20; Kay et al. submitted).

- Fire and competition in combination led to a dynamic, changing spatial clustering of oaks in mixed oak-grass vegetation at a 16-ha scale (Davis et al. 2005b). At finer scales, oak trees shade oak seedlings and facilitate ectomycorrhizal colonization thereby influencing spatial patterns of seedling colonization in savanna or old fields (Fig 21; Dickie et al. 2004, 2005, in prep.; Dickie and Reich 2005). Pine invasion in old fields is influenced by interannual climate variation and tree competition and facilitation (Figs 41, 42; Dovciak et al. 2005). Seed dispersal largely controls initial spatial patterns of pine seedling establishment, but over the long-term, resources and micro-environment lead to different spatial patterns for larger, older seedlings than for younger, smaller seedlings (Fig 43). Finally, the mosaic of woodland-grassland communities at CCNHA and nearby also influences bird community composition and diversity (Chapman and Reich submitted).
- Dynamics of soil C and N accumulation in successional grasslands depended on plant community composition, and had trajectories suggesting that 200 - 250 years may be required for field to attain pre-agricultural soil C and N levels (Knops and Tilman 2000).
- Detailed, small-scale mapping of spatial distributions and sizes of established and exotic plant species in the old field chronosequence showed that biodiversity influenced grassland invasions at both small and large scales (Naeem et al. in prep).
- The long-term annual data on plant species abundances in the old field chronosequence also showed that a 1988 drought synchronized plant population dynamics and led to sustained oscillations in aboveground plant biomass (Haddad et al. 2002).

### Future Research

During the past LTER cycle we studied community assembly in both grasslands and savannas, tree-grass interactions and ecosystem consequences with a variety of approaches, including long-term experiments, short-term manipulative experiments to test mechanistic hypotheses, and observations of across a range of ecosystem types. We will continue and expand these in 2006-2012. One focus will be on the spatial patterns and controls of invasion by both native and exotic herbaceous plant species. In addition, multi-scale data will be used to assess temporal and spatial patterns and mechanisms of oak woodland change. This will combine 1 to 100 m<sup>2</sup>-scale studies of competition and resource availability, 1 to 20 hectare scale long-term demographic studies, 1 to 1,000 hectare scale multiple date (1930s to 2000s) air photos, and 1,000 to 20,000 hectare-scale historical records (pre-settlement land office survey).

Another focus will be on tree-grass and tree-shrub-grass interactions and exotic and native woody invaders. Disturbances that alter the abundance of overstory trees in forest and woodland ecosystems can have complex impacts on both understory communities and woody regeneration because of interactions with the shrub layer (either native or exotic). In oak woodlands at CCNHA and elsewhere in the upper Midwest, the shrub layer, formerly dominated by native shrubs (e.g., *Corylus*) and brush (e.g., *Rubus*), is increasingly dominated by invaders such as *Robinia* (from further east in N. America) or *Rhamnus* (from Eurasia). Prior work at CCNHA has focused on the interactions at all life stages of dominant overstory tree species (e.g., oak or pine) with herbaceous vegetation, but has largely ignored the role of shrubs. In 2006-2012 we will use observations of spatially-explicit patch dynamics within long-term experiments to examine the roles of colonization processes, resource competition, species effects, and disturbances (e.g., fire, N deposition) on tree-shrub-herb dynamics. We will also use manipulative experiments of native diversity or cover and resource supply at sites nearby to CCNHA to evaluate hypotheses about invasion dynamics.

Besides studying invasion by exotic woody species, we will study invasion of old fields by native woody species, particularly *Pinus strobus*. We aim to determine 1) the patterns of *Pinus* invasion at CCNHA and on the Anoka sandplain more broadly, 2) the mechanisms facilitating *Pinus* invasion (including a new experiment in which half of each of 22 old fields will be burned regularly), 3) the consequences of *Pinus* invasion for ecosystem C and N stocks and cycling, and 4) the change in ecosystem services associated with a shift from C4 grassland to

*Pinus*-dominated vegetation. This complements and expands on our studies of interactions among fire, deer, and *Pinus* invasion in a single old field.

In summary, our studies in successional grasslands and in woodland-grassland in 2006-2012 will include: (1) continued measurements in the core fire frequency experiment of plant and soil C and N cycles to better understand roles of disturbance (fire), plant traits (woody vs. herbaceous), resource supply (N) and climate. These studies will be made at 2-3 year intervals in 12 plots spanning the range of fire frequency (we have annual data from these from 1998-2004, as well as in 1995); (2) measurement every 5-6 years of plant community composition, tree growth and demography, and resource availability in all 24 subplots of the 29 oak savanna burn unit plots; (3) studies of foliage and fine root traits for the entire plant community across light, N and fire gradients in the various oak woodland plots; (4) studies in the ecotonal region of pine, oak, and exotic tree species invasion into old fields and woodlands with varying fire and land use histories (e.g., Dovciak et al. 2005, Knight and Reich 2005) at multiple scales using ground-based, remote, and historical data sources; (5) studies of the dynamics of plants, arthropods, exotic invasive herbaceous plants, and soil C and N in the chronosequence; and (6) mechanistic studies of resource competition among trees, shrubs, and herbaceous vegetation using short-term manipulations embedded in long-term field experiments. These activities will enable us to 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. They will also provide data to test predictions of a variety of different theories of invasion ecology and community assembly (e.g., Davis and Thompson 2000; Davis and Pelsor 2001; Davis, Thompson and Grime 2005; Tilman 1999, 2004).

### **Set 3: How do herbivores, pathogens, seed predators and other natural enemies influence plant diversity, productivity and nutrient dynamics?**

#### **Introduction**

Herbivores, seed predators, and pathogens can have substantial effects on the growth, survival and reproduction of individual plants, and thereby on plant community composition and ecosystem function. Our experiments have shown that preferential feeding by deer on some legume species can have disproportionate impacts, over the long-term, on C and N dynamics, primary productivity, and plant community composition (Ritchie and Tilman 1995, Ritchie et al. 1998; Knops et al. 2000). We propose continuing our two current deer herbivory experiments to determine long-term effects of this herbivore on our grassland and savanna ecosystems.

Previous studies at CCNHA also have found significant effects of foliar fungal pathogens (Knops et al. 1999, Mitchell et al. 2002, Mitchell 2003, Mitchell et al. 2003), insect seed predators (Kitajima and Tilman in preparation), and soil pathogens (Schnitzer et al. in preparation) on productivity, biomass and/or reproductive output of individual plant species. Given these species-specific influences, we expect significant effects of these natural enemies on plant community composition and diversity, effects we propose to now directly test and compare through long-term removal experiments. Species differentiation in natural enemies, like species differentiation in resource use, could also be the basis for the increase in diversity at increased productivity observed in the Biodiversity experiment (Tilman et al. 2001b). We propose a second enemy removal study nested within the Biodiversity experiment to distinguish the enemy-based and resource-based contributions to the productivity-diversity relationship. We note that one of our new researchers, H. Muller-Landau, who also works on Barro Colorado Island (BCI) in Panama, will be comparing the role of natural enemies between CCNHA and BCI.

#### ***1. Impacts of Deer on Plant Productivity and Succession***

To evaluate the long-term effects of deer browsing on plant productivity and diversity via its impacts on legumes and on seed availability, and to investigate the interaction of deer

browsing with other anthropogenic environmental changes relevant to CCNHA, we propose to continue two long-term deer enclosure experiments.

*Savanna Herbivore Enclosures:* Within each of six oak savanna stands with different fire frequencies, we established a pair of 30 x 30 m plots, one fenced to exclude deer and one unfenced (**E140**). After 10 years, deer enclosure has led to increased legume abundances, especially of *Lathyrus venosus*. We hypothesize that this will lead to increased primary productivity via increased total soil N and N mineralization (Vitousek et al. 2002). Because deer preferentially feed on flowering heads of many forbs, we hypothesize that deer enclosure will lead to higher recruitment and abundance of these forb species and increased forb diversity. We will test these hypotheses by sampling species abundances, soil for total C and N, and available soil N.

*Interactive Effects of Deer, Fire and Nitrogen:* In 2000 we began to examine impacts of three anthropogenic effects on successional grasslands in an area with rapid woody encroachment toward white pine forest. We established a 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 deer (fenced or open to deer), with a total of 32 plots, each 20 x 20 m (**E153**). We hypothesized that the response of this ecosystem to the combined effects of fire, N, and herbivory would depend on the ability of pine and other species to invade and the magnitude of their response to the different disturbance factors: warm-season grasses increase with and encourage fire, resist herbivores, and inhibit woody plant invasion (Davis et al. 1998, Inouye et al. 1994); cool-season plants are favored by N deposition (Tilman 1987) but are fire-intolerant and palatable to herbivores; legumes tolerate fire but decrease with herbivory and N deposition; and finally, woody plants are fire-intolerant and may be more susceptible to herbivory. We are measuring treatment effects on composition and diversity of plants and consumers (insects, small mammals, lizards) as well as plant and soil C and N.

## **2. Impacts of Insects and Pathogens on Plant Diversity and Productivity:**

To evaluate the effects of natural enemies on plant community composition, diversity, and productivity, and to compare the relative importance of different groups of natural enemies to plant communities, we propose two new enemy removal experiments involving soil oomycete pathogens, above-ground fungal pathogens, and above-ground insect herbivores. We focus on these groups because of their demonstrated importance in this community and because of the relative feasibility of excluding them without major impacts on other organisms.

*Enemies and Native Savanna:* We propose an enemy removal experiment to elucidate the importance of four different groups of natural enemies for plant species composition, diversity, and productivity within native savanna. Specifically, 8 replicate blocks (4 in each of 2 stands of native savanna) will contain 6 treatments of 4 x 4 m each: (a) monthly soil metalaxyl drench to reduce soil oomycete pathogens; (b) weekly fungicide application to reduce fungal pathogens attacking foliage, flowers and seeds; (c) weekly insecticide application to reduce insect herbivores and seed predators; (d) deer exclusion via fencing; (e) a combination of all three; or (f) an untreated control. We will regularly survey plants for evidence of herbivory and disease to assess the effectiveness of the treatments (Coley 1983, Campbell and Madden 1990, Louda et al. 1997). Plant community responses will be assessed via monthly censuses of percent cover and annual clipping of above-ground biomass; seedling censuses; and counts of seed heads and viable seeds per seed head. Soil N will be measured annually. Foliage, root and soil samples will be collected at least once a year from all subplots, with some subsamples assayed for particular pathogens and others archived to facilitate later analyses (Beauchamp et al. 2005). With these data we will test the hypothesis that natural enemy removal leads to a reduction in plant species diversity because the species that are the best competitors in the absence of enemies competitively exclude the others. Using the seed and seedling data, we will specifically examine the role of enemy impacts on plant reproduction and recruitment limitation in driving changes in

community composition. We will also test whether enemy removal increases plant productivity or use of the limiting resource (soil N), and whether it increases or decreases interannual variation in productivity and composition. Comparisons among the treatments will permit an analysis of the relative effects of different enemy types.

*Enemies and Biodiversity Experiment:* To assess the relative contribution of natural enemies to the increase in productivity observed at high diversity in the Biodiversity experiment, and to determine how enemy impacts vary with diversity (even if they do not impact productivity), we propose experimental enemy removal treatments nested within monocultures, 2-, 4-, and 16-species plots of the Biodiversity Experiment, using 10 randomly chosen plots at each diversity level, and five treatment subplots of 2 m x 3.5 m each. The treatments and data collection will be as above minus the deer enclosure treatment (deer are excluded from the entire Biodiversity experiment). We will test for effects of the treatments on species composition and total productivity within plots, and on the overall among-plot diversity-productivity relationship, as well as on interannual variation in composition and productivity within plots and the diversity-stability relationship among plots. We hypothesize that productivity will be higher and the increase in productivity with diversity weaker when natural enemies are removed.

### C. REGIONAL AND CROSS-SITE RESEARCH

In keeping with the LTER's increasing emphasis on cross-site research and regionalization, we propose several new initiatives: 1) to move beyond the borders of CCNHA proper to compare the ecosystem consequences of the dominant land use change in the region (from agriculture to residential land use) with those of conversion to old fields; 2) to continue regional and global syntheses of plant traits; 3) to understand the role of photodegradation in decomposition across LTER sites spanning an aridity gradient; and 4) to compare the role of natural enemies in maintaining plant species diversity in temperate and tropical sites.

#### **1. Cedar Creek's changing borders: the consequences of land use/land cover change for organic matter dynamics**

The landscape surrounding CCNHA is changing rapidly, as agricultural lands are replaced by low-density residential land use at the fringes of the Twin Cities Metropolitan Area (TCMA). CCNHA is becoming an island within a sea of residential development. Such land use change is typical of the Upper Midwest: while urban areas occupy only 3% of the Upper Midwest land area, low-density residential land use occupies >11% (Hammer et al. 2004, Radeloff et al. 2005). Of the 100 fastest growing counties in the US during the period 2000-2004 (percentage population growth), seven were in the TCMA, including Isanti County (one of the counties in which CCNHA resides) (U.S. Census Bureau, 2005). Although the conversion of agricultural land to semi-natural perennial vegetation (e.g., old fields, restored prairie, CRP) has been relatively well-studied, including as part of CDR (Jastrow 1987, Knops and Tilman 2000, McLauchlan et al. 2006), the conversion of agricultural land to residential land use is relatively unstudied. Nevertheless, one recent estimate concluded that the US land area in turf grass is now three times larger than the area planted in irrigated corn (Milesi et al. 2005).

Relatively little is known about the ecosystem processes (particularly the C fluxes) associated with residential land cover. The Chicago Urban Climate Project produced detailed C budgets at the level of city blocks (Jo and McPherson 1995). Changes in soil C have also been quantified along urban-to-rural gradients (Pouyat et al. 2002). In addition, there are currently continuous measurements of CO<sub>2</sub> flux in two sites representing developed land use, the Baltimore urban LTER site (Grimmond et al. 2002) and a site operated by USGS near Denver (Anderson and Taggart 2002). Finally, a couple of studies have used biogeochemical simulation models to explore the consequences of different turfgrass management on soil and plant C fluxes (Qian et al. 2003, Milesi et al. 2005). However, with the exception of Qian et al. (2003), all of

these studies were essentially “snapshots” in time in that they ignored the temporal dynamics of C accrual in plant biomass and soil organic matter associated with conversion of other types of land use to residential landscapes or turfgrass. Yet, long-term agriculture is well-known to deplete soil organic stocks that generally increase over time with cessation of agriculture and restoration of perennial vegetation (McLauchlan et al. 2006). Thus, it is reasonable to hypothesize that conversion of agricultural lands to residential land use will result in C sequestration in soils and plant biomass, but with uncertain dynamics.

As part of our renewal, we propose determining the temporal dynamics of organic matter accumulation in soils and plant biomass in residential landscapes surrounding CCNHA by establishing a chronosequence of 50 residential landscapes in Anoka County in the CCNHA vicinity. This “residential chronosequence” will complement the old field chronosequence (E014) that has already been the focus of work on C and N dynamics following agricultural abandonment (Knops and Tilman 2000) and will enable us to directly compare the value of ecosystem services (in terms of C sequestration) provided by three major land use types: agriculture, conversion to semi-natural vegetation and conversion to residential landscape.

Using US Census housing data and County parcel data, we will select residential landscapes to hold constant slope, soil texture, depth to groundwater and minimum time in cultivation as much as possible, but varying time since conversion from agriculture. We will select sites in year 2 and concentrate sampling in year 3. We will establish plots conforming to USDA Forest Service Urban Forest Inventory protocols (developed in connection with the Baltimore urban LTER) and use data as input to the Urban Forest Effects (UFORE) model to estimate net C accumulation of trees (Nowak and Crane 2002). In addition to data on tree and shrub/seedling cover, the protocol includes data on percent cover of herbaceous vegetation, impervious surface, permeable surface, buildings, and water. Our sampling intensity (approx. 1 plot/120 acres) is similar to that used in previous urban forest inventory studies. The plots will be sampled once during the growing season by a team trained by FIA field personnel from the North Central Research Station. We will sample soil C and N pools, texture and bulk density to 0.5 m depth at each site and characterize C fluxes through static chamber-based flux measurements during years 3 and 4. The integration of all of these measurements will form the basis for regional scale comparisons between several land cover types currently being studied by investigators at the University of Minnesota. The results from this study will improve our understanding of impacts of suburbanization on ecosystem processes, enhance our ability to predict changes in regional C budgets with suburbanization, and provide data for economic valuation of ecosystem services such as C storage.

## **2. GLOPNET and related cross-site trait initiatives**

GLOPNET, a Reich-led coalition to develop a global plant physiological data base (Wright et al. 2004, 2005ab; Reich and Oleksyn 2004, Shipley et al. 2006), now includes >15,000 observations of >2,500 vascular plant species from >250 sites in 50 countries (including CDR and other LTER sites). These have uncovered fundamental trait relationships which have been incorporated into ecosystem-scale models tested at LTER sites (Ollinger et al. 2002, Wythers et al. 2003, 2005). The GLOPNET initiative is ongoing (e.g., Reich is a co-investigator of the Australia-New Zealand Research Network for Vegetation Function), supported by the activities of a large network of international collaborators, and is expanding to other traits such as roots, wood properties, etc. A new initiative supported in part by our renewal involves measures of leaf traits within dominant species along regional north-south and east-west gradients in central North America, including CCNHA, to test hypotheses about the effects of climate on soil biogeochemistry and adaptation and acclimation of plant traits. We anticipate substantial continued cross-site research on these themes during the next six years.

### **3. Photodegradation of plant litter in grassland ecosystems: a mechanism for uncoupling C and N biogeochemistry**

With separate funding (NSF Ecosystems Studies to King and Hobbie), we are quantifying the contribution of photochemical oxidation of organic matter by ultraviolet radiation to surface litter decomposition in grasslands across a gradient of solar radiation and aridity in the central US using a multi-year field decomposition experiment. We also use laboratory experiments to elucidate mechanisms by which photodegradation influences decomposition. The field decomposition experiment will be conducted at three LTER sites: CDR, SGS and SEV. Our LTER renewal will establish long-term measurement sites and monitoring protocols to go beyond the 3-year field study and will use this study to develop a database for monitoring UV radiation and the influence of photodegradation on C cycling. The results from this study will expand our understanding of the relative importance of photodegradation across the broader cross-site gradient and will enhance opportunities for LTER cross-site research and outreach.

### **4. The role of natural enemies in maintaining species diversity and composition in temperate grasslands vs. tropical forests**

In addition to the natural enemy removal experiments proposed for CCNHA (removal of fungal pathogens, aboveground insect herbivores, soil oomycete pathogens, and vertebrates), we are simultaneously planning similar enemy exclusion experiments in a wet tropical forest in Panama. While there are a number of differences in the experimental design necessitated by the different spatial scale of these plant communities (in Panama we will be treating only reproductive parts on trees and seedlings in the understory), the combination of these two studies should provide insight into the importance of different groups of natural enemies for controlling seed production and seedling regeneration within these two very different plant communities, and for maintenance of plant diversity.

## **D. SYNTHETIC RESEARCH**

Synthesis has been a hallmark of CDR since its founding. As in the past, the development, testing and refinement of concepts and theory are central features of the research and synthesis that we propose. We highlight, here, additional synthesis activities. Our synthesis activities often have come from approaching a question from many different perspectives, especially those of population, community and ecosystem ecology and addressing it with observations, experiments and theory. Synthesis can also come from using one perspective to approach many different questions. Although synthesis is central to all of our work, we highlight two activities that will be especially important parts of our proposed work. The first activity uses plant traits to explore the potential roles of interspecific tradeoffs and phylogenetic history in determining community assembly, composition and diversity, and also ecosystem functioning. The second takes our specific on-site results and uses them in combination with economic valuation theory to synthesize those aspects of ecology and economics relevant to maximizing the net long-term, sustainable value returned to society from natural and managed ecosystems.

### **1. Tradeoffs, Scaling, Phylogenetic History, and Community Assembly: A Trait-Based Approach to Synthesis**

#### **Introduction**

Plant traits (e.g. leaf %N, stem hydraulic conductance,  $A_{max}$ ) reflect interactions among (1) the ecological strategy and phylogenetic history of the species, (2) the plasticity of each trait, and (3) the current abiotic and biotic environment. They influence, if not regulate, whole-plant function, biotic interactions and plant-environment interactions, all of which determine the dynamics of communities and their aggregate structure and function (Fig 44). Patterns of functional trait variation and trait correlations within and among habitats are predictably related



to several environmental and trade-off axes, reflect natural selection, and can be considered plant strategies of resource capture and tolerance (Reich et al. 1997, 2003b). Plant trait variation typically involves multiple correlated traits that arise because of inevitable trade-offs among traits and across levels of whole-plant integration. That must be understood from a whole-plant perspective, which can provide a mechanistic underpinning for the facilitation and competition that drive community dynamics. As part of the CDR, we have studied ecosystem structure and function, community dynamics, trophic interactions (see other sections of proposal) and plant traits (e.g., Reich et al. 2003b, 2006b ; Wright et al. 2004, 2005ab). We have also searched for links between traits and ecological processes (e.g., Wedin and Tilman 1990, Tilman and Wedin 1991ab, Reich et al. 2001c, Craine et al. 2002ab, 2003abc; Dickie et al. 2005, Fargione and Tilman 2006, Harpole and Tilman 2006). We propose increased focus on this topic. We believe that studying plant traits across our diverse research landscape will uncover mechanisms that integrate evolutionary history, community assembly, and ecosystem structure and function.

Correlated leaf traits such as leaf lifespan, SLA, leaf N, leaf diffusive conductance,  $A_{\max}$ , and  $R_d$  form a fundamental spectrum of variation among plant species (Reich et al. 1997, Wright et al. 2004). At one end of the spectrum, species (typically characteristic of high-resource habitats or a high-metabolism strategy) can be characterized as having fast tissue turnover and high potential for resource capture and rapid short-term growth, whereas at the other end of the spectrum, species have slower tissue turnover and traits that enhance nutrient conservation. Abundant evidence shows the association of given traits with indices of fitness and the compositional dynamics of communities, but direct evidence of the underlying resource economics is much scarcer. Some authors have argued that particular suites of traits are adaptive in the face of many different resource stresses (Grime 1977, 1989; Chapin et al. 1993); others have emphasized that different suites of traits are advantageous according to the most limiting resource in question (Grubb 1998). We cannot resolve this debate here but note that a single multiple trait axis has been documented that represents a general trade-off strategy continuum for plant functional traits (Reich et al. 1997, 2003b, Wright et al. 2004). Testing the generality and applicability of these ideas can help us achieve synthesis across the range of CDR terrestrial ecosystems, by asking when, whether and how plant trait syndromes can explain the resource economics of individuals and how such economics regulate survival, growth, and community change. For instance, can resource economics determined by species traits explain the outcomes of competition that regulate the composition and diversity of assemblages under alternate fire,  $\text{CO}_2$ , N, climate, or other regimes? Moreover, plants do not have the same sets of traits for all environmental conditions. Identification of how or if trait syndromes vary with environmental conditions and influence biotic interactions is important to current and future CDR activities.

Measures of traits will be made for the following species along the following biological and environmental gradients: 1) 16 species in BioCON at all 16 combinations of species richness,  $\text{CO}_2$  and N (as many as 256 combinations); 2) most vascular plant species ( $\approx 45\text{-}60$ /plot, total of 180-192 in each of 1995, 2000, and 2005) found in the oak woodland-grassland continuum across patches varying in resource availability (light, soil N supply) because of fire regime, patch species composition and density; 3) many species in other experiments, including long-term N addition (**E001**), the old field successional chronosequence, the biodiversity experiment (**E120**); 4) within and across populations of species along regional north-south (temperature) and east-west (moisture) climate gradients. Each of these projects already has been initiated but will be greatly expanded from 2006-2012.

### **Key Results**

- Studies of species responses in CDR experiments have illuminated the importance of functional traits, integrated tissue-to-ecosystem attributes and helped explain responses of simple and diverse communities to perturbations (Lee et al. 2001, Reich et al. 2001abc, Craine et al. 2002a, 2003ac; Tjoelker et al. 2005, Harpole and Tilman 2006) such as  $\text{CO}_2$ , fire or N deposition.

- A CDR co-PI (PR) initiated and led a coalition that developed the first comprehensive global plant physiological data base (GLOPNET), focused on the nature of design alternatives in leaves (Reich et al., 1997, 1998, 1999; Wright et al. 2004, 2005ab; Reich and Oleksyn 2004).
- This work identified universal trade-offs between leaf traits that are common to all world biomes (Fig 25; Wright et al. 2004), demonstrating convergent evolution and broad generality. It has also highlighted a variety of geomorphic, environmental, evolutionary, and compositional forces that regulate plant chemistry across global gradients (Fig 27; Reich and Oleksyn 2004).
- Scaling of metabolism to size in plants was shown to be isotropic and driven by biochemical stoichiometry and refutes theoretical 3/4-power scaling (West et al. 1999, Gillooly et al. 2003) hypothesized to be a universal function of the fractal nature of vascular resource delivery systems (Fig 28; Reich et al. 2006b).
- These trait relationships have been incorporated into ecosystem-scale models that were validated against data from LTER sites or used to explore hypothesized global change scenarios (Ollinger et al. 2002, Craine et al. 2003ac; Wythers et al. 2003, 2005).
- Multi-year analysis of the phylogenetic structure of two long-term experimental communities at Cedar Creek, the oak savanna burn plots and the N addition plots, shows that phylogenetic clustering (i.e., “niche conservatism” Harvey and Pagel 1991, Ackerly 2003; Fig 45A) is the dominant pattern when environmental filtering (in the form of fire or N addition) is strong. We are currently examining the phylogenetic lability and conservatism of traits that could explain such patterns. We predict that traits of species that have similar values within the same plot will be phylogenetically conserved (C. Willis, J. Cavender-Bares, A. Keen and C. Lehman, in preparation). In successional fields where abiotic factors are less important, we expect phylogenetic overdispersion (neighbors are less related than expected; Fig 45B) if species interactions predominate over dispersal patterns.

### **Future Research**

In the renewal period we propose to greatly expand our studies of plant traits and their evolutionary and ecological causes and consequences (Fig 44). To do this we will develop traits data bases for species in many of the major CDR experiments, and couple these data with data on community composition and abundance that are available for several long-term experiments including i) the burn-frequency experiment in the oak savanna, ii) chronic N deposition in prairie communities, iii) natural succession of old fields abandoned at different times, and iv) diverse assemblages under ambient and elevated CO<sub>2</sub> and N in the BioCON.

In so doing we will address a specific hypotheses regarding (a) phylogenetic structure, dispersion and ecological sorting; (b) trade-off surfaces, trait-trait and trait-environment scaling relationships within and across communities; (c) causes and consequences of the distribution of traits in communities along succession, resource, or other gradients (including differentiating species replacements from phenotypic variation); and (d) the mechanisms whereby traits influence biotic interactions including facilitation, competition, and herbivory and thereby regulate the dynamics of plant community composition and the structure and function of ecosystems, including their C and N biogeochemistry.

We will greatly expand our trait measurement efforts, increasing the number of taxa, environments, and traits. We will measure the chemistry, architecture, phenology, metabolism, morphology, hydraulics and longevity of leaves, roots, stems, canopies, and root systems; as well as reproductive, seed and dispersal characteristics. In selected studies, detailed examination of plasticity of traits in space and time will allow characterization of resource uptake, pre-emption, storage and turnover and help to explain outcomes of competition and aggregate impacts of diversity on ecosystem processes. We will also further develop an incipient phylogenetic tree for species in the CCNHA region based on supertree methods (e.g., Webb and Donoghue 2005).

## **2. Valuing Ecosystem Services – A Synthesis of Ecological and Economic Perspectives**

## Introduction

Human society is, to a great extent, dependent on services that it receives from managed and natural ecosystems (Krutilla 1967, Daily 1997, Daily et al. 2000). But human actions that enhance certain ecosystem services, such as production agriculture, threaten to erode the ability of ecosystems to provide other services, such as supplies of clean water, sequestration of atmospheric C, regeneration of soil fertility and habitat to support biodiversity (MA 2005). There is a need for a systematic economic and ecological accounting of potential tradeoffs among ecosystem services, and their relative values, to better inform societal choices affecting ecosystems (NRC 1999, 2004, MA 2005). Most existing studies of ecosystem services have focused on the production of commodities (e.g., agricultural crops, fish, and timber). Our understanding of the factors affecting the supplies of other ecosystem services of societal importance – but not directly tied to income, such as climate regulation, nutrient cycling and habitat provision – lags far behind (MA 2005). To be able to close these gaps in understanding requires advances in the following areas:

- *Ecological production functions* that describe the relationship between the structure and function of ecosystems and the provision of various ecosystem services;
- *Economic valuation methods* that can be applied to generate estimates of the value of ecosystem services in monetary terms;
- *Integration of ecological production functions and economic valuation methods* in a unified approach to ecosystem services.

## Future Research

Ecological research conducted at CDR for the past 20 years provides detailed information on how the functioning of ecosystems depends on such human-driven variables as atmospheric N deposition, invasion of exotic species, loss of biodiversity, and elevated atmospheric CO<sub>2</sub>. We propose to use these existing data along with new data from CDR studies to define ecological production functions for ecosystem services and their dependence on various ecological conditions and management practices. We will begin by focusing on the biodiversity experiments, using them to elucidate the effects of species composition and diversity on the rates and sustainability of C sequestration, the quality (e.g., concentrations of NO<sub>3</sub> and other compounds) of water entering the water table, the rate of accumulation of soil total N and of other measures of soil fertility (such as in situ N mineralization), and the abundances of agriculturally-important pollinators and of biocontrol agents of crop pests (i.e., species of parasitoid or predatory insects).

The final step in the research will develop economic valuation of ecosystem services. Economists have developed a range of “non-market valuation” techniques that can be applied to valuing ecosystem services (Freeman 1993, NRC 2004), although the degree of confidence attached to estimates of non-market value varies widely depending on the services and the valuation methods used. In some cases, biophysical assessment of tradeoffs among services is sufficient without translation of services to dollar values.

In prior work, we have used CDR data to demonstrate the economic value of increased biodiversity in terms of increased system productivity (Tilman, Polasky and Lehman 2005). This work showed how to take ecological information and translate it into estimates of economic value and provides a foundation on which to work. However, it only scratched the surface of the research potential for integrating economic and ecological analysis of Cedar Creek data for valuing ecosystem services. Among the important next steps in this research are:

- Expanding the range of ecosystem services considered to include C sequestration, soil fertility, nutrient use and water quality, pollination and pest-regulation among others.
- Consideration of how human impacts, either from deliberate management decisions or as inadvertent byproducts of other decisions, affect the provision of various ecosystem services.
- Careful consideration of the geographic and temporal scale of the analysis.
- Consideration of cumulative effects.

- Consideration of interactions among effects.
- Consideration of changes in marginal value when levels of provision of ecosystem services change or the mix of services provided is altered.

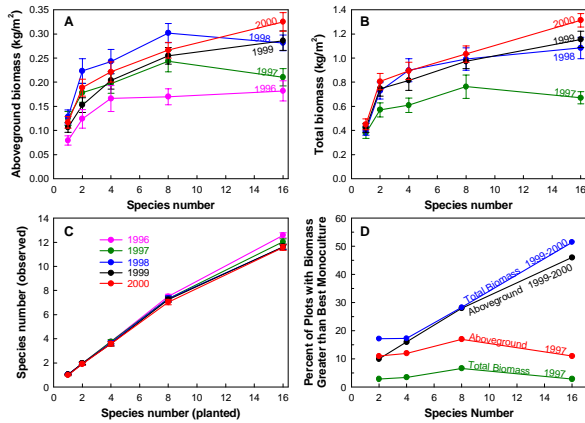
Our initial case study of ecosystem services, their economic valuation, and implications for policy will center on biofuel production. We have already evaluated the economic, energy, and environmental full-life-cycle costs and benefits of the use of food plants (corn and soybeans) as potential sources of transportation biofuels (ethanol and biodiesel; Hill et al, submitted). In particular, we propose evaluating the economic, energy, and environmental full-life-cycle costs and benefits, including those from ecosystem services, of biomass energy from prairie grass mixtures of different compositions and diversities. Much of our efforts would be supported by a grant from the MN Initiative on Renewable Energy and the Environment.

While the principles involved in valuing ecosystem services are clear, the practice of valuing ecosystem services is far from straightforward (“the devil is in the details”). Delivering credible scientific estimates of ecosystem services requires tackling tough problem within ecology and economics, but especially at the juncture of ecology and economics. With the work done at CDR over two decades, the work that Polasky has done on valuing ecosystem services for the National Research Council (National Research Council 2004), the Science Advisory Board of US EPA and the Millennium Assessment (Millennium Assessment 2005), and the prior combined work integrating ecology and economics (Tilman et al. 2005, Tilman and Polasky, 2005), we are well positioned to make fundamental advances in this field.

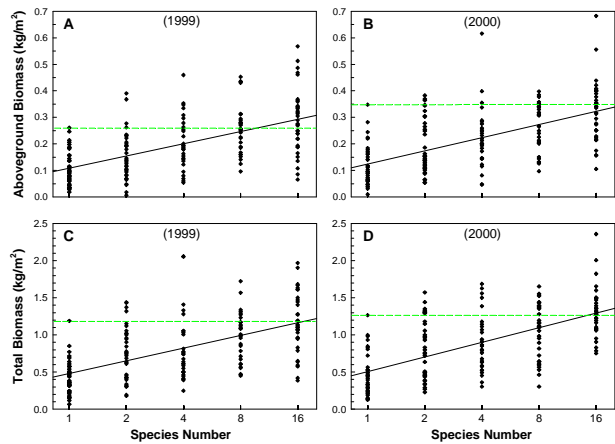
## **E. CONCLUSIONS AND SUMMARY**

The overarching goal of our research is to understand the processes, feedbacks and mechanisms that determine the dynamics and functioning of the grassland and savanna woodland ecosystems of CCNHA, including how and why they are impacted by various aspects of human-driven environmental change, and the societal implications of such changes. Our synthetic approach combines ecophysiological, population, community and ecosystem perspectives with long-term experiments, long-term observations and the development and testing of theory. Each of the core studies described in this proposal contributes to this effort (Fig 46). In particular, each of the core studies manipulates or otherwise determines how one or more environmental factors (e.g., biodiversity, climate change, elevated CO<sub>2</sub>, land use change, etc.) affects community composition and ecosystem structure and functioning. Related process-oriented studies allow us to test among potential underlying mechanisms for these effects. In addition, we will explore the potentially unifying role that species traits may play in moderating and determining the effects of environmental factors on both composition and diversity and on ecosystem structure and functioning.

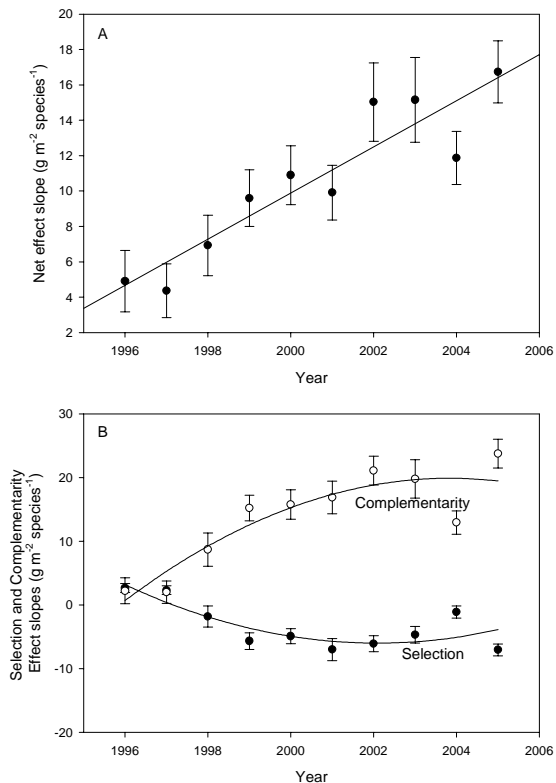
Our CDR team of scientists includes eight new co-investigators whose skills and interests add significant diversity to our LTER site, providing us with the full range of skills and interests to pursue the proposed research. Our proposed research includes the continuation of core long-term CDR studies that have potential to provide major insights, as well as the implementation of significant new initiatives, especially a biodiversity and climate experiment, two new natural enemy experiments, a study of ecosystem consequences of regional land use change, work on species traits, and work on the quantification and economic valuation of the effects of biodiversity on ecosystem services. In addition, we will continue to communicate our results to the media and government organizations, teach K-12 teachers and journalists about scientific research and recent results, provide science outreach for K-12 students and the public; provide research experiences for undergraduates, and train graduate students and post-docs.



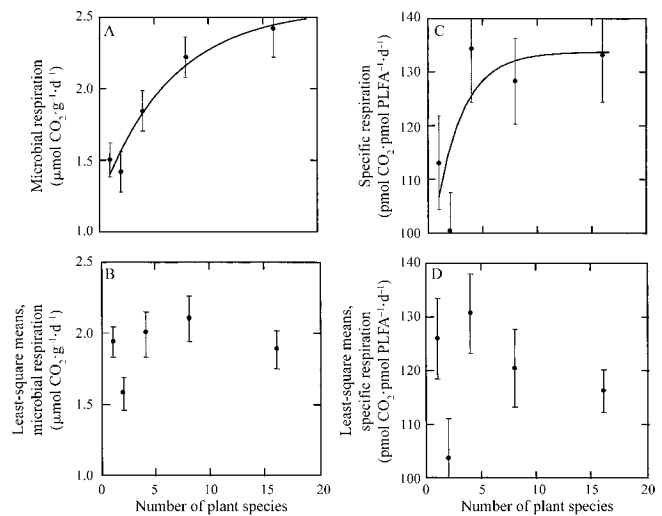
**Fig. 1.** The dependence of (A) plant aboveground biomass and (B) total biomass (aboveground plus belowground living plant mass) on the number of planted species. Data are shown as the mean  $\pm$  SE. (C) The relation between the number of species planted in a plot and the actual number (mean  $\pm$  SE) of planted species visually observed in a 2 m<sup>2</sup> area of each plot. (D) The percentage of all plots of a given planted diversity level, on average for 1999 and 2000 combined, or on average for 1997, that had greater biomass than the single monoculture plot with the greatest biomass. (From Tilman et al. Science 2001)



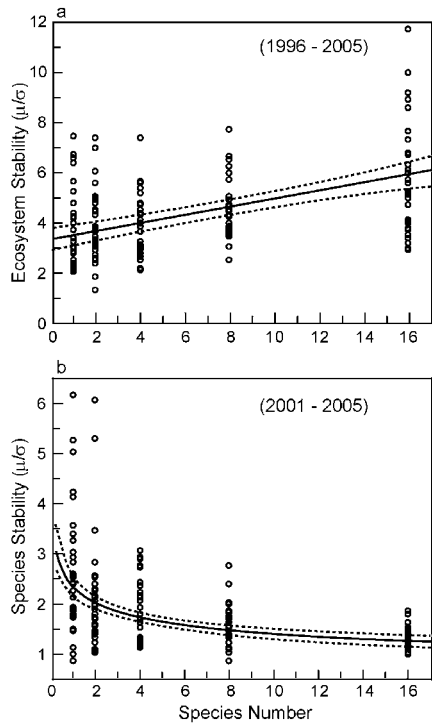
**Fig. 2.** The dependence of aboveground (A and B) and of total (C and D) biomass of each plot on planted species number for 1999 and 2000. The broken line shows the biomass of the top monoculture for a given year. The solid line is a regression of biomass on the logarithm of species number. Logarithm of species number was used in the figure because it gave slightly better fits, but was not used in Table 1 because it often gave slightly lower  $R^2$  values than species number. (From Tilman et al. Science 2001)



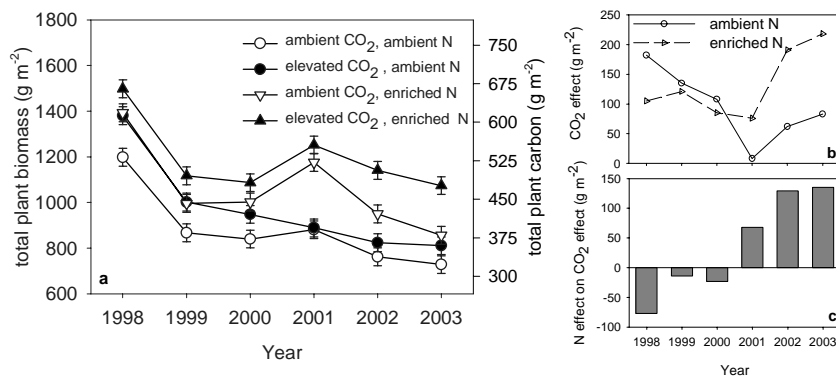
**Fig. 3.** Temporal trends in the slopes of (A) net and (B) selection and complementarity effects vs. species number 1996-2005. Error bars represent standard error. Only four of the slopes are not significantly different from zero: complementarity in 1996 and 1997, and selection in 1998 and 2004. (From Fargione et al., in prep.)



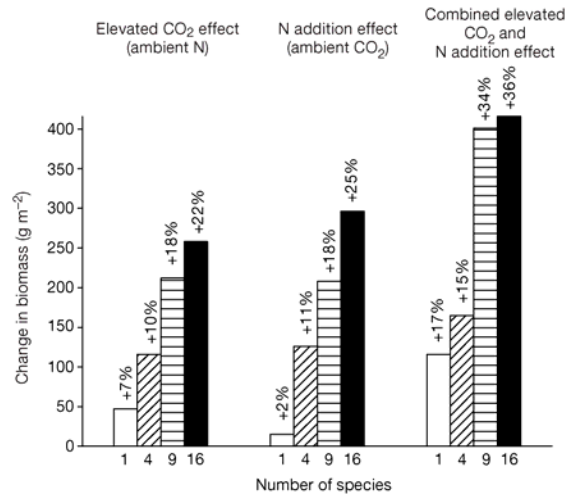
**Fig. 4.** Relationship of plant species diversity with (A) microbial respiration and (B) least-square means of microbial respiration, (C) specific microbial respiration, and (D) least-square means of specific microbial respiration. The best-fit line through treatment means of microbial respiration was  $\mu\text{mol CO}_2 \cdot \text{g}^{-1} \cdot \text{d}^{-1} = 1.35(1 - e^{-0.153 \text{ species}}) + 1.22$  ( $n = 5$ ,  $R^2 = 0.953$ ,  $P < 0.001$ ). The change in mean specific respiration with plant diversity (C) was described by the following equation:  $\text{pmol CO}_2 : \text{pmol PLFA}^{-1} \cdot \text{d}^{-1} = 37.55(1 - e^{-0.329 \text{ species}}) + 96.20$  ( $n = 5$ ,  $R^2 = 0.591$ ,  $P < 0.001$ ). There was no significant relationship between plant species richness and the least-square means of microbial respiration or specific microbial respiration. Error bars indicate  $\pm$  SE. (From Zak et al. Ecology 2003.)



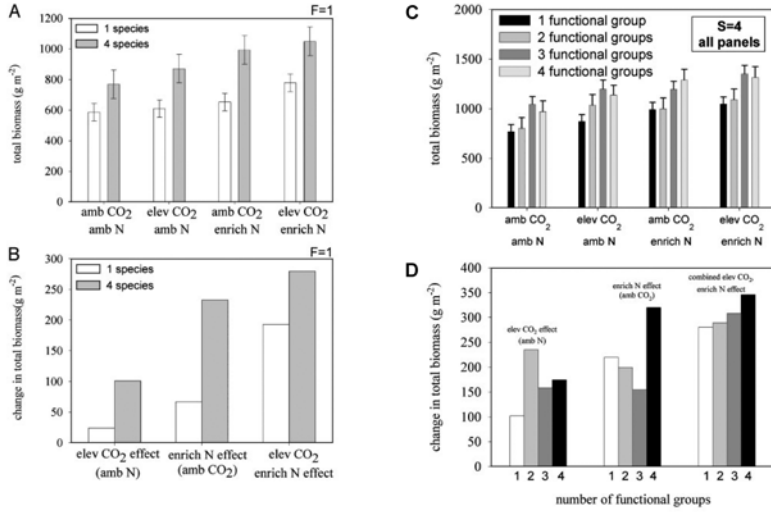
**Fig. 5.** Dependence of temporal stability of each plot on experimentally-controlled plant species numbers. **(a)** Ecosystem temporal stability for the decade from 1996-2005 was an increasing function of the number of planted species. Ecosystem stability is the ratio of mean plot total biomass to its temporal standard deviation determined after detrending. Regression line and its 95% confidence interval are shown, with  $F_{1, 159} = 43.7$ ,  $P < 0.0001$ . To reduce y-axis scale difference between the two parts of this figure, a single data point (species number of 16, ecosystem stability of 15.76) is not shown but was included in analysis. **(b)** Plot-average species temporal stability, determined using species biomass data for 2001-2005, was a declining function of the number of planted species. Regression curve and 95% confidence intervals based on fit of  $\text{Log}[\text{Species Stability}]$  on  $\text{Log}[\text{Species Number}]$ , with  $F_{1, 159} = 72.3$ ,  $P < 0.0001$ . (From Tilman et al. Nature, submitted.)



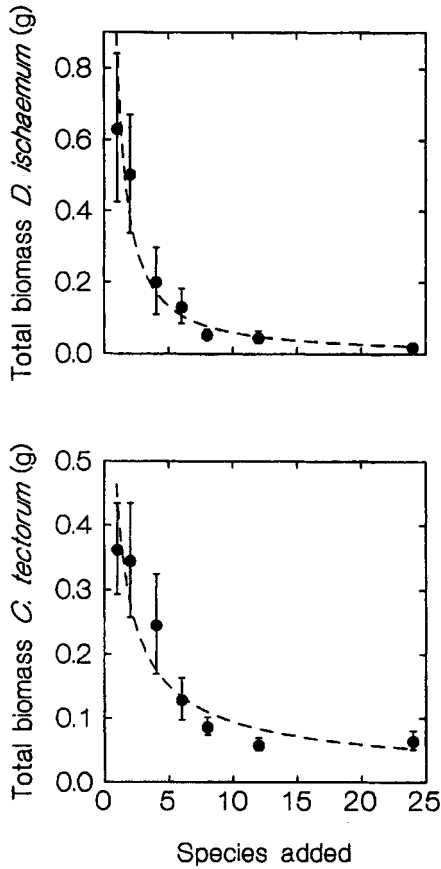
**Fig. 6.** Effects of CO<sub>2</sub> and N on total plant biomass over time in the BioCON experiment. **(a)** Total plant biomass (above-ground plus 0–20 cm below-ground) and carbon at ambient and elevated CO<sub>2</sub> and N levels from 1998 to 2003. Data were pooled across diversity treatments, and each point shows the annual mean (plus standard error) of 74 plots sampled twice per year. There was a significant interaction between CO<sub>2</sub>, N and year, plus significant main effects of year, CO<sub>2</sub> and N. Open circles, ambient CO<sub>2</sub> and ambient N; filled circles, elevated CO<sub>2</sub> and ambient N; open triangles, ambient CO<sub>2</sub> and enriched N; filled triangles, elevated CO<sub>2</sub> and enriched N. **(b)** The effect of CO<sub>2</sub> on total biomass: the CO<sub>2</sub> enhancement (assessed as (value at elevated CO<sub>2</sub>) minus (value at ambient CO<sub>2</sub>)) at ambient (circles) and enriched (triangles) N supply each year. **(c)** The effect of N availability on the CO<sub>2</sub> biomass effect, defined as the difference between the CO<sub>2</sub> effect at enriched N and that at ambient N, namely (CO<sub>2</sub> effect at enriched N) minus (CO<sub>2</sub> effect at ambient N). (From Reich et al. 2006a.)



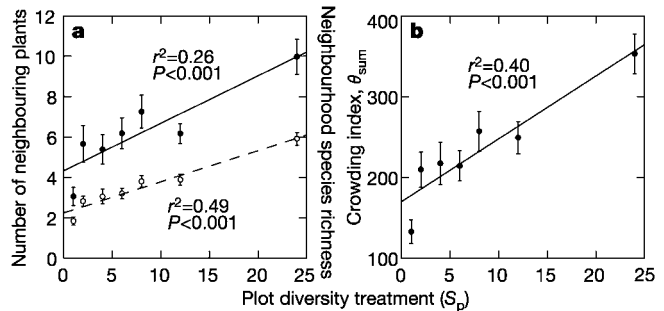
**Fig. 7.** Change in total (above-ground plus 0±20 cm below-ground) biomass (compared with ambient levels of both CO<sub>2</sub> and N) in response to elevated CO<sub>2</sub> alone (at ambient soil N), to enriched N alone (at ambient CO<sub>2</sub>), and to the combination of elevated CO<sub>2</sub> and enriched soil N, for plots containing 1, 4, 9 or 16 species. Data were averaged for 4 harvests over 2 yr. Per cent change is shown above each histogram for each diversity treatment. (From Reich et al. 2001a.)



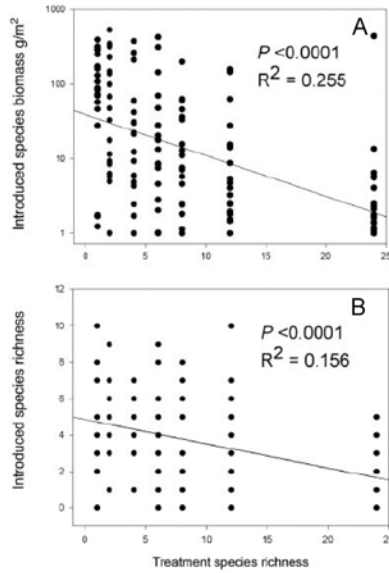
**Fig. 8.** Effects of  $S$  at a standardized  $F$  on biomass and biomass responses to elevated  $\text{CO}_2$  and enriched N. (A) In experiment I, total biomass (above-ground plus below-ground, 0–20 cm in depth; +1 SE) for plots planted with one functional group ( $F = 1$ ) and either one or four species, grown at four combinations of ambient ( $368 \mu\text{mol}\cdot\text{mol}^{-1}$ ) and elevated ( $560 \mu\text{mol}\cdot\text{mol}^{-1}$ ) concentrations of  $\text{CO}_2$  and ambient N and enriched N ( $4 \text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ). Data were averaged over two harvests in each year from 1998 to 2001. (B) In experiment I, the change in total biomass (compared with ambient levels of both  $\text{CO}_2$  and N) in response to elevated  $\text{CO}_2$  alone (at ambient N), to enriched N alone (at ambient  $\text{CO}_2$ ), and to the combination of elevated  $\text{CO}_2$  and enriched N, pooled across years, for plots with  $F = 1$  and  $S = 1$  or 4. Effects of  $F$  at a standardized  $S$  on biomass and biomass responses to elevated  $\text{CO}_2$  and enriched N. All data were from experiment III. (C) Total biomass (above-ground plus below-ground, 0–20 cm in depth; +1 SE) for plots planted with four species ( $S = 4$ ) drawn from 1, 2, 3, or 4 functional groups, grown at four combinations of ambient ( $368 \mu\text{mol}\cdot\text{mol}^{-1}$ ) and elevated ( $560 \mu\text{mol}\cdot\text{mol}^{-1}$ ) concentrations of  $\text{CO}_2$  and ambient N and enriched N ( $4 \text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ). Data were averaged over two harvests in each year from 1998 to 2001. (D) Change in total biomass (compared with ambient levels of both  $\text{CO}_2$  and N) in response to elevated  $\text{CO}_2$  alone (at ambient N), to enriched N alone (at ambient  $\text{CO}_2$ ), and to the combination of elevated  $\text{CO}_2$  and enriched N, in each year, for plots with  $S=4$  and  $F=1, 2, 3$ , or 4. (From Reich et al. PNAS 2004).



**Fig. 9.** Invading plant performance and species added to plots. Line represents fitted exponential curve using nonlinear regression. Filled circles represent means, and error bars are one SE. Top, regression parameter estimates; intercept =  $-0.34$  (SE =  $0.10$ ), exponent =  $-0.40$  (SE =  $0.13$ ),  $R^2 = 0.15$ ,  $P < 0.001$ . Bottom, regression parameter estimates; intercept =  $-0.61$  (SE =  $0.05$ ), slope =  $-0.14$  (SE =  $0.04$ ),  $R^2 = 0.45$ ,  $P < 0.001$ . (From Naeem et al. 2000.)



**Fig. 10.** Neighborhood characteristics and plot diversity treatment. Diverse plots tend to have neighborhoods with more neighboring plants (a, solid symbols and line), neighborhoods that are more species rich (a, open symbols and dashed line), and neighborhoods that are more crowded (b). Data points are mean values of 100 null points randomly placed into each of the 147 maps from 1998 that were then averaged within diversity treatments,  $\pm$ one standard error. (From Kennedy et al. 2002.)

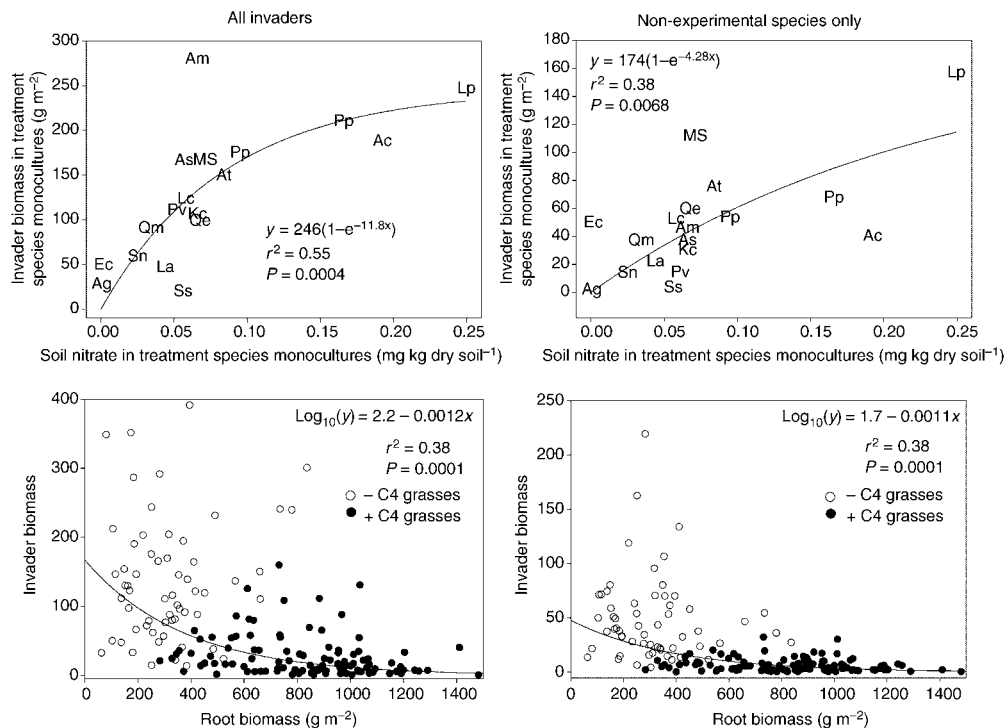


**Fig.11.** Relationship between species richness treatment and performance of introduced species. The lines are the best-fit simple linear regressions. Biomass of introduced species were log transformed before statistical analysis. (From Fargione, Brown, Tilman, PNAS 2003)

**Fig. 12.** Partial correlations from four multiple regression models in which the response of the  $\log(\text{cover} + 1)$  of each introduced functional guild in 1999 was regressed on the  $\log(\text{cover} + 1)$  of all four resident functional guilds in 1999

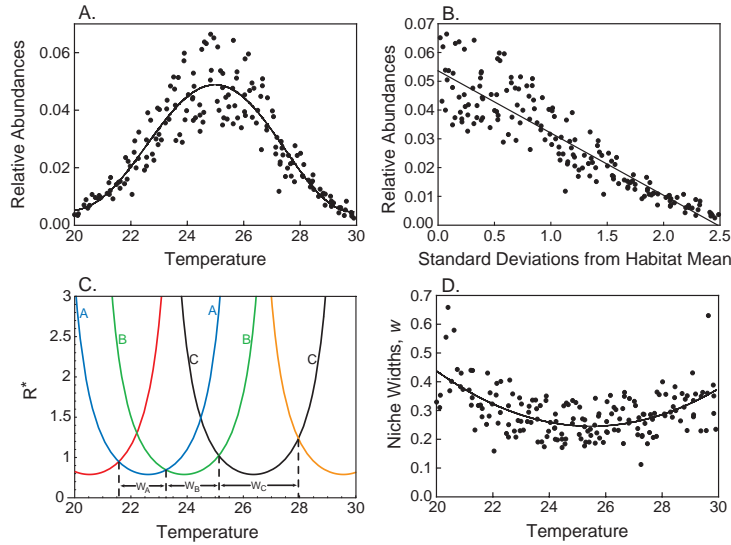
Resident functional guild	Introduced functional guild			
	Nonlegume forb	C3 grass	C4 grass	Legume
Nonlegume forb	-0.36***	-0.05	-0.12	-0.03
C3 grass	-0.11	-0.23**	0.01	-0.14
C4 grass	-0.47***	-0.32***	-0.48***	-0.24**
Legume	0.01	0.09	0.005	-0.12
Overall $r^2$	0.30	0.14	0.24	0.11
Overall $P$	<0.0001	0.0003	<0.0001	0.002

Significance levels were determined by using sequential Bonferroni (22) corrections for four multiple regressions (i.e., smallest  $P$  value < 0.0125, next smallest  $P$  < 0.0167, then  $P$  < 0.025, and the remainder  $P$  < 0.05). Uncorrected significance levels are presented for statistics that meet the sequential Bonferroni criteria: \*,  $P$  < 0.05; \*\*,  $P$  < 0.01; \*\*\*,  $P$  < 0.001. (From Fargione et al. 2003)

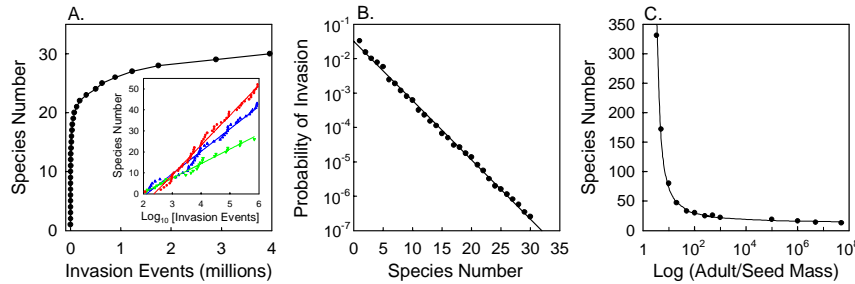


**Fig. 13.** Invader success is correlated with soil nitrate concentrations and root biomass. Soil nitrate concentrations explained most of the variation in invader biomass among monocultures of different species. Averages across monocultures are used for both invader biomass and soil nitrate, both of which were measured in the invasion strips. Root biomass, which was highly correlated with the presence of  $C_4$  grasses, was the best predictor of invader biomass across all 168 plots. Root biomass was measured in the adjacent unweeded plots. The regression results are for  $\log$  (invader biomass) regressed on root biomass. Analyses including  $C_4$  grasses are reported in the text. (From Fargione and Tilman, Ecology Letters 2005.)

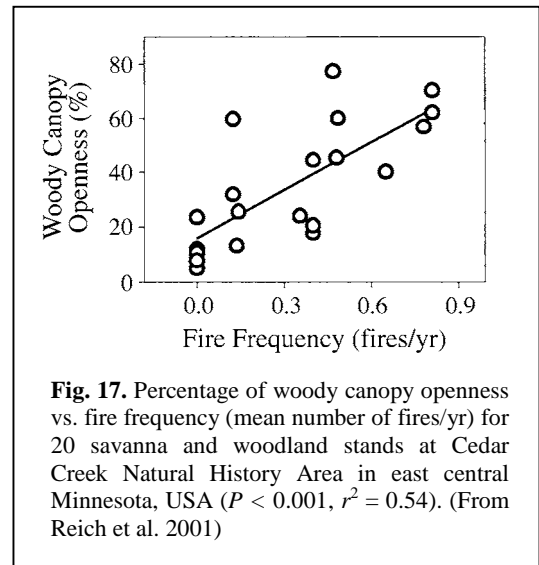
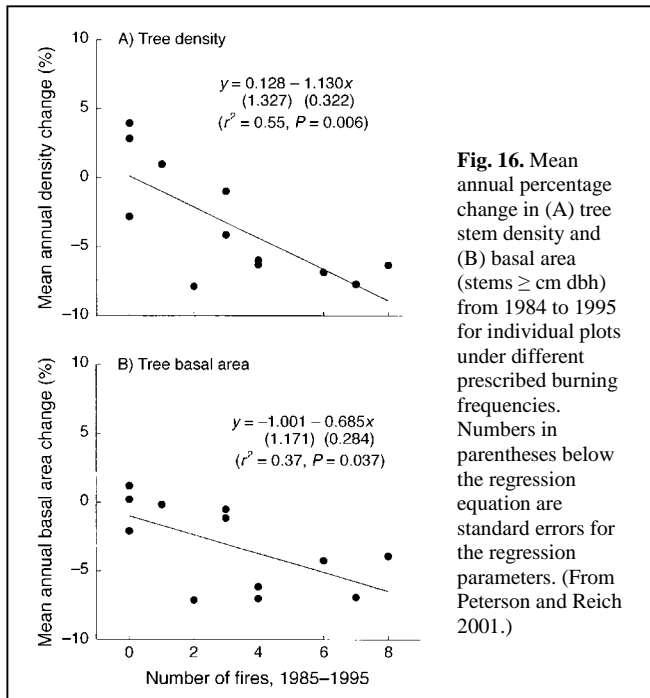


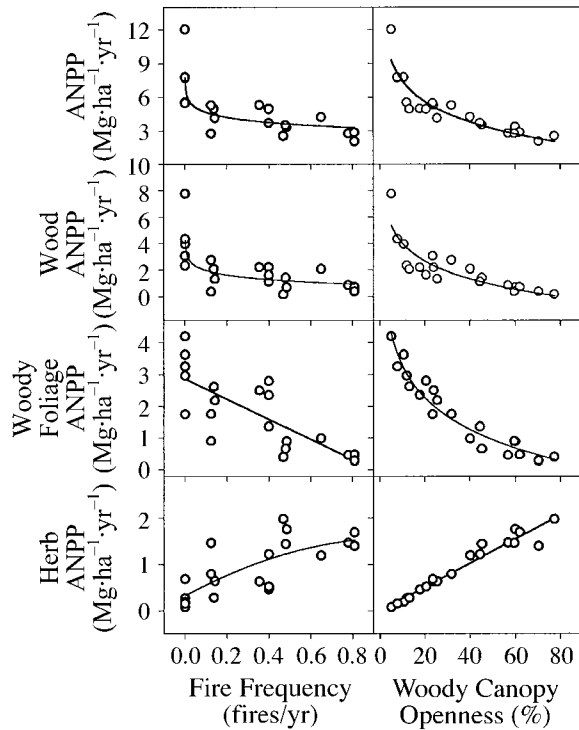


**Fig. 14.** A. Results of stochastic competitive assembly for five replicate simulations in which there were Gaussian distributions of both habitat temperatures and propagule  $t_{opt}$  values. Parameters as for Figure 4 A, B. The distribution of relative abundances of habitat temperatures (solid curve) closely mimics the observed relative species abundances (points). B. Relative abundance data of Part A graphed against the number of standard deviations of habitat heterogeneity (here  $\sigma = 2^\circ\text{C}$ ) by which optimum temperatures of species differ from habitat mean temperature. The most abundant species are those with  $t_{opt}$  values corresponding to the most common habitat types. C. Niche width is defined as the range of temperatures over which a species is the competitive dominant. D. Observed niche widths for the five simulations of Parts A and B. (From Tilman PNAS 2004)

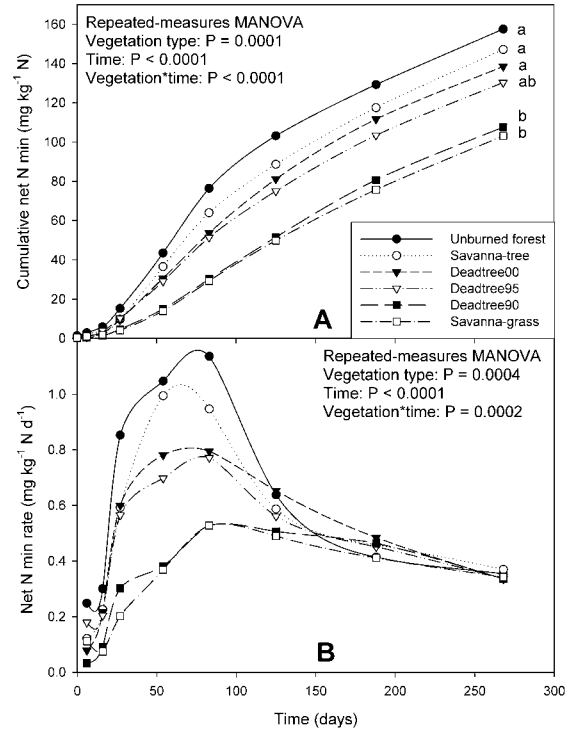


**Fig. 15.** Diversity and invasion. (A) Dynamics of species accumulation during stochastic competitive assembly shown for a simulation with Gaussian distributions of both habitat temperatures (mean,  $25^\circ\text{C}$ ;  $\delta = 2^\circ\text{C}$ ) and propagule  $t_{opt}$  values (mean,  $25^\circ\text{C}$ ;  $\delta = 2^\circ\text{C}$ ). Parameters were otherwise identical to those of Figs. 2 and 3, except that  $\delta_i = 0.4^\circ\text{C}$ . (Insert) Shown are three additional simulations differing only in the extent of habitat heterogeneity ( $\delta$ ), each illustrating that species number increases as the log of invasion events. (B) Log of the probability of future invasion (proportion of propagules that become established) declines linearly with species number. Results are for the same simulation shown in A. (C) Species number after  $10^6$  invasion events for cases like those of A but with a range of values for  $B_s$  and  $B_a$ . (From Tilman PNAS 2004)

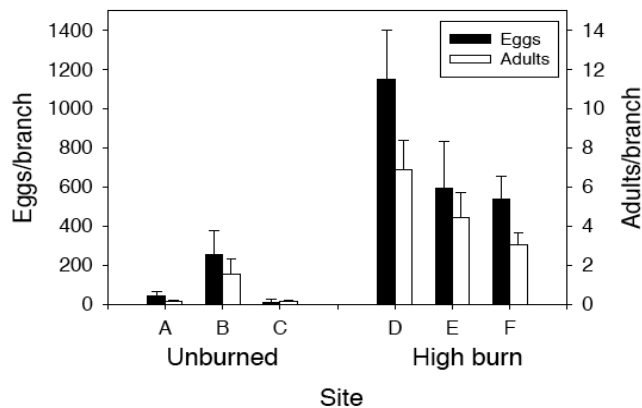




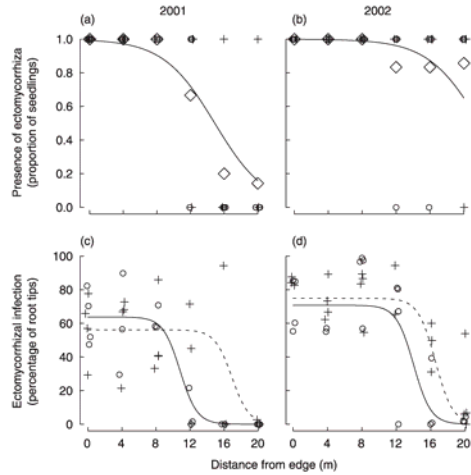
**FIG. 18.** Total aboveground net primary production (ANPP) and its components, aboveground wood NPP, woody foliage NPP, and herbaceous ANPP, in relation to fire frequency ( $r^2 = 0.59, 0.57, 0.58,$  and  $0.56,$  respectively) and percentage of woody canopy openness ( $r^2 = 0.83, 0.76, 0.94,$  and  $0.95,$  respectively) for 20 woodland and savanna stands. All relationships are significant at  $P < 0.001$ . (From Reich et al. 2001)



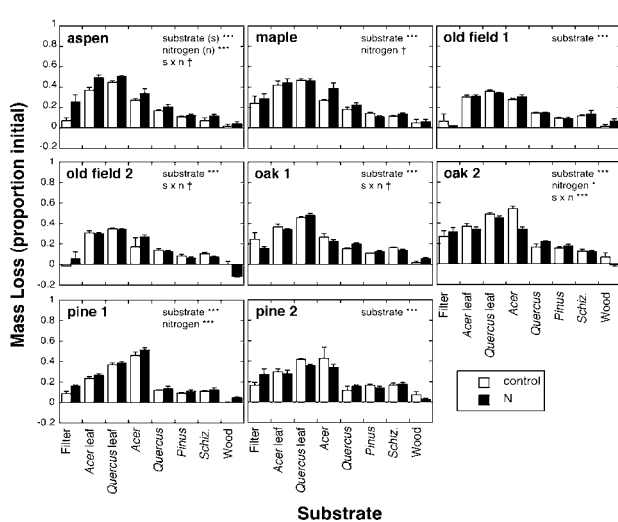
**Fig. 19.** Net N mineralization ( $\text{NH}_4^+ + \text{NO}_3^-$ ) over 268 days in laboratory incubations of soils from unburned forest, savanna-tree, savanna-grass, and dead tree plots. (A) Cumulative net N mineralization ( $\text{mg kg}^{-1}$  soil N). (B) Daily net N mineralization rates. Letters in (A) indicate significant differences in final cumulative net N mineralization (after 268 days) among treatments ( $P < 0.05$ ) with one-way ANOVA, with post hoc Tukey test. (From Dijkstra et al. (Ecosystems, in press))



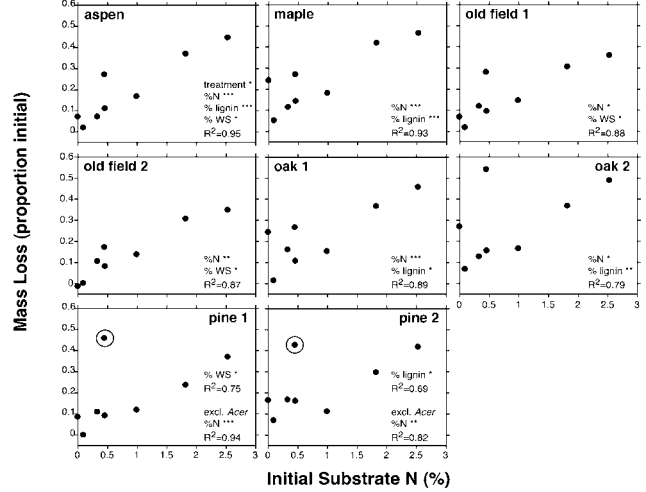
**Fig 20.** Lace bug abundance in unburned and high-burn units on trees sampled at random (irrespective of light conditions). Samples were taken from 4 branches on each of 10 trees per unit. Abundance was the number of individuals on a branch containing 80-120 leaves. Egg number per branch was estimated by categorizing egg clutches into size classes (small, medium, and large), then using the median values for each clutch size (30, 150, and 375 respectively) times the number of clutches of each size. (From Kay et al. submitted).



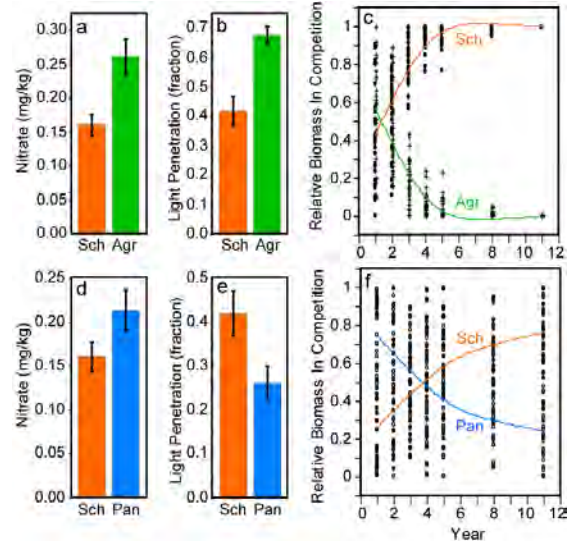
**Fig. 21.** Presence (a, b) and extent (c, d) of ectomycorrhizal infection as a function of distance from the forest edge for 2001 (a, c) and 2002 (b, d). Circles indicate data points from Field 56, crosses indicate data points from Field 57. A small amount of 'noise' has been added to distance to separate overlapping data points, all data points actually fell at the distances labeled on the x-axes. For the presence of ectomycorrhiza (a, b), lines indicate the linear fixed effect of distance on the probability of seedling infection for each year, back-transformed from logistic analysis (i.e. curvature is due to back-transformation), diamonds indicate mean values for each distance. Year and distance were both significant,  $P < 0.0001$  for both,  $r^2 = 0.41$ . For extent of mycorrhizal infection (c, d), lines indicate the most parsimonious model (two parameter logistic model, equation 2,  $r^2 = 0.46$ ). Including terms for both year and field resulted in lower AIC values than models without terms for year or field, solid line indicates fit for Field 56, dashed line indicates fit for Field 57. (From Dickie et al. 2005)



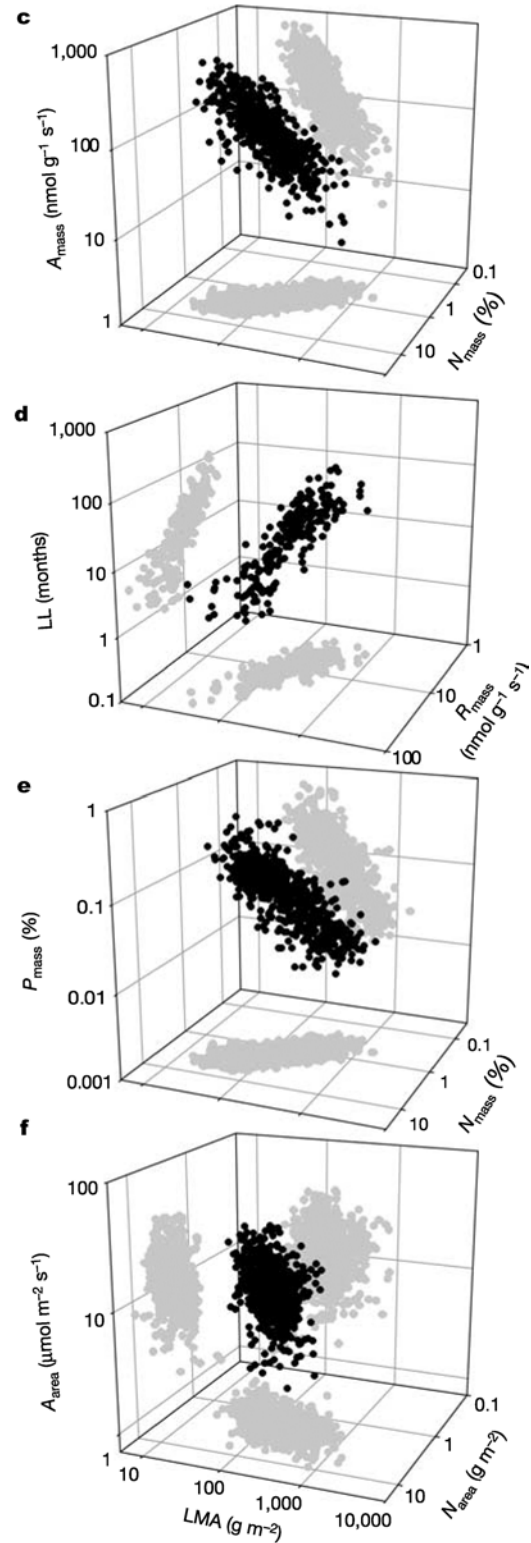
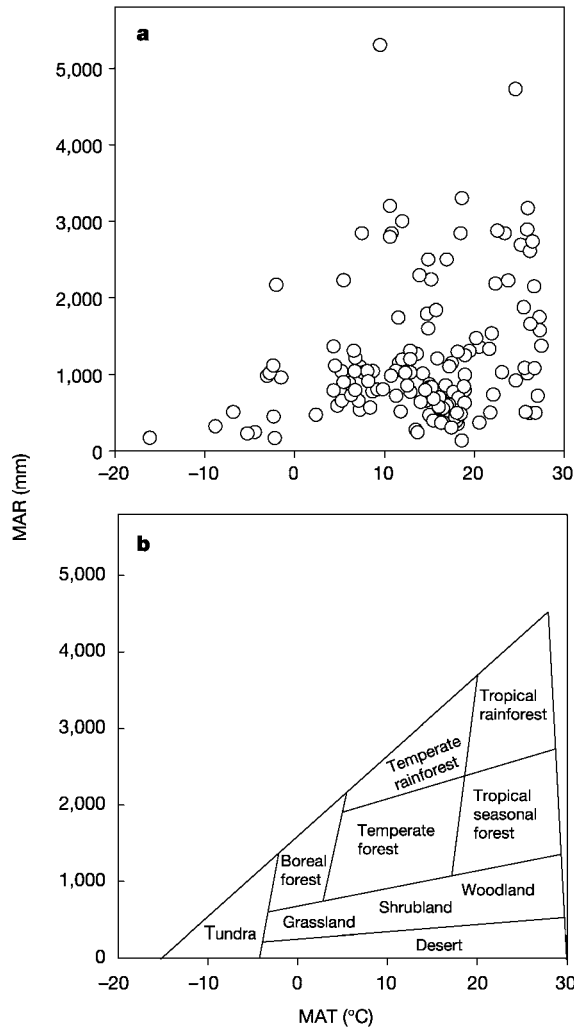
**Fig. 23.** Mass loss of eight substrates decomposed for ten months in control and N-fertilized plots ( $n = 6$ ) at all sites. For two-way ANOVA comparing substrates and N fertilization within each site: \*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$ , \_ $P < 0.10$ . (From Hobbie 2005)



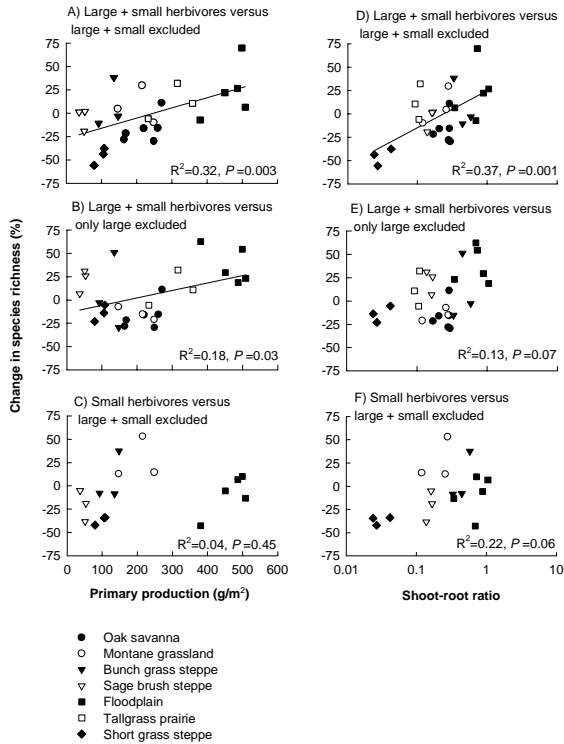
**Fig. 22.** Relationships between mass loss after ten months and initial substrate % N for eight substrates decomposed in control plots at each site. Statistics are from ANCOVAs of mass loss with fertilization treatment as the main effect and substrate N, lignin, WS, and NPE as covariates. ANCOVAs were run with and without *Acer* litter (circled) at both Pine sites. Significant relationships with N or WS were positive and those with lignin were negative. Percent AS was excluded from the analysis because of tight negative correlations with percent NPE and WS. (From Hobbie 2005)



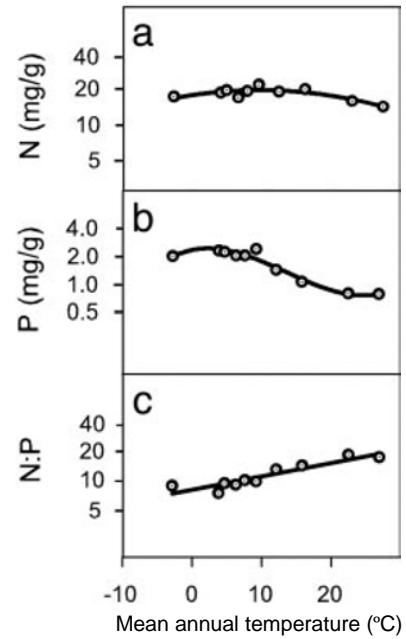
**Fig. 24.** Resource competition theory predicts that species that have lower equilibrium nitrate concentration and light penetration in monoculture should competitively exclude species that have higher equilibrium levels of those resources. *Schizachyrium scoparium* (Sch), *Agropyron smithii* (Agr), and *Panicum virgatum* (Pan) were grown in monoculture and pairwise competition for eleven years. Since *Schizachyrium* had lower equilibrium levels of both resources than *Agropyron* (a, b), it was predicted to win in competition, which it did (c). On the other hand, pairs of species that exhibit a tradeoff are predicted to coexist. *Schizachyrium* had lower equilibrium nitrate concentrations than *Panicum* (d), while *Panicum* had lower equilibrium light levels than *Schizachyrium* (e). These two species coexisted (f). Six other pairs of species exhibited similar relationships. (From Dybzinski and Tilman, in preparation)



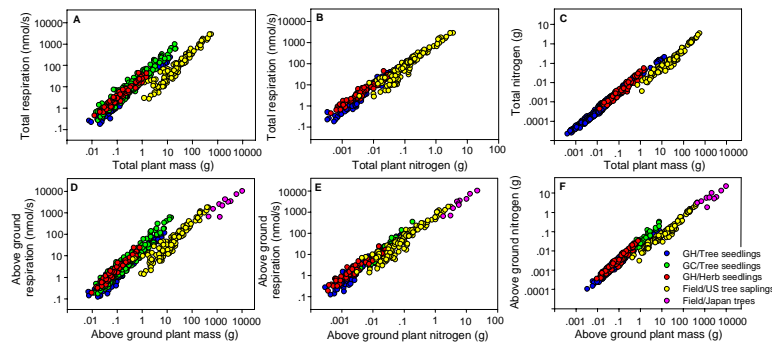
**Fig. 25.** Mean annual rainfall (MAR) and mean annual temperature (MAT) for 175 sites where leaf data were compiled (a), and in relation to major biome types of the world (b). Parts c-f: Three-way trait relationships among six leaf traits with reference to leaf mass per area (LMA), one of the key traits in the leaf economics spectrum. The direction of the data cloud in three-dimensional space can be ascertained from the shadows projected on the floor and walls of the three-dimensional space. (c) net photosynthetic capacity,  $A_{\text{mass}}$ , LMA and leaf N concentration,  $N_{\text{mass}}$ ; 706 species. (d) Leaf life span, LL; dark respiration rate,  $R_{\text{mass}}$  and LMA; 217 species. (e)  $N_{\text{mass}}$ ,  $P_{\text{mass}}$  and LMA; 733 species. (f)  $A_{\text{area}}$ , LMA and  $N_{\text{area}}$ ; 706 species. (From Wright et al. 2004)



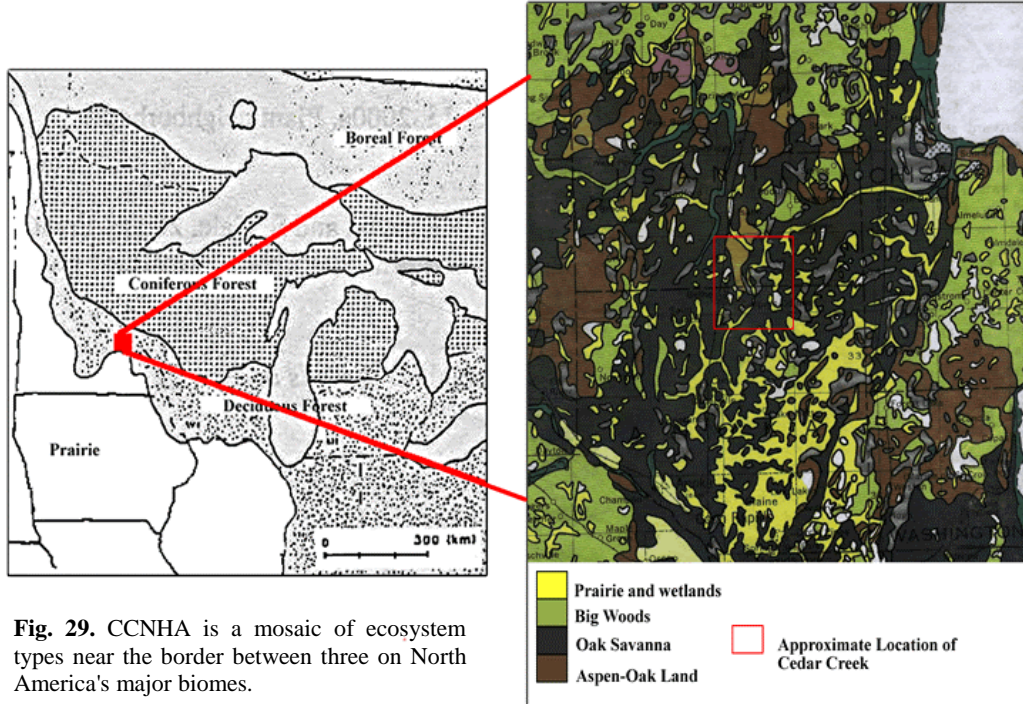
**Fig. 26.** Effect of each herbivore assemblage on plant species richness in relation to above ground primary productivity (A, B, C) and to the shoot-root ratio of the vegetation (D, E, F). (From Bakker et al., submitted.)



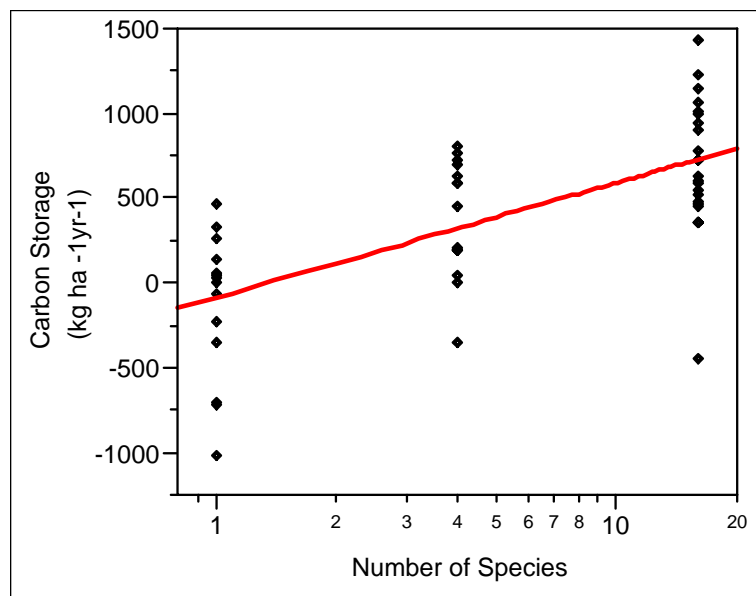
**Fig. 27.** Leaf N, P, and the leaf N:P ratio in relation to mean annual temperature. (From Reich and Oleksyn 2004.)



**Fig. 28** (Above). Scaling of respiration, N and plant mass for plants. Data are from studies of field, greenhouse (GH) and growth chamber (GC) plants. a, Whole-plant respiration in relation to total plant dry mass. b, Wholeplant respiration in relation to whole-plant N. c, Whole-plant N in relation to total plant dry mass. d, Above-ground plant respiration in relation to above-ground plant dry mass. e, Above-ground plant respiration in relation to above-ground plant N. f, Above-ground plant N in relation to aboveground plant dry mass. Respiration, determined as net CO<sub>2</sub> efflux, was adjusted to a common measurement temperature (see Methods and Supplementary Information). (From Reich et al. 2006b)

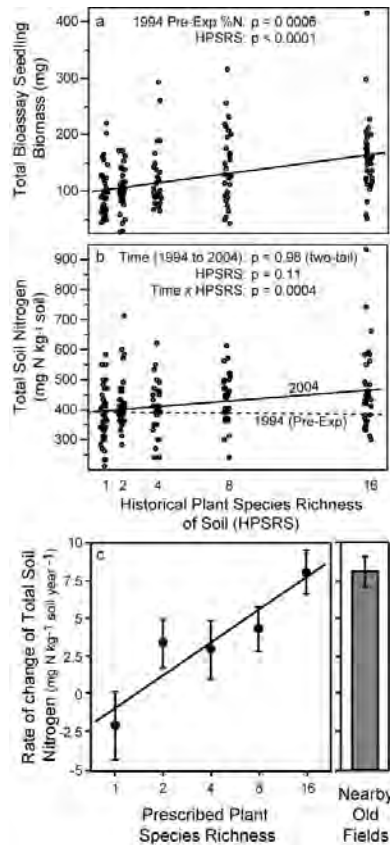


**Fig. 29.** CCNHA is a mosaic of ecosystem types near the border between three of North America's major biomes.



**Fig. 30.** Annual rate of accrual of carbon in soil in the Biodiversity Experiment plots. Soil cores for depths of 0-20 cm, 20-40 cm and 40-60 cm were collected in 1994 and in 2005 in the Biodiversity Experiment, sieved to remove roots, analyzed for total C, and used to calculate the annual rate of storage of carbon in the soil for the 0-60 depths. Note that there was no net storage of C, on average, in monoculture plots but that plots planted with 16 prairie perennials accrued about 750 kg of C per hectare each year (Tilman et al., in preparation).



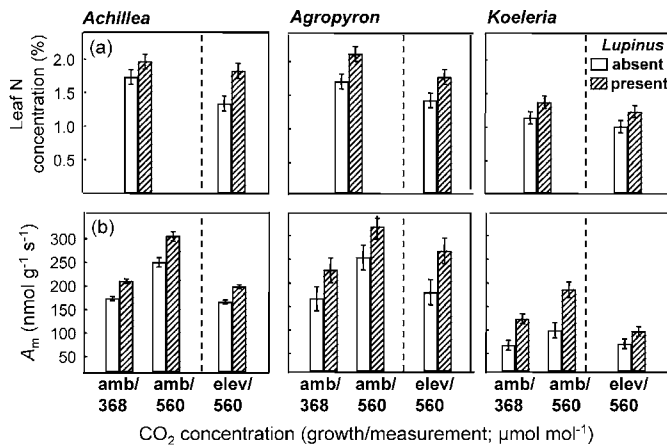


**Fig. 31.** (a) Seedlings grown in soil from high diversity plots were, on average, 63% larger than those grown in soil from low diversity plots. (b) This increased soil fertility was one more mechanism by which high diversity led to greater biomass. This was caused by greater total soil nitrogen in the high diversity plots. (c) The rate of soil nitrogen accumulation was higher at higher diversity. (From Dybzinski, Fargione and Tilman, in preparation.)

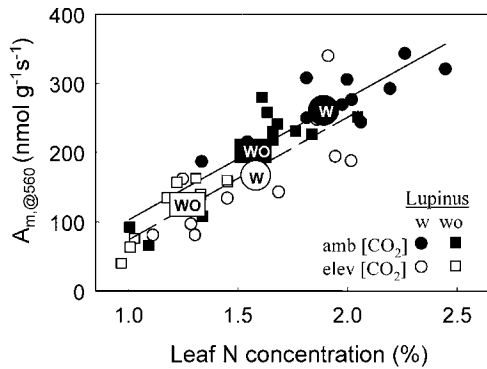
**Fig. 32. Variation in total biomass in relation to *S*, *F*, and functional group composition in experiments I and III**

Experiment	<i>F</i>	<i>S</i>	<i>C</i> <sub>4</sub> grasses	No <i>C</i> <sub>4</sub> grasses	<i>C</i> <sub>3</sub> grasses	No <i>C</i> <sub>3</sub> grasses	Forbs	No Forbs	Legumes	No legumes
I	1	1	728 ± 27		981 ± 37		538 ± 61		377 ± 31	
	1	4	805 ± 42		1,279 ± 60		966 ± 99		630 ± 50	
III	1	4		958 ± 33		800 ± 30		904 ± 31		1,016 ± 37
	2	4		979 ± 53		873 ± 56		972 ± 54		1,126 ± 49
	3	4		1,343 ± 46		988 ± 55		1,376 ± 52		1,188 ± 41
	4	4								

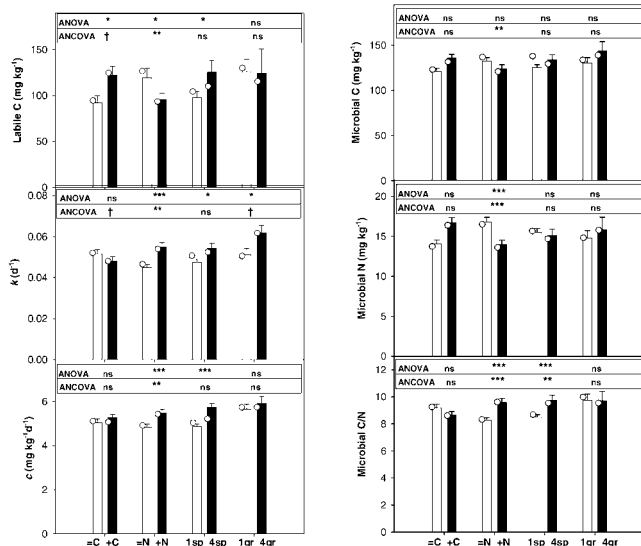
Biomass (mean ± 1 SE; average for two harvests in June and August of 1998–2001) in plots with various *F* (number of functional groups), *S* (number of species), and functional group treatments, averaged across CO<sub>2</sub> and N treatments, in experiments I and III. All values shown are in g·m<sup>-2</sup>. (From Reich et al. PNAS 2004)



**Fig. 33.** (a) Mean leaf N concentration (%) and (b) mean mass-based rates of leaf net photosynthesis ( $A_m$ ,  $\text{nmol g}^{-1} \text{s}^{-1}$ ) of three nonfixing species (*Achillea*, *Agropyron*, *Koeleria*) grown in nine species assemblages at ambient ( $368 \mu\text{mol mol}^{-1}$ ) and elevated ( $560 \mu\text{mol mol}^{-1}$ ) CO<sub>2</sub> concentrations and in the absence (*clear bars*) and presence (*shaded bars*) of *Lupinus*.  $A_m$  was measured at the CO<sub>2</sub> concentrations under which plants were grown: ambient ( $\text{amb}/368 \mu\text{mol mol}^{-1}$ ) and elevated ( $\text{elev}/560 \mu\text{mol mol}^{-1}$ ), and ambient grown plants were also measured at elevated CO<sub>2</sub> concentrations ( $\text{amb}/560 \mu\text{mol mol}^{-1}$ ). Shown are least squares means ( $\pm$ SE). Significant ( $P < 0.05$ ) ANOVA probabilities: (a) CO<sub>2</sub>  $P = 0.02$ , *Lupinus* presence  $P < 0.0001$ ; (b)  $A_{m@growthCO_2}$ : *Lupinus* presence  $P < 0.0001$ ,  $A_{m@560}$ : CO<sub>2</sub>  $P = 0.009$ , *Lupinus* presence  $P < 0.0001$ , *Lupinus* presence  $\times$  species  $P = 0.05$ , species  $\times$  CO<sub>2</sub>  $\times$  *Lupinus* presence  $P = 0.03$  (From Lee et al. 2003a.)

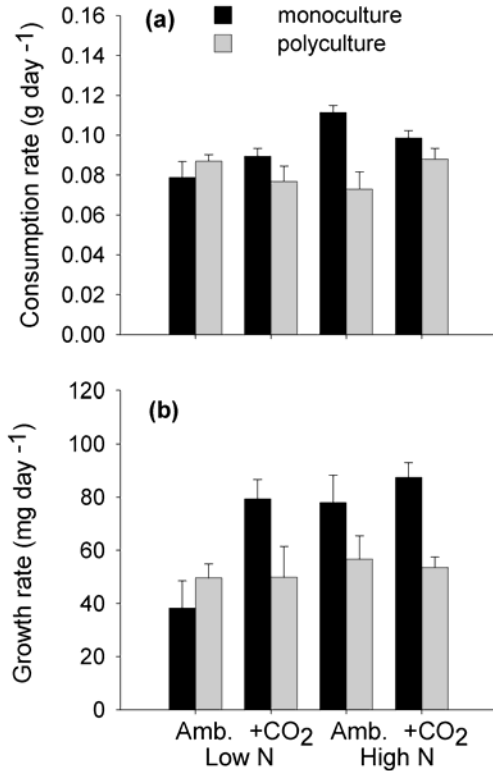


**Fig. 34.** Relationship between leaf net photosynthesis measured at a common CO<sub>2</sub> concentration of 560 μmol mol<sup>-1</sup> ( $A_{m, @560}$ , nmol g<sup>-1</sup> s<sup>-1</sup>) and leaf N concentration (%) for foliage of three non-fixing species (*Achillea*, *Agropyron*, *Koeleria*) grown in nine-species assemblages in the presence (black circles, clear circles) and absence (black squares, clear squares) of *Lupinus* or at ambient (black circles, black squares, 368 μmol mol<sup>-1</sup>) and elevated (clear circles, clear squares, 560 μmol mol<sup>-1</sup>) concentrations of CO<sub>2</sub>. Shown are plot averages of each of the three species. Separate regression lines are shown only where the elevation of the treatment lines was significantly different. ANOVA probabilities (P>F) for the main effects are: *Lupinus* presence, P=0.60; and CO<sub>2</sub> treatment, P=0.05 (ambient CO<sub>2</sub>: r<sup>2</sup>=0.83, P<0.0001, elevated CO<sub>2</sub>: r<sup>2</sup>=0.72, P<0.0001). Extra large symbols represent the data centroids of each treatment combination. (From Lee et al. 2003a.)

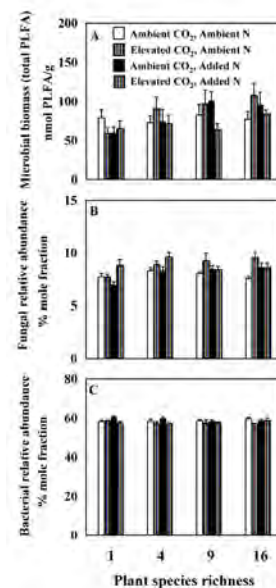


**Fig. 36.** Labile C, its respiration rate constant ( $k$ ), and the respiration rate of the more recalcitrant soil C ( $c$ ) affected by CO<sub>2</sub> (=C: ambient CO<sub>2</sub>, +C: elevated CO<sub>2</sub>), N fertilization (=N: unfertilized, +N: fertilized), species and functional group number. The CO<sub>2</sub>, N and species number effects were pooled across all other treatments (N = 196), while the functional group number effect was pooled across the CO<sub>2</sub> and N treatment in the four species plots only (N = 68). Error bars are standard errors. \*P < 0.1; \*\*P < 0.05; \*\*\*P < 0.01; \*\*\*\*P < 0.001 (shown for both ANOVA and ANCOVA with total plant biomass as covariate). No significant (P < 0.05) interactions were found. Least-square means adjusted for variation in total plant biomass (ANCOVA) are indicated with open circles.

Microbial C, N, and C/N ratio affected by CO<sub>2</sub> (=C: ambient CO<sub>2</sub>, +C: elevated CO<sub>2</sub>), N fertilization (=N: unfertilized, +N: fertilized), species and functional group number. The CO<sub>2</sub>, N and species number effects were pooled across all other treatments (N = 196), while the functional group number effect was pooled across the CO<sub>2</sub> and N treatment in the four species plots only (N = 68). Error bars are standard errors. \*\*P < 0.01; \*\*\*P < 0.001 (shown for both ANOVA and ANCOVA with total plant biomass as covariate). CO<sub>2</sub> x N interactions for microbial C and N are mentioned in the text. No other significant (P < 0.05) interactions were found. Least-square means adjusted for variation in total plant biomass (ANCOVA) are indicated with open circles. (From Dijkstra et al. 2005)

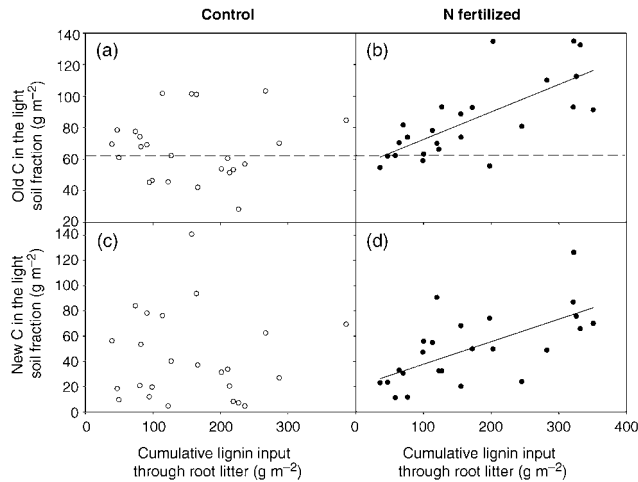


**Fig. 35.** Grasshopper responses when provided *Poa pratensis* grown under ambient or elevated CO<sub>2</sub> and ambient or elevated N conditions. Plants were either grown in monocultures or in polycultures (16 species). Panel (a) showing consumption rate, and (b) grasshopper growth rate. Error bar represent S.E. (From Strengbom et al. 2006 Oikos, submitted)

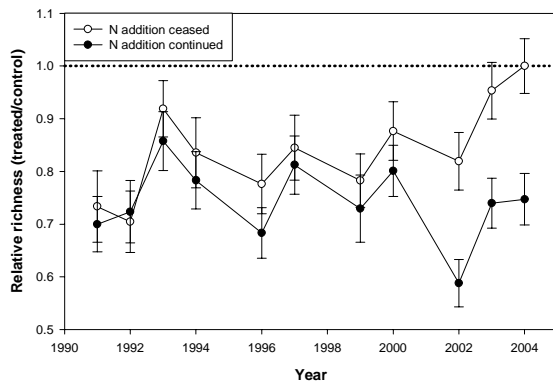


**Fig. 37.** Interactive effects of elevated CO<sub>2</sub>, experimental N deposition, and plant species richness on microbial biomass and community composition. Error bars indicate one standard error of the mean. (From Chung et al. submitted)

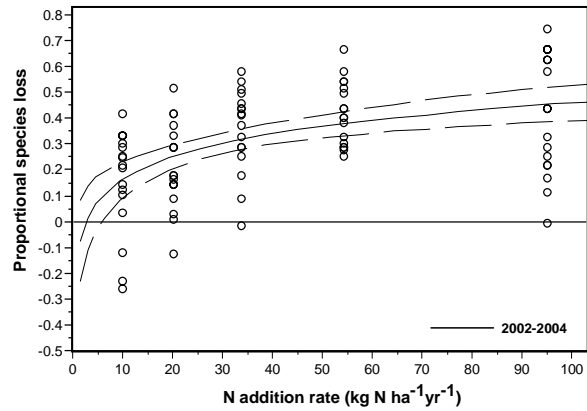




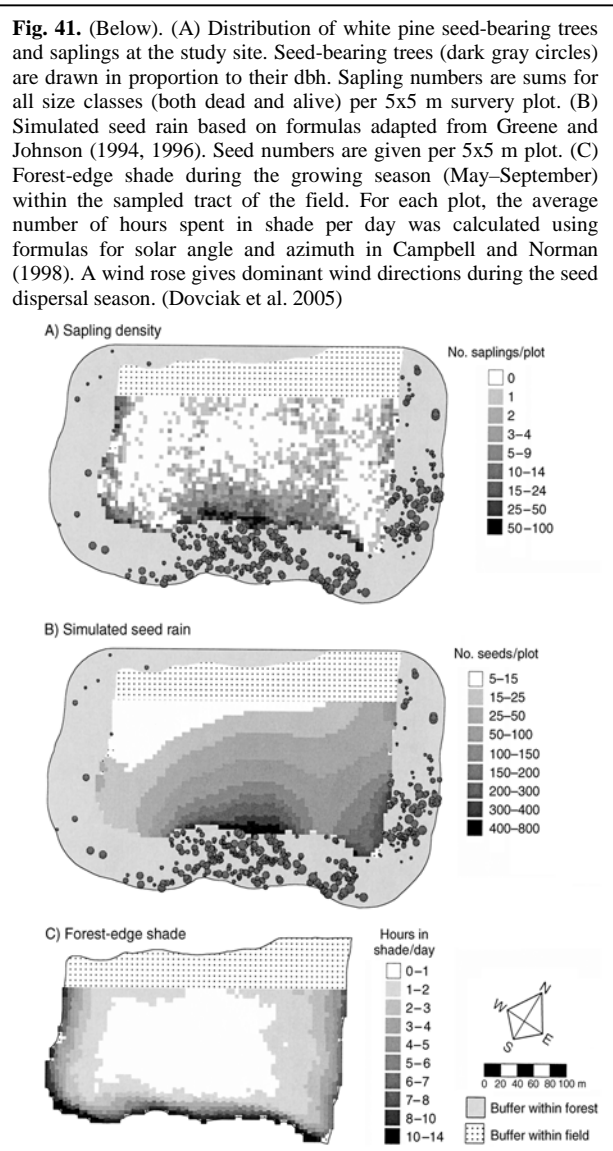
**Fig. 38.** (a and b) Old and (c and d) new carbon in the light soil fraction as a function of cumulative root lignin input for all 48 planted plots. After 5 years of treatment, there was a significant interaction between lignin input and N treatment in an analysis of their effects on old and new carbon in the light soil fraction (see text). Therefore, we did separate regressions of light fraction soil carbon against root lignin for control (a, c) and N fertilized (b, d) treatments. Old and new carbon in the light soil fraction were significantly positively related to root lignin input (total input from spring 1998 to autumn 2002) in the nitrogen fertilized plots (old C:  $R^2 = 0.54$ ,  $P < 0.0001$ , new C:  $R^2 = 0.25$ ,  $P = 0.01$ ), but not in the control plots ( $P > 0.1$ ). Dashed line in (a) and (b) shows the average pool size of the old carbon in the light soil fraction in the bare plots under ambient atmospheric  $\text{CO}_2$  ( $n = 6$ ) for comparison. (From Dijkstra et al. 2004)



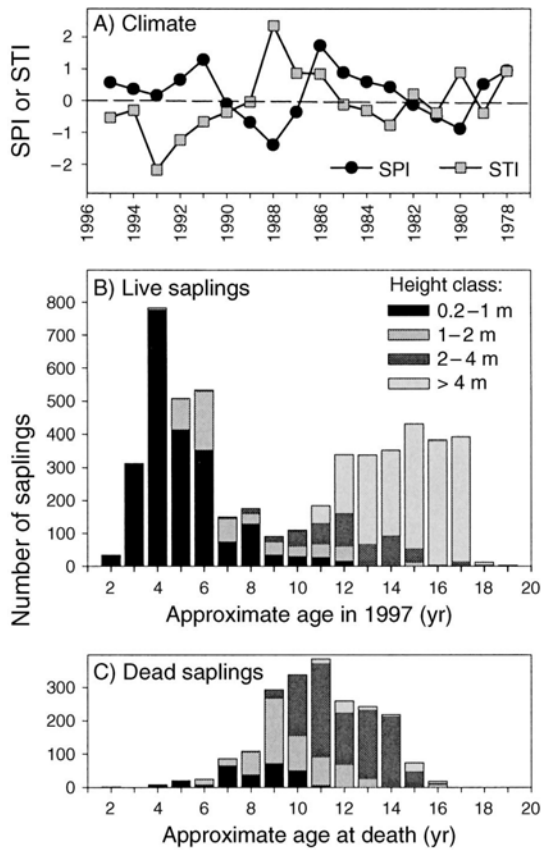
**Fig. 40.** Changes in richness relative to controls from 1991-2004 for plots that continue to receive N and those that do not. Shown are the averages after adjusting for N addition level. (From Clark and Tilman, submitted.)



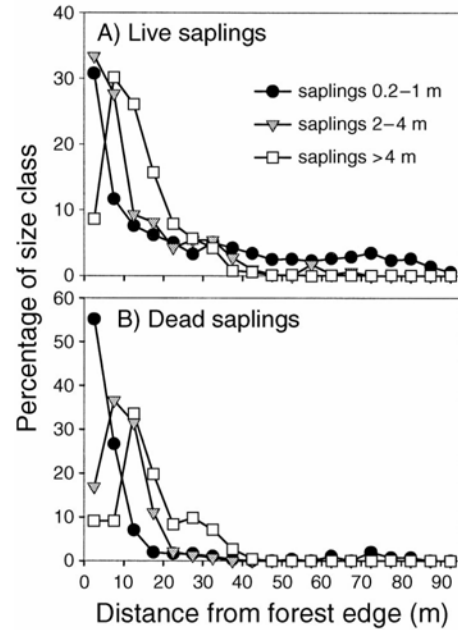
**Fig. 39.** Proportional species loss versus N addition rate for 2002-2004. Shown are plot averages for each field over the three year period fitted to a logarithmic curve. (From Clark and Tilman, submitted.)



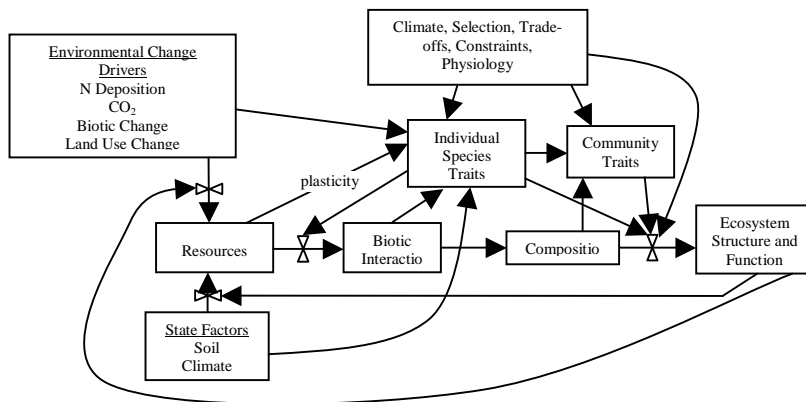
**Fig. 41.** (Below). (A) Distribution of white pine seed-bearing trees and saplings at the study site. Seed-bearing trees (dark gray circles) are drawn in proportion to their dbh. Sapling numbers are sums for all size classes (both dead and alive) per 5x5 m survey plot. (B) Simulated seed rain based on formulas adapted from Greene and Johnson (1994, 1996). Seed numbers are given per 5x5 m plot. (C) Forest-edge shade during the growing season (May–September) within the sampled tract of the field. For each plot, the average number of hours spent in shade per day was calculated using formulas for solar angle and azimuth in Campbell and Norman (1998). A wind rose gives dominant wind directions during the seed dispersal season. (Dovciak et al. 2005)



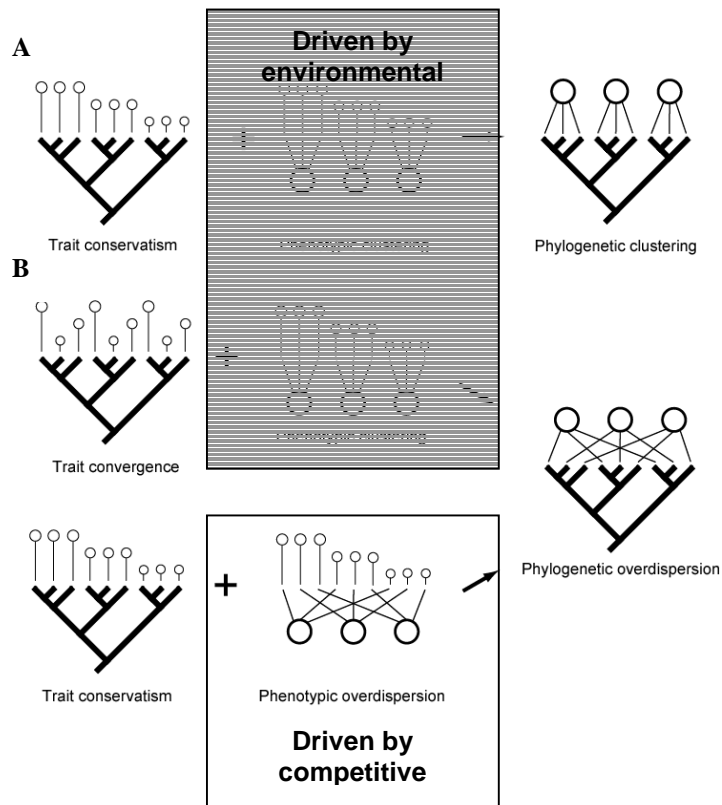
**Fig. 42.** Age structure of invading white pine relative to climate. (A) Growing-season climate (May–September) during the course of succession (1978–1995). SPI gives the average 12-month standardized precipitation index (a drought index) for each growing season. STI gives the average monthly standardized temperature index based on average monthly maximum temperature for each growing season. SPI and STI values above zero indicate wetter and hotter conditions than average; values below zero indicate drier and cooler conditions than average. (B) Total number of all living saplings within the surveyed area by approximate age and height classes. (C) Total number of all dead saplings within the surveyed area by approximate age at death and height classes; sapling height classes are as in (B). (From Dovciak et al. 2005)



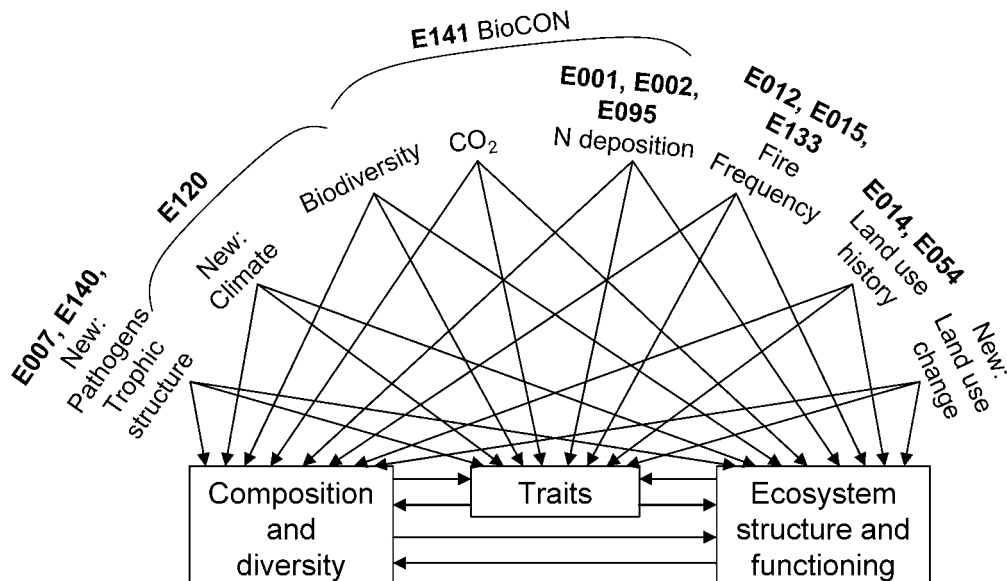
**Fig. 43.** Distribution of white pine height classes within the field relative to the forest edge. (A) Dispersion of live saplings; (B) dispersion of dead saplings. Height class 1–2 m was omitted for clarity because it is least common and its dispersion is intermediate between the dispersion of height classes 0.2–1 and 2–4 m. Percentages instead of absolute numbers of saplings are given to facilitate comparison of dispersion of the individual size classes (the sum of percentages at all distances is 100% for a given size class). The absolute sapling numbers were as follows: for 0.2–1 m class, ~2200 live and ~300 dead saplings; for 2–4 m class, ~500 live and ~1100 dead saplings; and for >4 m class, ~1900 live and ~100 dead saplings. Percentages were adjusted for varying area between distance classes. (From Dovciak et al. 2005.)



**Fig. 44.** Conceptual diagram of the causes and consequences of variation in plant functional traits, with respect to external drivers, resources, and the assembly and dynamics of plant communities.



**Fig 45.** Contrasting patterns in the phylogenetic structure of communities can arise. When neighbors are closely related (phylogenetic clustering, A) environmental filtering can be inferred to have acted on traits shared among close relatives. When neighbors are distantly related (phylogenetic overdispersion, B) competitive interactions can be inferred if traits are conserved. If traits are convergent, environmental filtering on convergent traits can also give rise to phylogenetic overdispersion. (From Cavender-Bares et al. 2004)



**Fig. 46.** The major topics addressed in CDR core long-term studies. Each of the core studies (indicated by its CDR experiment number) addresses how one or more factors (e.g., pathogens or climate or biodiversity, etc.) affects ecosystem structure and functioning and community composition and diversity. Some of these effects are direct; many will result of how the factor is moderated by the traits of species or how species abundances are impacted by the factor. The information gained from these interacting and interdependent studies is directly relevant to the quantification and valuation of ecosystem services, and how this value is impacted by human-driven environmental change.

### **Section 3. MANAGEMENT OF CDR AND CCNHA**

Although the Cedar Creek LTER project (CDR) and the Cedar Creek Natural History Area (CCNHA) each have their own missions, funding sources, personnel and management teams, they are interdependent and supportive of each other. Each has grown immensely in the past decades. About a dozen individuals worked at CCNHA on a summer day in 1982 when our LTER began. This past summer, this had increased to about 120. Facilities have undergone several expansions during this time; the largest is currently underway. Funds raised from 10 sources now total about \$1.3M for a new Science and Outreach Center at CCNHA. Construction should begin late summer of 2006. In addition, the University of Minnesota is seeking, as part of its biennial request to the Minnesota Legislature, \$750,000 for construction of CCNHA housing.

#### **CCNHA Management**

CCNHA is the 5400 acre site and its facilities at which CDR research related projects are performed. CCNHA operates under the authority of the Dean of the College of Biological Sciences of the University of Minnesota. In response to the greatly increased research, outreach and educational activities at CCNHA, CCNHA management recently has undergone significant changes. As of the start of 2006, and for the first time in its history, CCNHA is now directed by a full-time, on-site Manager and Associate Director, Dr. Jeff Corney, for whom directing CCNHA is his sole responsibility. Until now, CCNHA has been overseen by a faculty Director (D. Tilman) and led by an Associate Director, both of whom were housed on campus (30 miles away) and had numerous other responsibilities (teaching loads, research, etc.).

With help from an Administrative Assistant (also a new position for CCNHA), Dr. Corney directs, manages and coordinates all issues and budgets related to CCNHA facilities and their use for research, education, outreach and community relations. Corney chairs the CCNHA Research Review Committee (members: S. Hobbie, M. Davis, J. Knops) that evaluates proposals for research done at CCNHA. He coordinates recruitment of Summer Research Interns, and leads the Summer Research Intern program. Corney reports to the CCNHA Executive Committee, the members of which are appointed by the Dean of the College of Biological Sciences. The CCNHA Executive Committee members are researchers and educators, from both the University and other institutions, who are active at CCNHA. It is chaired by David Tilman, the faculty Director of CCNHA, a position appointed by the Dean of the College of Biological Sciences.

#### **Management of the CDR LTER Project**

Our group of CDR scientists is the largest and the most intellectually diverse that it ever has been. As we have grown, we have learned that maintaining communication among us is of central importance to our success. Frequent meetings focused on science, and especially on opportunities for synthesis and cooperation, are the heart of our team management plan. Our meetings include informal weekly gatherings of researchers (those on site) during the field season; monthly on-campus LTER science discussions and seminars during the academic year; an annual winter Science Synthesis Workshop for PI's, post-docs, graduate students and staff; our all-day Science Symposium, which initiates the field season and introduces our Summer Research Interns to CDR; and our Summer Science Retreat and Field Day.

Our LTER is coordinated by its lead Principle Investigator (Tilman) with the advice and guidance of the LTER Executive Committee. The LTER Executive Committee meets regularly (about every six weeks) to discuss and reach consensus on all matters related to the project, focusing especially on strategic issues related to science, personnel and their responsibilities and budgets. The lead PI manages (with rare exception) based on this consensus. The LTER Executive Committee is composed of the lead PI and three members elected by the CDR PI's and co-investigators. The Manager and Associate Director of Cedar Creek (Corney) serves as an ex officio member of the committee. Of the three elected members, one is to be a senior PI, one represents newer members of the team, and one represents non-EEB members of the team. Members are elected for staggered 2 year terms during the annual summer meeting of the team.

The four senior PI's (Tilman, Reich, Hobbie, Polasky) share project responsibilities. Among other duties, the lead PI supervises LTER staff, tracks LTER budgets, tracks publications and other products and contributions from the LTER, prepares the Annual Report for NSF,

organizes and leads the regular meetings of the Executive Committee, organizes weekly meetings of PI's and staff during the field season and monthly on-campus LTER science discussions and seminars during the academic year, and represents CDR at one of the National LTER Coordinating Committee Meetings. To allow the other CDR investigators to learn about the LTER Network, each will take a 2-year turn attending the other National LTER Coordinating Committee Meeting. The next such meeting, in Spring 2006, is hosted by CCNHA, allowing our full team, many of them new to LTER, to learn about the LTER Network. Each of the three other senior PI's will take responsibility for organizing one additional CDR activity: our annual winter Science Synthesis Workshop, Science Symposium; or Summer Science Retreat and Field Day.

Major decisions about allocation of project resources to individual investigators and particular studies were made as we planned the research proposed herein, and are reflected in our budget, thus allowing our future discussions to focus more on science than finances. However, scientific discussions inevitably lead to ideas for new research. Major new ideas would, of course, require new grants. However, as our CDR-funded science evolves, we will change, as a team, how we allocate our time and resources. We will continue our tradition that this evolution occurs "from the bottom, up," i.e., that individuals choose to change use of the funds allocated to them because of their excitement about new research opportunities. Similarly democratic, bottom-up processes will be used to determine how we allocate a portion of our core funds. Most core CDR funds are dedicated to long-term observations and experiments that are a central focus of CDR. Portions, though, are more flexible, and will be redirected as new ideas develop and gain support within the team.

#### **Participation of Other Scientists**

We strongly believe that intellectual diversity increases scientific creativity and productivity. We openly encourage non-project scientists to pursue their interests at CCNHA and to join in and use CDR research as a base for their own work. We have found that such interactions can be particularly beneficial when the other scientists have skills and/or ideas that differ from those already at CCNHA. During the current LTER, more than a dozen other senior scholars have worked with the CDR team, with about half of these individuals being faculty at other institutions. In particular, Walt Carson (University of Pittsburg), Don Zak (University of Michigan), Kirk Larson (Luther College), Dave Ellsworth (University of Michigan), Jim Elser (Arizona State University), Nancy Johnson (Northern Arizona University), Tali Lee (University of Wisconsin- Eau Claire), Mark Davis (Macalaster College), Michael Russelle (ARS), Ross McMurtrie (University of New South Wales), Phil Grime (University of Sheffield, UK) and M. Blinnikov (St. Cloud State University) have worked with us, as have the following University of Minnesota faculty: Peter Tiffin (plant evolutionist), Ruth Shaw (community genetics), David McLaughlin (fungal biology), Steve Polasky (economist), Jennifer King (soil sciences), Karen Oberhauser (evolution and environmental education), and Rob Blair (environmental education). In addition, Nick Haddad (University of North Carolina) and Rudolfo Dirzo (Stanford University) have expressed strong interest in collaborating with the CDR team in the near future. It is worth noting that a portion of these individuals have now 'joined the team' and have funding allocated to them in this proposal. Although Karen Oberhauser and Rob Blair, who head our Schoolyard LTER and other education and outreach activities at CCNHA, have no funds formally allocated to them in this proposal, they have received, and will continue to receive, NSF supplemental support to our LTER for education, assuming such funds continue to be available.

#### **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 4. INFORMATION MANAGEMENT AND TECHNOLOGY

CDR data are managed according to the following principles: (1) data quality and availability must be assured for the long term, (2) data organization and availability must enhance and promote both research and data analysis at our site as well as globally, (3) data must be archived and protected from any chance of loss. The CDR information management team is involved in the entire experimental process, from experimental design (e.g. plot placement and treatment randomization) to the final analysis of data. This involvement allows us to insure that data are collected in a standardized manner, rigorous standards of quality control are enforced, and information is made available to researchers as quickly as possible. It is the responsibility of the information management team to maintain our extensive systems of automated data collection and backup. These systems help to assure data quality and alleviate most human-introduced data entry errors. This approach was started for core LTER projects, but has been adopted by most projects at Cedar Creek. By funneling data through a centralized collection system, data management personnel are better able to assure the quality, backup, and availability of data to the research community.

The Rothamsted England site serves as a case in point, as experiments there have been in place for more than 150 years, and the original data, including archive samples, continue to enhance and complement modern research studies (see Leigh and Johnston, *Long-term Experiments in Agricultural and Ecological Sciences*, 1993). With this example as a model, we have developed a data storage and archival system that we feel better fits a timescale based on data availability for centuries to come, rather than the short-term life of current computer media.

After CDR data have been collected, validated, edited, and backed up, they are stored in a simple non-proprietary ASCII format (Fig 47). This simple ASCII text archive format is central to our data storage policy. Documentation (i.e., meta-data) is added directly to each archive file. Data are also archived for the long term using a data storage technique called “PERM1” which incorporates column, line and page checksums to ensure data validity in the event that they need to be scanned or re-entered (Fig 48). This system insures that data can be printed, read, and directly understood without the use of proprietary software, and also makes our data extremely versatile as it can be imported into virtually any proprietary software package. A non-proprietary format is the most reliable way to store data for long periods, during which time computers and storage media inevitably change. The full CDR data and metadata set is backed up both locally and remotely in both electronic form and as printed text. For example, sites with full electronic backup include CCNHA, the Ecology Building of U of MN, the U of MN College of Biological Sciences Computing Services (which also has its own remote backup), in houses and offices of the primary PI’s (including with J. Knops at the University of Nebraska) and the Data Manager, and at the Luquillo and Baltimore LTER sites via cooperation with their Data Managers. Luquillo also backs up our full web site.

**Data Acquisition:** When possible, data are acquired directly from the machines that generate them, without unnecessary human intervention. Data collection on paper has been virtually eliminated. Field data are collected with palm-top computers and pass directly through our downloading, processing, and backup programs to a centralized computing system. Software created for palm-top computers allows data entry based on specific CCNHA data types and contains scientific names and units, which helps to alleviate misnaming and spelling errors.

Numerical analyses and output from autoanalyzers pass through error correcting software that was developed at CCNHA to assure data quality. Balances used for weight measurements are connected directly to computers and data are imported into a spreadsheet-like software environment with error correction capabilities directly built into it. Samples are labeled with a unique barcode ID (Fig 49) that remains with the sample for its lifetime. This labeling system allows us to virtually eliminate sample misidentification and misplacement.

Light measurement readings—such as below- and above-canopy light intensity—are taken with recording light meters (*Decagon*), annotated with plot number or appropriate code, and directly downloaded.

Climatological data such as temperature, rainfall, wind speed and direction, and solar radiation are monitored by a permanent weather station (*Campbell*) located at Cedar Creek. Weather data are downloaded daily to a computer at the field station, uploaded to a remote server, backed up, and made available via the world-wide web. Data are summarized hourly and daily.

Researchers collecting and compiling data from non-LTER experiments are also encouraged to utilize CCNHA data management practices. Information management personnel are available to help all Cedar Creek researchers in their data collection efforts in an attempt to increase data synthesis and collaboration among researchers. Researchers that choose to use collection techniques other than, or in addition to, standard Cedar Creek practices are solicited by Cedar Creek information management staff and encouraged to include their data in the long term archive.

Data collected for core LTER projects have always been available to investigators within weeks of their collection, and it is our goal to ensure equally fast processing time for all Cedar Creek data sets. Timely data validation allows researchers to confirm the integrity of their data within the relatively small sampling window of a typical field season.

**Data Availability:** Principal and original investigators receive full access to data gathered for their projects, as well as privileged use of these data for a period of time following collection. In an effort to protect the rights of researchers while promoting broad use and availability of data, Cedar Creek data are divided into the following categories:

1. *Directly available on the web.* Data in this category are free for public use and can be obtained from the Cedar Creek website (<http://www.cedarcreek.umn.edu>) at any time, without special registration. Data in this category include meteorological data, description and identification guides for flora and fauna (including the high resolution photographs that comprise our on-line herbarium and our on-line insect collection), background information on LTER experiments, and publication information.

2. *Available on the web following electronic registration.* This class of data includes experimental core data sets from all CDR and CDR-related research projects, and contains such information as biomasses or other measures of species abundances (such as direct counts of individuals of insect species), percent covers of plant species, soil moisture, nitrate, ammonia, total carbon and total N, and light penetration. Access to these data requires the registration and acceptance of a data use and ethics pledge, after which data are immediately accessible. In completing the registration process, researchers must provide their name, institution type, and intended use, thus providing us with a viable means to track data use information.

Although some data, such as meteorological data, are made available daily, the core data sets associated with LTER projects are made available in accordance with our data use and sharing philosophy and ethics, which we articulated in Davis et al. (2001) and is available at <http://www.cedarcreek.umn.edu/biblio/fulltext/t1803.pdf>. In accordance with LTER Network policy, we make all data available for use by non-CDR researchers two years after they have been collected. They may be used sooner with permission of the CDR investigator who gathered the data (see "Data Use and Ethics Pledge"). Cedar Creek has an extensive and well defined data use and access policy that can be found at <http://www.cedarcreek.umn.edu/cgi-bin/register>. We realize that the area of ecoinformatics is quickly evolving and expanding, and we will continue to be flexible in order to adhere to the guidelines established by NSF and by the LTER information management community.

3. *Available through CDR investigators.* All major experiments at Cedar Creek are documented on the web with pertinent, up to date contact information, including the name of the lead investigator. This allows off-site researchers to contact the relevant CDR investigators about data that are not yet available on the web, and prevents dissemination of data that have not yet

undergone final quality verification by the original investigators and/or that the original investigators are still in the process of analyzing or publishing.

***Anticipated major changes:*** Due to the dynamic and rapidly changing environment of information management, Cedar Creek has committed itself to remain at the forefront of technological exploration. In the past we have relied heavily on in-house software solutions to resolve issues that were unique to our situation. As the field of ecology has expanded and informatics has grown and developed, we have found that cooperation and synthesis are increasingly more important. Network wide collaboration and cooperation are now the goals of the Cedar Creek information management team.

The main portal to information management at Cedar Creek has become, and will remain, the world-wide-web. Cedar Creek's web site (<http://www.cedarcreek.umn.edu>) has grown to include more than 15,000 pages, including more than 10,000 images. Special care needs to be taken to insure the integrity of the information carried on our web pages. In order to promote collaborative research initiatives, our data need to remain available to all interested researchers. With this in mind, we have begun a collaborative effort with the University of Minnesota, College of Biological Sciences Computing Services (<http://www.cbs.umn.edu/main/ComputingServices/>). This relationship provides us with access to the professional services of web developers, web hosting, and database and systems administration. As a result of this collaboration, we are planning major upgrades in areas of our website such as the flora and fauna sections, the insect key, data access pages, and our bibliography. Many areas of our website have become valuable tools for researchers, as well as the general public.

During the past year and a half, we have been adopting and implementing EML. All CDR core data are now EML compliant to Level 2. We have been working with Inigo Sangil in the Network Office and are on schedule to reach Level 5 compliance by July 2006. We then plan to expand EML compliance to include all projects, not just LTER based experiments.

We will continue to maintain and improve upon our intranet as well. A major upgrade to our archival labeling system is planned. We also hope to facilitate easier access to data collection, validation, and storage options through improvement of our internal network. We plan to develop a web portal that allows "one-stop" access to our suite of information management utilities. This will allow researchers to access information management tools regardless of access to information management personnel, and makes these utilities more "user-friendly". We also provide wireless networking to enhance network access for visiting researchers and seasonal staff, and plan to expand our network area to include large portions of our entire research area.



```

Data set: Biomass data
Project: E001
Year: 2000
Accession:
Source: /data/e001/ascii/pl00e001

Note: The use of any parts of these data requires written permission
from David Tilman, c/o LTER Data Management, 100 Ecology Building,
University of Minnesota, St. Paul, MN 55108.

Label Field: Field name
Label Exp: Experiment number
Label Plot: Plot number
Label Ntrt: Nitrogen treatment
Label NitrAdd: Nitrogen fertilizer addition (g/m2/yr)
Label Date: Sampling date (YYMMDD10)
Label Taxon: Species Taxon code
Label Species: Species Name
Label Biomass: Species Biomass (g/m2)
Label Prop: Species proportion of total biomass

Additional notes:
Sample size = 0.30 m2

Constant Exp: 1

|Field|Plot|Ntrt|NitrAdd|Date|Taxon|Species          |Biomass |Prop  <== Labels
|A  |N2  |N  |N2  |A10|N3  |A31          |N4.4   |N1.6  <== Format
|A  |1  |9  |0  |2000-07-05|99  |Miscellaneous litter          |337.0333|.
|A  |1  |9  |0  |2000-07-05|100 |Agropyron repens             |0.7     |0.004899
|A  |1  |9  |0  |2000-07-05|103 |Schizachyrium scoparium     |101.    |0.706788
|A  |1  |9  |0  |2000-07-05|117 |Poa pratensis                |41.1667|0.28808
|A  |1  |9  |0  |2000-07-05|130 |Buchloe dactyloides         |0.0333 |0.000233
|A  |2  |2  |3  |2000-07-05|99  |Miscellaneous litter          |464.7  |.
|A  |2  |2  |3  |2000-07-05|100 |Agropyron repens             |5.5    |0.037835

```

Figure 47. An example of our Ascii text archival data format.

```

46393: E990 Plot 00 (CLL/CEM)          9/11/95 11:47am (Monday)
37404: 501 Achillea millefolium        13.5
28274: 572 Agastache foeniculum        4
34317: 102 Andropogon gerardi           16
55318: 105 Bromus inermis               4
08844: 730 Heliopsis helianthoides     5
45832: 000 Open ground/litter           7
40669: 117 Poa pratensis                7
10186: 103 Schizachyrium scoparium     42
50048: 810 Tragopogon pratensis        1.5
60933;
41071.

```

Figure 48. Example of Perm1 archival format with error checking codes.

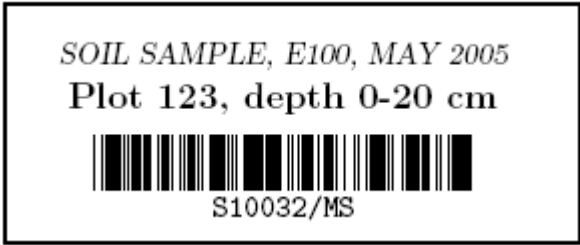


Figure 49. Example of Cedar Creek soil sample barcode label which has helped greatly to reduce labeling errors.

## Section 5. PUBLIC OUTREACH AND EDUCATION

We believe in communicating relevant findings not just with the scientific community, but also with governmental officials, educators and the general public, especially when research addresses issues of significance to society. Through outreach and education activities, we seek to inform decision makers of recent scientific findings, increase public understanding of research, and encourage and train the next generation of scientists. We use a variety of approaches to disseminate information about CCNHA research, including communicating with media and government organizations, teaching both K-12 teachers and journalists about scientific research and recent results. We also provide science outreach for K-12 students and the public, and research experiences for undergraduates. Our outreach and education program has expanded significantly since 2000 through funding from other NSF programs and the Bush Foundation. Moreover, a new CCNHA Outreach and Science Center will have space dedicated to education and outreach.

### Media and government communications:

From 2000 to the present, at least 38 *newspaper and magazine articles* have been written about the work at CCNHA (<http://cedarcreek.umn.edu/about/news.html>). Articles appeared in publications including the *Washington Post*, *Newsweek*, *Popular Science*, the *Minneapolis Star Tribune*, the *St. Paul Pioneer Press*, *US News and World Report*, the *Baltimore Sun*, the *National Post*, *Newsday*, the *Montreal Gazette*, and *NRC Handelsblad* (a major Dutch newspaper).

We gave 29 *radio and TV interviews* that were aired on a variety of media outlets including National Public Radio's *Science Friday*, NPR's *DNA Files*, BBC World Service, *DÉCOUVERTE* a science and technology TV program from Canadian Broadcasting Corporation, ABC News, Twin Cities Public Radio, Twin Cities Public Television, Great Lakes Radio Consortium, Earthwatch Radio, and Oregon Public Broadcasting. Also, from 2000 to the present we presented more than 150 invited talks on our research.

We have participated in *government meetings* at a variety of administrative levels. We advised local city councils on green space in city planning, and worked with the Anoka County Conservation District, Anoka County Parks, and the Minnesota Department of Natural Resources on Metro Greenways and the Remediation Fund Grant. We have given invited testimony to the MN legislature on biodiversity, and on impacts of climate change. We hosted an ecological research field trip for 20 MN state senators and representatives. In addition, we were an invited speaker at the White House's Office of Management and Budget, have twice given testimony on the importance of biodiversity to the United Nations, and were an invited speaker at an international conference on Biodiversity convened by the President of France, Jacques Chirac.

### Student and Teaching training:

CCNHA is committed to providing educational opportunities for teachers and students at all levels of education, ranging from elementary school to post-doctorate.

CCNHA's *Schoolyard LTER Program* (<http://truffula.fr.umn.edu/schoolyard/>) impacted over 4000 elementary and junior high students in the White Bear Lake School District from 2001 to 2004. We helped teachers set up a miniature biodiversity experiment where students learn about topics such as biodiversity, plant functional groups, productivity, soil chemistry, and plant-insect interactions. We also coordinated professional development opportunities for teachers, including workshops at CCNHA and funding to attend education sessions at ESA.

Since 2000, 290 undergraduate interns (including 23 minorities) from 97 universities have participated in our *Summer Internship* program. Each intern receives training in field

research techniques, participates in weekly seminars and other programs, and has the opportunity to conduct independent research. The field season begins with the *CCNHA Research Symposium* (<http://www.cedarcreek.umn.edu/events/2004/symposium/sym2004.html>) at which interns find potential mentors for their independent projects. From 2000-2005, interns presented 99 summer research projects (12 *REU* funded) at the *CCNHA Intern Symposium*, held at the end of each summer. CCNHA also offers a *Summer Seminar Series* at which scientists present their research and discuss scientific issues with interns. In 2002 we began offering the annual *Summer Field Trip*, a 3-4 day intern excursion to different ecological field sites, including other LTER sites.

CCNHA is also extensively used as a site for *graduate and post-doctoral research*. Since 2000, 40 PhD and MS students (of whom 24 completed their degrees during this period) and 26 post-docs have conducted research on site.

### **Other educational services:**

*CCNHA's website* (<http://www.cedarcreek.umn.edu>) is designed to be used both by scientists and the general public with ease. Ranging from data and experiment descriptions to plant and insects identification and pictures, our site receives around 3000 hits per day.

Each year, nearly 500 people attend *public tours* at CCNHA. Tour participants have included a variety of groups including St. Francis High School, Cambridge Community College, Northwestern College, the St. Paul Garden Club, and many individual members of the public. Most tours are led by an LTER staff member. (<http://www.cedarcreek.umn.edu/public/2005/>)

The *Prairie Maze* (<http://www.smm.org/bigbackyard/>) is a 17,000 sq foot maze of that explores how landscapes could be managed with perennial covers to provide biomass energy and environmental services such as ground water purification (Fig 50). The maze is a joint initiative of CCNHA and the Science Museum of Minnesota, funded by the Initiative for Renewable Energy and the Environment. We proposed, helped design, planted and continue to help maintain the maze, which has received over 98,000 visitors since it opened in June 2004.

### **Future directions:**

Two new developments at CCNHA will facilitate the expansion of our outreach program. We are in the process of designing a new outreach and science building, which will provide additional space for educational exhibits and programs. In addition, we recently hired a new Manager and Associate Director with extensive outreach experience.

We are working to enhance relationships with local governments and communities and hope to culture an appreciation for natural areas and offset the potentially negative impacts of encroaching suburbia. For example, we are discussing hosting DNR prescribed burning training at CCNHA. We also are working with the city of East Bethel to set up interpretative hiking and cross-country skiing trails inside CCNHA.

In 2005, with grants from the Bush Foundation, the NEST Foundation, Monarchs in the Classroom and the NSF's Education Environment Venture Fund, we launched our newest education program called *Schoolyards, Science and Sustainability*. K-12 teachers learn about CDR research, environmental science and sustainability in a curriculum that relates existing CDR long term data sets to small-scale student projects in their schoolyards. A similar program will be offered to working journalists starting spring of 2006. We are also planning a U of MN class in which summer interns receive college credit for independent research projects.

## Welcome to the Prairie Maze!

In June 2014, students, parents, and staff from the University of Minnesota's Cedar Creek Natural History Area, led by staff from The Science Museum of Minnesota's Science Watershed Research Station, planted more than 120 species of prairie grasses and forbs in this maze.

### Learn more about prairie plants

The prairie plants you see around you do lots of important work for us. They help clean our soil, air, and water. And the many plant species a prairie has, the more productive it will be at these important tasks.

But check this out—plants like these could be a good source of renewable energy, too! Explore the Prairie Maze to find out more.

Take an Explore the Prairie Maze guide to begin your adventure.

# Enter Here

---

Not very diverse

Now that's biodiversity!

## Lots of different plants make a prairie

Look closely at the patch of prairie in front of you. How many different kinds of plants do you see? We've put over 30 different species of grasses and forbs (plants with broad leaves) in this part of the Maze.

A prairie is much more than just grass. Prairies have oodles of different kinds of plants and animals living together, forming an *ecosystem*. Since prairies have many different kinds of plants and animals, we say they have a lot of *biodiversity*.

## Plants store energy

# 7

Plants are like solar collectors. They convert and store energy from the sun.

We tap the stored energy in plants when we burn plant material—called *biomass*—for fuel.

All plants need sunlight, nutrients, CO<sub>2</sub>, and water to grow.

Most byproducts of plant combustion can be reused by living plants.

Plant power can heat your water, cool your air, and keep your computer humming.

**Fig. 50.** Excerpts from educational materials on display at the Prairie Maze, a 17,000 sq ft maze at the Science Museum of Minnesota. Cedar Creek initially proposed the maze, and has since been involved in its design, construction, and maintenance. (From Science Museum of Minnesota. 2005)

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(Note: Cited papers that resulted from 2000-2006 CDR research are in Supplemental Documentation -- Table 1: *Publications of the Cedar Creek LTER*)

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- Vitousek, P.M., K. Cassman, C. Cleveland, T. Crews, C. B. Field, N. B. Grimm, R. W. Howarth, R. Marino, L. Martinelli, E. B. Rastetter and J. Sprent. 2002. Towards and ecological understanding of nitrogen fixation. *Biogeochemistry* 57-58:1-45.

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- Webb, C. O., and M. J. Donoghue. 2005. Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes* 5:181.
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- West, G. B., J. H. Brown and B. J. Enquist. 1999. A general model for the structure and allometry of plant vascular systems. *Nature* 400:664-667.
- White, A. S. 1983. The effects of thirteen years of annual prescribed burning on a *Quercus ellipsoidalis* community in Minnesota. *Ecology* 64:1081-1085.

## **Biographical Sketch - G. David Tilman**

Department of Ecology, Evolution and Behavior, University of Minnesota,  
100 Ecology Building, 1987 Upper Buford Circle, St. Paul, Minnesota 55108-6097  
Phone: (612) 625-5743; Fax: (612) 624-6777; Email: tilman@umn.edu

### **Professional Preparation**

University of Michigan, Zoology, B.S., 1971  
University of Michigan, Zoology, Ph.D., 1976

### **Professional Appointments**

Regents Professor (University of Minnesota)	2002-present
McKnight Presidential Chair in Ecology	2001-present
Director, Cedar Creek Natural History Area	1992-present
Professor (University of Minnesota)	1984-present
Associate Professor (University of Minnesota)	1980-1984
Assistant Professor of Ecology (University of Minnesota)	1976-1980

### **Five Most Relevant Publications**

Tilman, D., S. Polasky and C. Lehman. 2005. Diversity, productivity and temporal stability in the economies of humans and nature. *Journal of Environmental Economics and Management* 49:405-426.

Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences* 101:10854-10861.

Fargione, J., C. S. Brown and D. Tilman. 2003. Community assembly and invasion: An experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences* 100:8916-8920.

Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294:843-845.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80:1455-1474.

### **Synergistic Activities and Service**

Founding Editor, "Ecological Issues," *Ecological Society of America*, 1995-2003

Member, Board on Environmental Studies & Toxicology, NRC, 2002-2005

President's Committee of Advisors on Science and Technology (White House; PCAST), Biodiversity and Ecosystems Panel, 1997-1998

Member, Search Committee for NSF Assistant Director for Biology, 2004-2005

Member of Editorial Board for: *Proceedings of the National Academy of Science* (2002-2004), *International Journal of Plant Sciences* (1999-2005), *American Naturalist* (1990-1994), *Science* (1996-1999), *Ecological Society of America* (1982-1984), *Limnology and Oceanography* (1978-1981)

### **Other Scholarly Activities Relevant to Scientific Merit**

John Simon Guggenheim Fellow, 1984-1985

MacArthur Award (1997) & Cooper Award (1989) of the Ecological Society of America

American Academy of Arts and Science, 1995

Designated the Most Highly Cited Environmental Scientist of the Decade (1990-2000) by Essential Science Indicators

National Academy of Sciences, 2002

Total of 28 graduate students advised and of 17 post doctoral scholars sponsored.

## **BIOGRAPHICAL SKETCH--Sarah E. Hobbie**

Department of Ecology, Evolution, and Behavior  
University of Minnesota  
1987 Upper Buford Circle  
St. Paul MN 55108  
(612) 625-6269  
shobbie@umn.edu

### **Professional Preparation**

Carleton College, Biology, B. A., *magna cum laude*, 1986  
University of California, Berkeley, Integrative Biology, Ph.D. 1995  
Stanford University Post-Doctoral Fellow, Ecosystem Ecology, 1995-1998

### **Appointments**

Director of Graduate Admissions, Ecology, Evolution and Behavior Graduate Program,  
2005-present  
Associate Professor, University of Minnesota, 2004-present  
Assistant Professor, University of Minnesota, 1998-2004  
Post-Doctoral Research Fellow, Stanford University, 1995-1998  
Graduate Student Instructor, University of California, Berkeley, 1990-1991  
Research Assistant, Limnological Research Center, University of Minnesota, 1986-1989

### **Five Related Publications**

Dijkstra, F. A., **S. E. Hobbie**, and P. B. Reich. in press. Soil processes affected by sixteen grassland species grown under different environmental conditions. *Soil Science Society of America Journal*

Dijkstra, F. A., **S. E. Hobbie**, P. B. Reich, and J. M. H. Knops. 2005. Divergent effects of elevated CO<sub>2</sub>, N fertilization, and plant diversity on soil C and N dynamics in a grassland field experiment. *Plant and Soil* 272:41-52

Dijkstra, F. E., **S. E. Hobbie**, J. M. H. Knops, and P. B. Reich. 2004. Nitrogen deposition and plant species interact to influence soil carbon stabilization. *Ecology Letters* 7:1192-1198.

**Hobbie, S. E.** 2005. Contrasting effects of substrate and fertilizer nitrogen on the early stages of decomposition. *Ecosystems* 8:644-656.

Reich, P. B., **S. E. Hobbie**, T. Lee, D. S. Ellsworth, J. B. West, D. Tilman, J. M. H. Knops, S. Naeem, J. Trost. In press. Nitrogen limitation constrains sustainability of ecosystem response to CO<sub>2</sub>. *Nature*

### **Synergistic Activities**

LTER All Scientists Meeting Program Committee, 2005-2006  
NCEAS Science Advisory Board, 2002-2004  
National Science Foundation LTER Panel, 2/02  
National Phytotron at Duke University Strategic Planning Workshop, 10/01  
Steering Committee, How Nutrient Cycles Constrain Carbon Balances in Boreal Forests and Arctic Tundra, Abisko, Sweden, 1998-1999

Total of 8 graduate students advised, 7 postdoctoral scholars sponsored.

## CIRRICULUM VITAE: STEPHEN POLASKY

### EDUCATION

Williams College	Political Economy	B.A. 1979
University of Michigan	Economics	Ph.D.1986

### POSITIONS HELD

Fesler-Lampert Professor of Ecological/Environmental Economics, University of Minnesota  
1999-present  
Senior Staff Economist, President's Council of Economic Advisers, 1998-99  
Associate Professor, Agricultural and Resource Economics Department, Oregon State University,  
1993-99  
Visiting Senior Research Fellow, Marine Policy Center, Woods Hole Oceanographic Institution,  
1997  
Assistant Professor, Economics Department, Boston College, 1986-93  
Visiting Research Fellow, Marine Policy Center, Woods Hole Oceanographic Institute, 1990-93  
Visiting Scholar, Economics Department, M.I.T., 1990

### FIVE SIGNIFICANT PUBLICATIONS:

Polasky, S., E. Nelson, E. Lonsdorf, P. Fackler and A. Starfield. 2005. Conserving species in a working landscape: land use with biological and economic objectives. *Ecological Applications* 15(4): 1387-1401.  
Tilman, D., S. Polasky and C. Lehman. 2005. Diversity, productivity and temporal stability in the economies of humans and nature. *Journal of Environmental Economics and Management*. 49(3): 405-426.  
Polasky, S., C. Costello and A. Solow. 2005. The economics of biodiversity. In *The Handbook of Environmental Economics, Vol. 3*, J. Vincent and K.-G. Maler (eds.). Elsevier – North Holland.  
Polasky, S. (Editor). 2002. *The Economics of Biological Diversity*. Ashgate International Library of Environmental Economics and Policy. Ashgate Publishing.  
Ando, A., J. Camm, S. Polasky and A. Solow. 1998. Species distributions, land values, and efficient conservation. *Science* 279: 2126-2128.

### SYNERGISTIC ACTIVITIES

Economic and Social Aspects of Conservation Biology: developed curriculum for interdisciplinary conservation biology course as part of the core curriculum for the Graduate Program in Conservation Biology, University of Minnesota.  
Co-Leader of DIVERSITAS Core Project 3 on “Developing the science of conservation and sustainable use of biodiversity.”  
Committee on “Assessing and valuing ecosystem services from aquatic and related terrestrial ecosystems.” National Research Council.  
Committee on “Valuing protection of ecological systems and services.” Science Advisory Board, US EPA.  
Bibliography on biodiversity ([www.apec.umn.edu/faculty/spolasky/Biobib.html](http://www.apec.umn.edu/faculty/spolasky/Biobib.html))

Total of 29 graduate students advised, 2 postdoctoral scholars sponsored.

## **Biographical sketch - Peter B. Reich**

Department of Forest Resources  
1530 Cleveland Avenue North, University of Minnesota, St. Paul, MN 55108  
Phone: 612-624-4270; FAX 612-625-5212; E-mail preich@umn.edu

### **Professional Preparation**

B.A. (1974) Writing and Physics, Goddard College, Plainfield, VT  
M.S. (1977) Forest Ecology, University of Missouri, Columbia, MO  
Ph.D. (1983) Environmental Biology and Plant Ecology, Cornell University, Ithaca, NY

### **Appointments**

Distinguished McKnight University Professorship, University of Minnesota, 2003-  
F.B. Hubachek, Sr., Professor, Dept Forest Resources, U. Minnesota, St. Paul, MN, 1991-  
Assistant /Associate Professor, Dept Forestry, U. Wisconsin, Madison, WI, 1985-1991.  
Postdoctoral Associate, Boyce Thompson Institute; Ithaca, NY, 1982-1985.

### **5 publications relevant to this project:**

- Dijkstra, F, S Hobbie, P Reich, J Knops. 2005. Divergent effects of elevated CO<sub>2</sub>, N fertilization, and plant diversity on soil C and N dynamics in a grassland field experiment. *Plant and Soil* 272:41-52.
- Lee, TD, PB Reich, & MG Tjoelker. 2003. Legume presence increases photosynthesis and N concentrations of co-occurring non-fixers but does not modulate their responsiveness to carbon dioxide enrichment. *Oecologia* 137:22-31
- Reich, PB, SE Hobbie, T Lee, DS Ellsworth, JB West, D Tilman, J Knops, S Naeem, J Trost. 2006. Nitrogen limitation constrains sustainability of ecosystem response to CO<sub>2</sub>. *Nature* (in press).
- Reich, PB, D Tilman, S Naeem, D Ellsworth, J Knops, J Craine, D Wedin, J Trost. 2004. Species and functional diversity independently influence biomass accumulation and its response to CO<sub>2</sub> and N. *Proc Nat Acad Sci USA* 101:10101-10106.
- Wright I, PB Reich, M Westoby, and GLOPNET researchers. 2004. The worldwide leaf economics spectrum. *Nature* 428:821-827.

### **Synergistic Activities, Honors, Recognition, and Service (selected recent)**

National Science Foundation, Biocomplexity and the Environment Program, Coupled Biogeochemical Cycles Panel member, 2004  
Invited speaker at >50 (since 2000) international symposium, research conferences, university seminars;  
GLOPNET, Founder and co-leader, International Network of Global Plant Traits, 1998-  
Member of the Editorial Review Board (or equivalent) for the journals *Tree Physiology*, (1987-88, 1993-95, 2004-) *Trees* (1991- 97), *Canadian Journal of Forest Research* (1992-98) and *Ecology/Ecological Monographs* (1995-99)  
*Teaching-* Dynamics of Global Change: Plant Ecology; Forest Ecology; Tree Physiology; Plant Physiological Ecology; Plant Responses to Air Pollution; Tropical Forest Ecology; Patch Dynamics Seminar; Climate Change Seminar

Total of 24 graduate students advised, 11 postdoctoral scholars sponsored.



## Jeannine M. Cavender-Bares

### **Professional Preparation**

Cornell University	College Scholar in Environmental Studies <i>Magna cum laude</i> , Distinction in all Subjects	A.B., 1990
Yale University	Forest Ecology and Global Change	M.E.S., 1992
Harvard University	Biological Sciences	Ph.D., 2000

### **Appointments**

Assistant Professor, University of Minnesota, Dept. of Ecology, Evolution and Behavior;  
Graduate Faculty in Dept. of Plant Biological Sciences; 2003 - present  
Chateaubriand Postdoctoral Fellow, Centre d'Ecologie Fonctionnelle et Evolutive, Centre  
National de la Recherche Scientifique, France, 2-8/2003  
Smithsonian Institution Postdoctoral Fellow, Smithsonian Environmental Research Center,  
9/2000-2/2003  
Adjunct Assistant Professor, Georgetown University, Center for the Environment, 2001  
Research Fellow, Harvard University, Dept. of Org. and Evolutionary Biology, 1994-2000.  
Teaching Fellow, Harvard University (1994, 1995, 1996, 1999)  
Research Fellow, Center for Science and International Affairs, Harvard University, 1993-1994  
Fulbright Scholar, University of Bonn, Germany, 1992-1993

### **5 Related Publications**

- Cavender-Bares, J.**, A. Keen, and B. Miles. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology* (in press, accepted July 2005).
- Cavender-Bares, J.**, D. D. Ackerly, D. A. Baum, and F. A. Bazzaz. 2004. Phylogenetic overdispersion in Floridian oak communities. *American Naturalist* 163:823-843.
- Cavender-Bares, J.**, K. Kitajima, and F. A. Bazzaz. 2004. Multiple trait associations in relation to habitat differentiation among 17 Florida oak species. *Ecological Monographs* 74:635-662.
- Cavender-Bares, J.**, and A. Wilczek. 2003. Integrating micro- and macroevolutionary processes in community ecology. *Ecology* 84:592-597.
- Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, **J. Cavender-Bares** et al. 2004. The worldwide leaf economics spectrum. *Nature* 428:821-827.

### **Synergistic Activities**

- *Reviewing and Editing*: served on Ecology DDIG review panel, Feb. 2005; Associate Editor for Physiological Ecology, *Journal of the Torrey Botanical Society*
- *Advising/Mentoring*: Currently advising and co-advising 3 graduate students, 2 undergraduates, and 1 NSF Postdoctoral Fellow. Mentored 16 undergraduates over ten years (4 for Cedar Creek LTER research); five have been coauthors on publications, ten have gone on to graduate school in science.
- *Outreach and Networking*: Invited lecturer at 26 universities in five countries; Symposium invitee and yearly participant at the Ecological Society of America (ESA).
- Co-organizer of the national Symposium on Community Genetics and Phylogenetics (Minneapolis, U of M, April 2005);
- Developed statistical methods and computer programs (in Visual Basic) to analyze community data using phylogenetic information.

### **Other Scholarly Activities Relevant to Scientific Merit**

- Ecological Society of America's Billings Award for Physiological Ecology (1999)
- Derek Bok Award for Excellence in Teaching, Harvard University (1996-1997)
- Six major scholarships for academic study and public service.

Advisor to two graduate students and one post-doctoral scholar.

## JENNIFER Y. KING

### Professional Preparation

Rice University	Ecology and Evolutionary Biology	BA, 1994
University of California, Irvine	Earth System Science	MS, 1997
University of California, Irvine	Earth System Science	PhD, 1999

### Appointments

Assistant Professor, University of Minnesota, Department of Soil, Water, and Climate and Department of Ecology, Evolution, and Behavior (joint appt.), 2002-present  
Postdoctoral Research Fellow, USDA-ARS, Fort Collins, Colorado, Soil-Plant-Nutrient Research Unit, 1999-2001  
Graduate Student Researcher, Univ. of California, Irvine, Earth System Science, 1994-1999  
Teaching Assistant, Univ. of California, Irvine, Earth System Science, 1996  
Research Assistant, Rice Univ., Wetland Center for Biogeochemical Research, 1991-1994

### Related Publications

King, J.Y., A.R. Mosier, J.A. Morgan, D.R. LeCain, D.G. Milchunas, and W.J. Parton. 2004. Changes in aboveground plant nitrogen in shortgrass steppe following growth under elevated atmospheric CO<sub>2</sub>. *Ecosystems* 7: 147-160.

Milchunas, D.G., J.Y. King, A.R. Mosier, J.C. Moore, J.A. Morgan, M.H. Quirk, and J.R. Slusser. 2004. UV radiation effects on plant growth and forage quality in a shortgrass steppe ecosystem. *Photochemistry and Photobiology* 79(5): 404-410.

Pendall, E., S. DelGrosso, J. King, D. LeCain, D. Milchunas, J. Morgan, A. Mosier, D. Ojima, W. Parton, P. Tans, and J. White. 2003. Elevated atmospheric CO<sub>2</sub> effects and soil water feedbacks on soil respiration components in a Colorado grassland. *Global Biogeochemical Cycles* Vol. 17 No. 2 10.1029/2001GB001821.

King, J. Y., D. G. Milchunas, A. R. Mosier, J. C. Moore, M. H. Quirk, J. A. Morgan, and J. R. Slusser. 2003. Initial impacts of altered UVB radiation on plant growth and decomposition in shortgrass steppe. Pages 384-395 *In* Ultraviolet ground- and space-based measurements, models, and effects III (J. R. Slusser, J. R. Herman, and W. Gao, eds.). International Soc. Optical Eng., SPIE Proceed. Vol. 5156, Bellingham, WA.

Mosier, A.R., J.A. Morgan, J.Y. King, D.R. LeCain, and D.G. Milchunas. 2002. Soil-atmosphere exchange of CH<sub>4</sub>, CO<sub>2</sub>, NO<sub>x</sub>, and N<sub>2</sub>O in the Colorado shortgrass steppe under elevated CO<sub>2</sub>. *Plant and Soil* 240: 201-211.

### Synergistic Activities and Service

Session convener, Biogeosciences, American Geophysical Union Fall Meeting, 2000  
Invited participant, NEON, Stable Isotope Network, 2004  
Panel member: USDA/NASA Interagency Panel on Carbon Cycle Science, 2004  
Reviewer for agencies and journals: National Science Foundation, U.S. Department of Agriculture (USDA), Research Council of Norway, Swiss National Science Foundation  
*Global Change Biology, Global Biogeochemical Cycles, Journal of Environmental Quality, Soil Biology and Biochemistry, Journal of Geophysical Research, Agricultural and Forest Meteorology, Oecologia, Biogeochemistry, Ecology, Photochemistry and Photobiology, Atmospheric Environment*  
Teaching: Introduction to Environmental Science, Biogeochemical Processes, Global Change Honors Colloquium, Biogeochemistry Graduate Seminar, Undergraduate Directed Research, Environmental Science May Session (7<sup>th</sup> and 8<sup>th</sup> grade students)  
Advisor for: Leslie Brandt, Harriet Van Vleck, Diego Riveros, Laura Van Riper (4 graduate students); Peter Weishampel (postdoc); 15 undergraduate students

## Linda L. Kinkel

### Professional Preparation:

Saint Olaf College	Biology and Psychology	B.S. with honors, 1981
University of Wisconsin-Madison	Plant Pathology	M.S., 1985
University of Wisconsin-Madison	Biometry	M.S., 1987
University of Wisconsin-Madison	Plant Pathology	Ph.D., 1988
University of California-Berkeley	Plant Pathology	1988-1989

### Appointments:

Professor, University of Minnesota, Department of Plant Pathology, 2001-present.  
Associate Professor, University of Minnesota, Department of Plant Pathology, 1996-2001.  
Assistant Professor, University of Minnesota, Department of Plant Pathology, 1990-1996.  
Postdoctoral Scientist and Instructor, University of California-Berkeley  
Department of Plant Pathology, 1988-1989.

### Publications:

- Davelos, A. L., Xiao, K., Martin A. P., Samac, D. A., Kinkel, L. L. 2004. Spatial variation in *Streptomyces* genetic composition and diversity in a prairie soil. *Microb Ecol* 39 (1):1-11.
- Davelos, A. L., Kinkel, L. L., Samac, D. A. 2004. Spatial variation in the frequency and intensity of antibiotic interactions among Streptomycetes from Prairie Soil. *Appl. Environ. Microbiol.* 70: 1051-1058.
- Lee, S. D., Kinkel, L. L., and Samac, D. A. *Amycolatopsis minnesotensis* sp. nov. isolated from a prairie soil. *Intl. J. Syst. Evol. Microbiol.* 56: 265-269.
- Davelos, A. L., Xiao, K., Flor, J. M., Kinkel, L. L. 2004. Genetic and phenotypic traits of streptomycetes used to characterize antibiotic activities of field-collected microbes. *Can. J. Microbiol.* 50: 79-89.
- Barnes, C. W., Kinkel, L. L., and Groth, J. V. 2005. Spatial and temporal dynamics of *Puccinia andropogonis* on *Comandra umbellata* and *Andropogon gerardii* in a native prairie. *Canadian Journal of Botany* 83:1159-1173.

### Synergistic Activities

- \*Contributor to local Minnesota Science Museum symposium on integration of current university research into the high school curriculum.
- \*Active mentor to undergraduate research students. I have advised more than 50 undergraduate research projects in the last decade; the majority of these have been women.
- \*Collaborator with research scientists at small colleges, including University of Texas Pan American (Dr. Anita Davelos Baines), UW-River Falls (Dr. Kim Mogen) and Northern Michigan University (Dr. Donna Becker). These scientists have little access to research funds. Through our collaborations, they have enhanced access to research funds and I am happy to provide cultures, equipment, and research support as needed.
- \*I have worked with Dr. Kim Mogen to develop undergraduate microbiology lab exercises based upon the techniques in our research. These exercises are currently used at UW-River Falls, and are being published as part of the ASM MicrobeLibrary resource for teachers of Microbiology, and have been presented for the past 2 years at the ASM National Meetings.
- \*Just completed 3-year term as Senior Editor, *Phytopathology*.

Total of 10 graduate students advised, 5 postdoctoral scholars sponsored.

## JOHANNES (JEAN) M. H. KNOPS

School of Biological Sciences & School of Natural Resource Sciences  
University of Nebraska, Lincoln, 348 Manter Hall, Lincoln, NE 68588  
Phone: (402) 472-6449, FAX: (402) 472-2083, e-mail: jknops2@unl.edu

### EDUCATION

1982	Ing.	Horticulture	Higher Agricultural College
1989	Drs.	Plant Ecology	University of Utrecht
1994	Ph.D.	Botany	Arizona State University

### PROFESSIONAL EXPERIENCE

2005 - current	Director Cedar Point Biological Station.
2004 - current	Associate professor, University of Nebraska
1999 – 2004	Assistant professor, University of Nebraska.
1995 - 1999	Research director, Long-Term Ecological Research program at the Cedar Creek Natural History Area, and adjunct assistant professor, Department of Ecology, Evolution and Behavior, University of Minnesota.

### PEER REFEREED JOURNAL PUBLICATIONS

Kennedy, T., S. Naeem, K. Howe, J.M.H. Knops, D. Tilman & P. Reich. 2002. Biodiversity as a barrier to ecological invasion. *Nature* **417**: 636-639

Knops, J.M.H., K.L. Bradley & D.A. Wedin. 2002. Mechanisms of species impacts on ecosystem nitrogen cycling. *Ecology Letters* **5**: 454-466.

Knops, J.M.H., D. Wedin & D. Tilman. 2001. Biodiversity and decomposition in experimental grassland ecosystems. *Oecologia* **126**: 429-433.

Knops, J.M.H. & D. Tilman. 2000. Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. *Ecology*, **81**: 88-98.

Knops, J.M.H., D. Tilman, N.M. Haddad, S. Naeem C.E. Mitchell, J. Haarstad, M.E. Ritchie, K.M. Howe, P.B. Reich, E. Siemann & J. Groth. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insects abundances and diversity. *Ecology Letters* **2**: 286-293

### AWARDS

2005 Sigma Xi Outstanding young scientist

### SYNERGISTIC ACTIVITIES

1. 2000- current. Environmental Studies coordinator and advisor for the School of Biology (approximately 45 undergraduate students)
2. Editor for *Ecology Letters* (2002 – ongoing) and *Plant Biology* (2003 – ongoing)
3. Review panel member, *Ecology*, National Science Foundation 2004 and 2005

Total of 5 graduate students advised, 2 postdoctoral scholars sponsored.

**Biographical Sketch, Rebecca A. Montgomery**  
Department of Forest Resources, University of Minnesota  
St. Paul MN 55108

**Professional preparation**

Occidental College, Biology, A. B. Magna cum laude, 1994  
University of Connecticut, Ecology and Evolutionary Biology, Ph.D., 1999  
University of Wisconsin-Madison, Botany, 2000-2003

**Appointments**

2004-present Assistant Professor, Forest Resources, University of Minnesota  
2003-2004 Research Associate, Forest Resources, University of Minnesota  
2003-2004 Instructor, Forest Resources, University of Minnesota

**Publications**

- Givnish T.J., **R.A. Montgomery** and G. Goldstein. 2004. Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: static light responses. *American Journal of Botany* 91: 228-246.
- Montgomery, R. A.** 2004. Relative importance of photosynthetic physiology and biomass allocation for tree seedling growth across a broad light gradient *Tree Physiology* 24:155-167.
- Montgomery, R. A.** 2004. Effects of understory vegetation on patterns of light attenuation near the forest floor. *Biotropica* 36: 33-39.
- Montgomery, R. A.** and R. L. Chazdon. 2002. Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. *Oecologia* 131:165-174.
- Montgomery, R. A.** and R. L. Chazdon. 2001. Forest structure, canopy architecture and light transmittance in old-growth and second-growth stands of lowland rainforest in NE Costa Rica. *Ecology* 82: 2707-2718.

**Recent Synergistic Activities**

I am currently developing a database of plant functional traits for the entire Hawaiian flora in collaboration with several scientists based in Hawaii (U Hawaii at Manoa, U Hawaii at Hilo, USGS and USDA Forest Service). • Over the past four years, I have been involved in an international collaboration (>15 countries) examining leaf decomposition rates in tropical forest around the globe. This project is coordinated by Dr. Jennifer Powers (U Minnesota) • In 2003, Dr. Tom Givnish (U Wisconsin) and I provided plants to the US National Arboretum to help mount a display on endangered Hawaiian flora. • Over the past 3 years, I have presented > 10 presentations of my research at national and international meetings. • During this past year, I participated in an Early Career Teaching Program and various workshops on improving teaching and learning at the college level.

Total of 2 graduate students advised, 1 postdoctoral scholar sponsored.

## Helene C. Muller-Landau

**Research interests:** Plant community ecology, both theoretical and empirical, especially species coexistence, Janzen-Connell effects, seed dispersal, plant life history strategies.

### Professional Preparation:

Swarthmore College	Mathematics and Statistics	BA 1995
Princeton University	Ecology and Evolutionary Biology	MA 1997
Princeton University	Ecology and Evolutionary Biology	PhD 2001
National Center for Ecological Analysis and Synthesis, UCSB		Postdoc, 2002-2003
Princeton University	Ecology and Evolutionary Biology	Postdoc, 2004

### Appointments:

July 2004 – present: Assistant Professor, Ecology, Evolution and Behavior, U. of Minnesota

### Five Most Relevant Publications:

- Muller-Landau, H.C.** In press. Competition-colonization tradeoffs in tropical forests and their role in the maintenance of plant species diversity. *Tropical Forest Community Ecology*. W. P. Carson and S. A. Schnitzer, editors. Blackwell Scientific.
- Wills, C., K. E. Harms, R. Condit, D. King, J. Thompson, F. He, **H. Muller-Landau**, P. Ashton, E. Losos, L. Comita, S. Hubbell, J. LaFrankie, S. Bunyavejchewin, H.S. Dattaraja, S. Davies, S. Esufali, R. Foster, I.A.U.N. Gunatilleke, C.V.S. Gunatilleke, P. Hall, A. Itoh, R. John, S. Kiratiprayoon, S. Loo de Lao, M. Massa, C. Nath, Md. N. S. Noor, A. Rahman Kassim, R. Sukumar, H. S. Suresh, I-F. Sun, S. Tan, T. Yamakura, J. Zimmerman. In press. Non-random processes contribute to the maintenance of diversity in tropical forests. *Science*.
- Adler, F. R. and **H. C. Muller-Landau**. 2005. When do localized natural enemies increase species richness? *Ecology Letters* 8:438-447.
- Wright, S. J., **H. C. Muller-Landau**, O. Calderón, and A. Hernández. 2005. Annual and spatial variation in seedfall and seedling recruitment in a Neotropical forest. Putative mast seeding, seed fate, and El Niño climate fluctuation in a Neotropical forest. *Ecology* 86(4):848-860.
- Muller-Landau, H. C.**, S. J. Wright, O. Calderón, S. P. Hubbell, and R. B. Foster. 2002. Assessing recruitment limitation: concepts, methods and examples for tropical forest trees. Pages 35-53 in *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. J. Levey, W. R. Silva and M. Galetti, editors. Oxfordshire, UK: CAB International.

### Synergistic Activities:

1. Member of the Editorial Board, *Ecological Research*. 2004-present.
2. Reviewer for the journals *Science*, *PNAS*, *Ecology Letters*, *American Naturalist*, *Ecology*, *Journal of Ecology*, *Oecologia*, *Oikos*, *Journal of Theoretical Biology*, *Theoretical Population Biology*, *Bulletin of Mathematical Biology*, *Journal of Applied Ecology*, *Ecological Applications*, *Biotropica*, *Journal of Tropical Ecology*, *Plant Ecology*, *Ecoscience* and *Annales Botanici Fenici*, as well as for Princeton University Press, NSF, WOTRO (the Netherlands NSF equivalent), and the Swiss National Science Foundation.
3. Outreach to Minnesota students through the Bell Museum of Natural History at the U. of Minnesota as part of the 2003-04 JASON curriculum on “Rainforests at the Crossroads.”
4. Developed and made freely available R programs to implement numerical methods for estimating seed shadows from data on seed traps within mapped plots, and led workshops to teach these methods in Quito, Ecuador (April, 2003) and Pasoh, Malaysia (August, 2003).

Total of 2 graduate students advised, 1 postdoctoral scholar sponsored.

## BIOGRAPHICAL SKETCH

Jennifer S. Powers  
Dept. of Ecology, Evolution & Behavior  
University of Minnesota  
St. Paul, MN 55108

tel: 612 625-5721  
email: powers@umn.edu

### Professional Preparation

Reed College	Biology	B.A.	1991
Oregon State University	Forest Science	M.S.	1995
Duke University	Biology	Ph.D.	2001
SUNY-Stony Brook	Ecology	Postdoc	(2001-2004)

### Appointments

2006	Assistant Professor, Depts. of Ecology, Evolution & Behavior, Plant Biology, and Soil, Water & Climate University of Minnesota. Start date, fall, 2006
2004-fall 2006	NSF ADVANCE Postdoctoral Research Fellow, UMN.
2001-2004	Postdoctoral Research Associate, Dept. of Ecology and Evolution, State University of New York--Stony Brook
1996-2001	Graduate Research Assistant, Biology Dept., Duke University
1995	Research Assistant and Intern in the GIS lab, La Selva Biological Station, Costa Rica
1992-1995	Graduate Research Assistant, Forest Science Dept., Oregon State University

### Five Publications

Powers, J.S., K.K. Treseder, and M.T. Lerdau. 2005. Fine roots, arbuscular mycorrhizal hyphae and soil nutrients in four neotropical rain forests: patterns across large geographic distances. *New Phytologist* 165: 913-921.

Powers, J.S., and E. Veldkamp. 2005. Regional variation in soil carbon and  $\delta^{13}\text{C}$  in paired forests and pasture of Northeastern Costa Rica. *Biogeochemistry* 72: 315-336

Powers, J.S. 2004. Soil carbon and nitrogen storage following contrasting land-use transitions in Northeastern Costa Rica. *Ecosystems* 7: 134-146

Powers, J.S., J.M. Read, J.S. Denslow, and S.M. Guzman. 2004. Estimating soil carbon fluxes following land-cover change: a test of some critical assumptions for a region in Costa Rica. *Global Change Biology* 10: 170-181.

Powers, J.S., and W.H. Schlesinger. 2002. Relationships between soil carbon distributions and biophysical factors at nested spatial scales in rain forests of Northeastern Costa Rica. *Geoderma* 109: 165-190.

### Synergistic Activities

Gave talks on carbon cycling and tropical forests to school groups: YWCA Girl Power Group of 6<sup>th</sup> graders (April 2004), Kennedy High 10<sup>th</sup> graders (May 2004), Edina High 12<sup>th</sup> graders (May 2005).

Educational outreach with 8<sup>th</sup> grade students in Earth Sciences classes at Breck School, Minneapolis, MN. Includes giving annual guest lectures and designing year-long field experiments on leaf litter decomposition (2002 – present).

## Facilities, Equipment, and Other Resources

### Laboratory:

Cedar Creek Natural History Area is large (2200 hectares, or 9 square miles), convenient (40 minutes north of Minneapolis/St. Paul), and ecologically diverse (at the meeting point of the western prairies, northern coniferous forests, and eastern deciduous forests). It is comprised of a rich mosaic of habitats---savannas, forests, prairies, marshes, lakes, ponds, and successional habitats of various ages. Its sandy soils are typical of about 30% of terrestrial ecosystems.

CCNHA has one laboratory building, and is currently finalizing plans for construction of additional laboratory and office space (about 6500 sf, in total, for new building). The existing building, with a total of 5700 square feet (sf) contains eleven offices, two work rooms, two chemistry rooms each with a fume hood, a collections room (insects and herbarium), a computer room, and a lunch room with limited kitchen facilities. Each work room (about 500 sf each) accommodates 14 to 18 people doing tasks at large tables, such as plant or insect sorting or preparation of soils for chemical analyses. The largest room in the building is the kitchen - lunch room (780 sf), which doubles as the meeting room and as informal space for many other needs. Equipment housed within the laboratory facility includes an NH<sub>4</sub> and NO<sub>3</sub> Alpkem RFA-300 Autoanalyzer, used for soil and water analyses, analytic balances, shaker tables, centrifuges, two fume hoods, three drying ovens, a pH meter, a large-capacity Barnstead Nanopure II water purification system, top-loading balances, Licor LI-6200 portable photosynthesis system, a Licor leaf area meter with automatic feed, two Decagon SF-40 Sunfleck Ceptometers, and a UDY cyclone mill. A Costech total C/N autoanalyzer performs analyses for CDR projects and is currently at the University of Nebraska.

### Computer:

Our computing system is a distributed network containing Unix and Linux servers, personal computers, and hand-held computers. We use personal computers for originating and maintaining data and web pages. The central Unix and Linux machines act as servers and provide multiple redundant backup sites for the data and the website.

Specifically, the network includes: (1) A Sun Ultra 450 Unix computer at the field site. This computer is dedicated to CCNHA functions. It serves one copy of the CCNHA website and contains a copy of all the CCNHA data. It is also available for computation. (2) An additional offsite Linux computer (35 miles away on the University campus in the College of Biological Sciences Computing Facility) that serves the main web site and contains a redundant copy of the data. Data are also backed up at many other sites. (3) Eight personal computers in a dedicated computer room, used by visitors, research interns, and others for web access and general processing. (4) Twelve personal desktop computers permanently connected to laboratory instruments. Ten of these are connected to scales and bar-code readers used in soil analysis and other weighing operations, one is dedicated to the nitrogen analysis machine, and one serves the weather station and communicates its results to the dedicated Unix server at the field site. (5) Four personal computers dedicated to origination and maintenance of web sites and geographic information sites. (6) Approximately 18 personal computers in individual offices. (7) Ten handheld computers for data acquisition in the field.

The computing machinery is used for email, data management, data analysis, word processing, experimental design (randomization, labels, etc.), documenting experiments, acquiring data (hand-held units), storing data, modeling, and other purposes.



**Office:**

The laboratory building at CCNHA currently provides the facility's office space. There are 11 offices each measuring approximately 9' x 12'. An additional 6 or 7 offices are planned for the new building. These new offices would be available for use by researchers, including off-campus scientists on long-term research visits to CCNHA, and for outreach and public education staff.

**Other:**

In addition to the main laboratory facility, CCNHA has a number of auxiliary wood-frame buildings, including a workshop with power equipment and hand tools; a 2000 sf storage barn containing lockers and storage bins for research equipment; a 5000 sf storage building currently under construction; a 1200 sf post-frame building with a walk-in drying room and areas for archived samples; a screened root washing building; and several household garages.

Housing facilities include four year-round family homes, two summer cabins, a duplex apartment building, and a garage that was converted into a dormitory. One residence is configured for visiting scientists, with one double bed per room. Other residences generally have 2 or more beds per bedroom (total of 65 beds). In addition to the permanent housing structures, we also maintain a number of tent pads for summer interns who choose to use them.

**Major Equipment:**

Transportation equipment available to researchers at CCNHA includes 4 full size pickup trucks and 2 utility passenger vehicles (e.g., Chevrolet Suburban). There are also 2 tractors available at CCNHA: a Ford 4100, and a John Deere 4350. Tractor implements include a tiller, brush mover, lawn mower, grater, and disk. ATVs available at the facility include 2 Polaris Rangers and an Argo 8 wheeled amphibious vehicle. Prescribed burn equipment includes 5 gas powered water pump: 3 pickup truck mounted units with 125 gallon capacity and 11 hp engines, and 2 ATV mounted units with 55 gallon capacities and 5 hp engines. Other fire equipment includes Nomex fire clothing, backpack sprayers, and various hand tools. The CCNHA facility also provides various types of field equipment such as soil corers, chain saws, battery powered biomass trimmers, hand tools, rototillers, lawn mowers, a generator, and gas powered portable water pumps. There are also 5 large refrigerators and 4 standard freezers available to researchers.

**Other Resources:**

CCNHA is owned by the University of Minnesota which provides a number of important resources to the facility. Electrical power required to run experiments, accounting and secretarial staff in the college of Ecology Evolution and Behavior, and Electronic Instrument services are just an example of the services provided by the University. CCNHA has also entered into a relationship with the College of Biological Sciences Computing Services which has increased our access to professional dedicated computing staff, as well as physical computing resources. CBS Computing Services is now the host for the CCNHA web site (<http://www.cedarcreek.umn.edu>), and provides off campus data storage and backup facilities. The University also provides access to field equipment such as wood chippers and vehicles on a rent or loan basis. CCNHA also has access to University of Minnesota Fleet Services for maintenance and repair of vehicles.

Researchers associated with CCNHA also have access to an analytical chemistry laboratory located at the University of Nebraska maintained by Dr. Jean Knops. Soil and plant tissue samples from CCNHA can be sent to this laboratory to be analyzed for total Carbon and Nitrogen.

**Table 1: Publications of the Cedar Creek LTER (2000-2006)**

**1. Journal Articles**

- Avis, P. G., D. J. McLaughlin, B. C. Dentinger and P. B. Reich. 2003. Long-term increase in nitrogen supply alters above- and belowground ectomycorrhizal communities and increases the dominance of *Russula* spp. in a temperate oak savanna. *New Phytologist* 160:239-253.
- Barnes, C. W., Kinkel, L. L., and Groth, J. V. 2005. Spatial and temporal dynamics of *Puccinia andropogonis* on *Comandra umbellata* and *Andropogon gerardii* in a native prairie. *Can. J. Bot.* 83:1159-1173.
- Bassirirad, H., J. V. H. Constable, J. Lussenhop, B. A. Kimball, R. J. Norby, W. C. Oechel, P. B. Reich, W. H. Schlesinger, S. Zitzer, H. L. Sehtiya, S. Salim. 2003. Widespread foliage  $\delta^{15}\text{N}$  depletion under elevated  $\text{CO}_2$ : inferences for the nitrogen cycle. *Global Change Biology* 9:1-9.
- Bradley, K. L., E. I. Damschen, L. M. Young, D. Kuefler, S. Went, G. Wray, N. M. Haddad, J. M. H. Knops and S. M. Louda. 2003. Spatial heterogeneity, not visitation bias, dominates variation in herbivory. *Ecology* 84:2214-2221.
- Bradley, K., R. A. Drijber, and J. Knops. 2006. Increased N availability in grassland soils modifies their microbial communities and decreases the abundance of arbuscular mycorrhizal fungi. *Soil Biology and Biochemistry*, In press.
- Burrows, R. L. and F. L. Pflieger. 2002. Arbuscular mycorrhizal fungi respond to increasing plant diversity. *Canadian Journal of Botany* 80:120-130.
- Burt-Smith, G. S., J. P. Grime and D. Tilman. 2003. Seedling resistance to herbivory as a predictor of relative abundance in a synthesized prairie community. *Oikos* 101:345-353.
- Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Diaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. ter Steege, H. D. Morgan, M. G. A. van der Heijden, J. G. Pausas and H. Poorter. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51:335-380.
- Craig, T. P., J. D. Horner and J. K. Itami. 2001. Genetics, experience and host-plant preference in *Eurosta solidaginis*: implications for host shifts and speciation. *Evolution* 55:773-782.
- Craine, J. M., P. B. Reich. 2005. Leaf-level light compensation points in shade-tolerant woody seedlings. *New Phytologist* 166:710-713.
- Craine, J. M. and D. A. Wedin. 2002. Determinants of growing season soil  $\text{CO}_2$  flux in a Minnesota grassland. *Biogeochemistry* 59:303-313.
- Craine, J. M. and P. B. Reich. 2001. Elevated  $\text{CO}_2$  and nitrogen supply alter leaf longevity of grassland species. *New Phytologist* 150:397-403.
- Craine, J. M., D. A. Wedin and P. B. Reich. 2001c. Grassland species effects on soil  $\text{CO}_2$  flux track the effects of elevated  $\text{CO}_2$  and nitrogen. *New Phytologist* 150:425-434.

- Craine, J. M., D. A. Wedin, F. S. Chapin III., and P. B. Reich. 2003c. The dependence of root system properties on root system biomass of 10 North American grassland species. *Plant and Soil* 250:39-47.
- Craine, J. M., D. A. Wedin, F. S. Chapin III., and P. B. Reich. 2002b. Relationship between the structure of root systems and resource use for 11 North American grassland plants. *Plant Ecology* 165:85-100.
- Craine, J. M., D. Tilman, D. A. Wedin, P. B. Reich, M. J. Tjoelker and J. M. H. Knops. 2002a. Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Functional Ecology* 16:563-574.
- Craine, J. M., D. A. Wedin, P. B. Reich. 2001b. The response of soil CO<sub>2</sub> flux to changes in atmospheric CO<sub>2</sub>, nitrogen supply, and plant diversity. *Global Change Biology* 7:947-953.
- Craine, J. M., J. Froehle, D. G. Tilman, D. A. Wedin and F. S. Chapin III. 2001a. The relationships among root and leaf traits of 76 grassland species and relative abundance along fertility and disturbance gradients. *Oikos* 93:274-285.
- Craine, J. M., P. B. Reich, D. Tilman, D. Ellsworth, J. Fargione, J. Knops and S. Naeem. 2003b. The role of plant species in biomass production and response to elevated CO<sub>2</sub> and N. *Ecology Letters* 6:623-630.
- Craine, J., W. Bond, W. Lee, P. Reich and S. Ollinger. 2003a. The resource economics of chemical and structural defenses across nitrogen supply gradients. *Oecologia* 137:547-556.
- Daily, G. C., T. Soderqvist, S. Aniyar, K. Arrow, P. Dasgupta, P. R. Ehrlich, C. Folke, A. Jansson, B-O. Jansson, N. Kautsky, S. Levin, J. Lubchenco, K-G. Maler, D. Simpson, D. Starrett, D. Tilman and B. Walker. 2000. The value of nature and the nature of value. *Science* 289:395-396.
- Davelos, A. L., L. L. Kinkel, and D. A. Samac. 2004. Spatial variation in the frequency and intensity of antibiotic interactions among Streptomycetes from Prairie Soil. *Applied and Environmental Microbiology* 70:1051-1058.
- Davelos, A. L., K. Xiao, J. M. Flor, and L. L. Kinkel. 2004. Genetic and phenotypic traits of streptomycetes used to characterize antibiotic activities of field-collected microbes. *Canadian Journal of Microbiology* 50:79-89.
- Davelos, A. L., K. Xiao, A. P. Martin, D. A. Samac and L. L. Kinkel. 2004. Spatial variation in *Streptomyces* genetic composition and diversity in a prairie soil. *Microbial Ecology* 48:601-612.
- Davis, M. A. and K. Thompson. 2000. Eight ways to be a colonizer; two ways to be an invader. *Bulletin of the Ecological Society of America* 81:226-230.
- Davis, M. A. and L. B. Slobodkin. 2004. Restoration ecology: the challenge of social values and expectations. *Frontiers in Ecology and Evolution* 2:44-45.
- Davis, M. A. and L. B. Slobodkin. 2004. The science and values of restoration ecology. *Restoration Ecology* 12:1-3.

- Davis, M. A. and M. Pelsor. 2001. Experimental Support for a Resource-Based Mechanistic Model of Invasibility. *Ecology Letters* 4:421-428.
- Davis, M. A. 2003. Biotic Globalization: Does Competition from Introduced Species Threaten Biodiversity? *BioScience* 53:481-489.
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**Table 2a. CDR Electronic Data Sets**

The following list briefly describes the long-term data sets available electronically via the world wide web (<http://www.cedarcreek.umn.edu>). Detailed descriptions of the experiments and data are on our web site. Data are available for download in a number of different commonly used formats to insure that data are useful to a wide audience. All data files include pertinent metadata and contact information.

**Data Sets Available on the WWW:**

<b>Data Set Name</b>	<b>Data Set Description</b>
Weather ( <a href="http://www.cedarcreek.umn.edu/weather/">http://www.cedarcreek.umn.edu/weather/</a> )	Historical regional weather data for Fort Snelling, MSP, MN, 1837-2006, the oldest weather record for the state; Cedar, MN (NOAA weather Station), 1982-2006; daily precipitation and temperature. Cedar Creek meteorological station, 1988-2006; hourly precipitation, temperature, radiation, wind, and other measurements, updated daily.
Rainfall Chemistry ( <a href="http://www.cedarcreek.umn.edu/weather/nadp">http://www.cedarcreek.umn.edu/weather/nadp</a> )	Data Collected at CCNHA for the National Atmospheric Deposition Program (NADP) and Minnesota Pollution Control Agency (MPCA), 1996-2006. Includes precipitation acidity and conductivity. (Data also available at <a href="http://nadp.sws.uiuc.edu">http://nadp.sws.uiuc.edu</a> , Site MN01.)
Ground Water Levels ( <a href="http://www.cedarcreek.umn.edu/research/exper/e084">http://www.cedarcreek.umn.edu/research/exper/e084</a> )	83 Sites spread across CCNHA at which ground water levels are measures 7 times per year.
Online Insect Collection ( <a href="http://www.cedarcreek.umn.edu/insects">http://www.cedarcreek.umn.edu/insects</a> )	High resolution photographs 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. 1700 web pages with over 1500 images.
Online Plant Herbarium ( <a href="http://www.cedarcreek.umn.edu/plants1">http://www.cedarcreek.umn.edu/plants1</a> )	Photographs and high resolution scanned images of the more abundant plant species of Cedar Creek as an aid in plant identification.

<p>Flora of Cedar Creek (<a href="http://www.cedarcreek.umn.edu/flora">http://www.cedarcreek.umn.edu/flora</a>)</p>	<p>A Floral list for Cedar Creek prepared by Professor John Moore and updated by Barbara Delaney.</p>
<p>Birds of Cedar Creek (<a href="http://www.cedarcreek.umn.edu/birds">http://www.cedarcreek.umn.edu/birds</a>)</p>	<p>A bird checklist for CCNHA prepared by James Horowitz and David Bosanko</p>
<p>Effects of nitrogen supply on ecosystem dynamics (E001) (<a href="http://www.cedarcreek.umn.edu/research/exper/e001/data.html">http://www.cedarcreek.umn.edu/research/exper/e001/data.html</a>)</p>	<p>An experiment consisting of 207 permanent plots in 4 grassland sites. Annually sampled for biomass, sorted to species (1982-2005). Plant biomass and light penetration (treatment means), species richness and its derivatives, 1982-2005.</p>
<p>Long-Term Nitrogen Deposition: Effects of Succession Following Major Disturbances (E002) (<a href="http://www.cedarcreek.umn.edu/research/exper/e002/data.html">http://www.cedarcreek.umn.edu/research/exper/e002/data.html</a>)</p>	<p>An experiment with N addition treatments identical to E001 (above) except experimental areas were initially disturbed via disking. Same data gathered as for E001 (above; 1982-1993). In 1993, the experiment was modified to be either an N cessation experiment or an N addition x Fire experiment.</p>
<p>Effects of fire frequency on successional vegetation (E012) (<a href="http://www.cedarcreek.umn.edu/research/exper/e012/data.html">http://www.cedarcreek.umn.edu/research/exper/e012/data.html</a>)</p>	<p>A fire experiment, with treatments of no burning, annual burning, burning every other year, burning every fourth year. Biomass by species (treatment means), 1983-2003. Plant biomass and light penetration (treatment means), species richness and its derivatives, 1983-2003.</p>
<p>Successional dynamics in a resampled chronosequence (E014) (<a href="http://www.cedarcreek.umn.edu/research/exper/e014/data.html">http://www.cedarcreek.umn.edu/research/exper/e014/data.html</a>)</p>	<p>A study to observe the long-term dynamics of plant, insect and mammal species in successional fields. Percent cover by species and associated total N and C measured every 5 or 6 years from 1983-present in each of ca. 2200 permanent plots. Insect and small mammal abundances measured annually in these 22 old fields.</p>
<p>Productivity in an old-field chronosequence (E054) (<a href="http://www.cedarcreek.umn.edu/research/exper/e054/data.html">http://www.cedarcreek.umn.edu/research/exper/e054/data.html</a>)</p>	<p>Annual measurement of plant biomass by species, in 14 of the fields of E014 (above), performed from 1988-2003.</p>

Biodiversity Experiment (E120) ( <a href="http://www.cedarcreek.umn.edu/research/exper/e120/data.html">http://www.cedarcreek.umn.edu/research/exper/e120/data.html</a> )	The "Big" Biodiversity Experiment. Annual data on plant percent cover by species (treatment means) or on aboveground biomass sorted to species; total aboveground plant biomass; root biomass, total percent plant cover, soil nutrients, light penetration (treatment means), species richness and its derivatives, 1996-2003.
Arthropod size and Diversity (E122) ( <a href="http://www.cedarcreek.umn.edu/research/exper/e122/data.html">http://www.cedarcreek.umn.edu/research/exper/e122/data.html</a> )	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 including abundances across fields and sampling dates.
Biodiversity, productivity, and nutrient dynamics (E123) ( <a href="http://www.cedarcreek.umn.edu/research/exper/e123/data.html">http://www.cedarcreek.umn.edu/research/exper/e123/data.html</a> )	The "Small" Biodiversity Experiment -- No Longer Active. Percent cover by species (treatment means), 1995-2003. Aboveground biomass, root biomass, total percent plant cover, soil nutrients, light penetration (treatment means), species richness and its derivatives, 1995-2003.
Biocomplexity: Interacting responses to C and N cycles to altered biodiversity, elevated CO2 and N (E141) ( <a href="http://www.cedarcreek.umn.edu/research/exper/e141/data.html">http://www.cedarcreek.umn.edu/research/exper/e141/data.html</a> )	The "BioCON" Experiment. Aboveground biomass, root biomass, total percent plant cover, soil nutrients, light penetration (treatment means), species richness and its derivatives, 1998-2003.
Archived Soil, Plant and Other CDR Samples ( <a href="http://www.cedarcreek.umn.edu/samples">http://www.cedarcreek.umn.edu/samples</a> )	Records of over 60,000 soil, plant tissue, and litter samples archived for access by researchers for future reference. Archived samples are stored in archival quality glass containers labeled and curated in a room dedicated solely to this task, much as a library.

**Table 2b. Documented non-LTER uses of Cedar Creek Data**

The CDR web site was visited by more than a third of a million individuals during 2005, about a fifth of whom found our site via Google. Interestingly, the most common kind of 'data' accessed from our site were photographic images, especially images of insects.

Type of Hit	Number of Hits per Year
Unique Visitors	375,762
Visitors Referred by Google (web search)	83,322
Images Requested (downloaded)	6,672

We currently do not have a way to track downloads of weather data, lists of flora and fauna, and other data sets that visitors use without registration. Because users must register to download the detailed core data sets that have been gathered in the core CDR experiments (e.g., our Biodiversity Experiment, our N Addition Experiment, etc.), we know that these are downloaded approximately 100 times per year. The institutions that access core CDR data can be broken into the following categories (numbers represent data for calendar year 2005):

Institution Type	Downloads per Year
Colleges and Universities	92
Government Agency	8
Other agencies and personal use	6

Most of the “college and universities” are major research universities. The major reasons given for data use were research and education:

Specified Use	Downloads per Year
Education	40
Research	64
Other	2

Once researchers have downloaded data, they are free to use it (in any way that is consistent with the Data Use Pledge). We only learn of its use in publications if a researcher who uses the data in a paper notifies us or if we happen to encounter such a paper in the literature.