APPENDIX III

COVER SHEET FOR PROPOSALS TO THE NATIONAL SCIENCE FOUNDATION

FOR CONSIDERATION BY NSF ORGANIZATIONAL UNIT (Indicate the most specific unit known, i.e. program, division, etc.) Division of Biotic Systems & Resources	PROGRAM ANNOUNCEMENT/SOLICITATION NO./CLOSING DATE Long-Term Ecological Research/Feb 1, 1988

SUBMITTING INSTITUTION CODE (if known)	FOR RENEWAL ☒ CONTINUING AWARD ☐ ACCOMPLISHMENT BASED RENEWAL ☐ REQUEST, LIST PREVIOUS AWARD NO.:	IS THIS PROPOSAL BEING SUBMITTED TO ANOTHER FEDERAL AGENCY? Yes____ No X; IF YES, LIST ACRONYM(S)

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

ADDRESS OF ORGANIZATION (INCLUDE ZIP CODE)
1919 University Ave., St. Paul, MN 55104

IS SUBMITTING ORGANIZATION: ☐ For-Profit Organization; ☐ Small Business; ☐ Minority Business; ☐ Woman-Owned Business

TITLE OF PROPOSED PROJECT LTER: Successional Dynamics and Spatial Patterning in Ecosystems at the Prairie-Forest Border

REQUESTED AMOUNT $2,001,773	PROPOSED DURATION 5 Years	DESIRED STARTING DATE January 1, 1989

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

☐ Animal Welfare
☐ Endangered Species
☐ Human Subjects
☐ Marine Mammal Protection
☐ Pollution Control
☐ National Environmental Policy Act
☐ Research Involving Recombinant DNA Molecules
☐ Historical Sites
☐ Interdisciplinary
☐ International Cooperative Activity
☐ Research Opportunity Award
☐ Facilitation Award for Handicapped
☐ Proprietary and Privileged Information

PI/PD DEPARTMENT Ecology & Behavioral Biology	PI/PD ORGANIZATION University of Minnesota	PI/PD PHONE NO. & ELECTRONIC MAIL (612) 625-9922

PI/PD NAME/TITLE	SOCIAL SECURITY NO.*	HIGHEST DEGREE & YEAR	SIGNATURE
G. David Tilman, Professor		Ph.D. 1976	
ADDITIONAL PI/PD (TYPED) Eville Gorham, Regents Professor		Ph.D. 1951	Eville Gorham
ADDITIONAL PI/PD (TYPED) David Grigal, Professor		Ph.D. 1968	
ADDITIONAL PI/PD (TYPED)			
ADDITIONAL PI/PD (TYPED)			

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AUTHORIZED ORGANIZATIONAL REP.	SIGNATURE	DATE	TELEPHONE NO.
NAME/TITLE (TYPED)			
OTHER ENDORSEMENT (optional)			
NAME/TITLE (TYPED) Franklin H. Barnwell, Head	Franklin H Barnwell	1/25/88	(612) 625-4466

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

NSF FORM 1207 (1-87)

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Summary of Results of Previous NSF Support

This is a request for renewal of the Cedar Creek LTER grant (NSF/BSR 8612104; **Succession, Productivity and Dynamics in Temperate Mixed Ecosystems in Minnesota**; $275,000/yr; 1/15/87 to 1/14/89; D. Tilman and D. Grigal, Co-PI's). The goals and achievements of the first 6 years of LTER at Cedar Creek Natural History Area (CCNHA) are summarized below and discussed in relation to future research in the proposal. Publications documenting our achievements are listed at the end of this summary.

Our central goal is to understand the causes of the successional dynamics and spatial structure of CCNHA ecosystems. CCNHA, which is located at the prairie-forest boundary, contains a mosaic of old fields, prairie, oak savanna, oak forest, and wetlands. These landscape elements differ in productivity, herbivory, disturbance history, soil processes, and landscape position. Each of these factors interacts with and covaries with the other factors. To understand the cause of spatial and temporal dynamics, we uncouple these factors through long-term experiments, find how they are linked in nature through long-term observations, and synthesize these data through ecosystem models and general ecological theory. Our work looks at the direct, indirect, and feedback effects of ecosystem elements on each other.

Succession is a universal ecological process, but it is slow. Only long-term observations can adequately describe succession. Only long-term experimentation can unravel paths of causation, and distinguish spurious correlation from causation. At CCNHA, 60 years after cessation of agriculture, fields have neither returned to pre-agricultural nitrogen levels nor re-attained their woody cover. Our highest priority initially was to establish long-term experimental and observational plots in old fields. We now have over 1100 permanent experimental plots, as well as 2300 permanent observational plots distributed among 22 fields in a successional chronosequence. **We are building a systematic, long-term data set that has already proven useful, but that becomes increasingly unique and powerful with each additional year of data.**

Field experiments, each well-replicated within a given field and most repeated in 4 different successional fields, fall into 4 major classes: studies of (1) soil carbon and nitrogen dynamics and controls, (2) primary productivity, (3) herbivory, and (4) disturbance regimes. Studies of **C and N dynamics** include (a) litter-decomposition experiments; (b) effects of nitrogen addition on nitrification and leaching losses; (c) experimental studies of N fixation by soil algae, legumes, free-living soil bacteria, and associative N-fixers; (d) studies of denitrification; (e) studies of microbial biomass, dissolved organic C, and N dynamics; and (f) changes in the composition and structure of the microbial community. **Primary productivity experiments** include (a) addition of nutrients one at a time or in combination to determine which limit production; (b) experimental productivity gradients of natural vegetation within deer and gopher exclosures; and (c) similar experimental productivity gradients with all herbivores present. **Herbivore experiments** include (a) selective removal of herbivore guilds (foliage-feeding insects; xylem- and phloem-feeding insects; below-ground feeding insects; Microtus pennsylvanicus; Geomys bursarius; all herbivores); (b) deer exclosures at the margins of old fields to determine the role of deer herbivory in succession; and (c) comparisons of fenced and unfenced N gradients to determine effects of gophers and deer. **Disturbance experiments** include (a) comparisons of disturbed versus undisturbed plots that receive different N additions; (b) a 24-yr running set of prescribed burns in large blocks of native oak savanna designed to test effects of fire frequency; (c) prescribed burns at various frequencies in a 25-yr old field; and (d) manipulations of water table depth to mimic the potential impact of climate change. Most studies have been done in the same fields in a coordinated manner, so that results of one study are directly relevant to others.

Permanent observational plots are located in a chronosequence formed by 22 old fields of different ages. Within each field we established 100 permanent quadrats (150 in two fields) for repeated, non-destructive sampling of vegetation to species, soils (total N, pH, organic matter, sand silt, clay), and disturbance events. Other quadrats have been sampled for total plant biomass (aboveground and belowground, the former separated to leaves and stems), soil chemistry (total N; pH; dissolved organic C; total organic C; extractable NH_4 and NO_3), microbial biomass, microfungi (identified to species by M. Christensen), mycorrhizal fungi, small mammals (to species), and grasshoppers (to species). This chronosequence has provided a rich description of the changing importance of various processes during succession. By periodic resampling, we will determine the extent to which inferences based on a chronosequence are indicative of the actual pattern of dynamic change during succession.

Our observational studies suggest that N dynamics, light, disturbance history, and herbivory are the major factors influencing successional dynamics and spatial patterning at CCNHA. Low levels of N in newly abandoned fields, and the 100+ years required for soil N levels to return to that of undisturbed savanna, may partially explain the pattern and rate of succession, especially the slow revegetation by woody plants. However, this can not explain the domination of early successional, N-poor fields by annuals and short-lived perennials. Might their dominance be the result of the transient dynamics of competitive displacement? Our experiments have shown that transient dynamics are a general response of ecosystems to perturbation. Are the results that we have observed after 6 years of nutrient addition indicative of the eventual relations between ecosystem structure and productivity? Or are the species that dominate after 6 years also transients to be displaced by other species? We do not yet know how long an experiment must proceed before it is possible to distinguish between transient dynamics and long-term effects. Our models predict that transient dynamics may last for 30 to 40 years in grasslands. If this is so, our experiments may need to proceed for another 25 to 35 years.

Slow increases in soil N and plant biomass during secondary succession at CCNHA suggest that the successional gradient is also a productivity gradient. However, contrary to our initial hypothesis, there are dramatic differences between the correlational patterns observed between ecosystem structure and productivity in successional fields and those observed in native, undisturbed ecosystems. We do not know what causes these differences. Why, for instance, do plants that dominate the poorest soils of secondary succession have root:shoot ratios almost 5 times **lower** than plants that dominate the least productive areas of non-successional ecosystems? Why is Agropyron repens dominant on N poor soils during succession, but on the most N-rich soil in our experimental N gradients? Given the length of time that successional fields remain free of a woody overstory, why do woody plants of N-poor, undisturbed soils, such as Corylus and ericaceous species, not come to dominate the old fields? In other words, why is species composition along the successional productivity gradient so different from that along a non-successional productivity gradient, though both have similar physiognomic characteristics? We shall address these questions by continuing our existing research and by expanding it to include studies of productivity gradients in additional post-successional habitats.

Our work has demonstrated the power of combining observational, experimental, and theoretical approaches, and the need for long-term studies. It has led us to formulate a series of general theoretical predictions that we now wish to test not only at CCNHA, but also by performing comparisons across the North American productivity gradient represented by the LTER network. CCNHA is an important member of this network because it is the only LTER site on the prairie-forest boundary. This boundary between herbaceous and woody species is a major transition point for North American biomes, and is similar to the transition from herbaceous to woody vegetation that occurs during succession at CCNHA.

Publications of the Cedar Creek LTER (1982-1988)

Book

1. Tilman D. 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities.* Monographs in Population Biology, Princeton University Press, in press. (Includes a 61 page chapter on Cedar Creek LTER, and new theory relevant to Cedar Creek and cross-site comparisons.)

Published Papers

2. Goldburg, R.J. 1987. Sequential flowering of neighboring goldenrods and the movements of the flower predator *Epicauta pennsylvanica*. Oecologia 72:in press.

3. Huntly, N.J. and R.S. Inouye. 1987. Small mammal populations of an old-field chronosequence: successional patterns and associations with vegetation. Journal of Mammalogy 68: 739-745.

4. Huntly, N. J. and R. S. Inouye. 1988. Effects of gophers (*Geomys bursarius*) on ecosystems. BioScience, in press.

5. Inouye, R.S., N.J. Huntly and D. Tilman. 1987. Response of *Microtus pennsylvanicus* to fertilization with various nutrients, with particular emphasis on sodium and nitrogen concentration in plant tissues. Holarctic Ecology, 10:110-113.

6. Inouye, R.S., N.J. Huntly, D. Tilman, J.R. Tester, M. Stillwell and K.C. Zinnel. 1987. Old field succession on a Minnesota sandplain. Ecology 68: 12-26.

7. Inouye, R.S., N.J. Huntly, D. Tilman, and J.R. Tester. 1987. Pocket gophers, vegetation and soil nitrogen along a succession sere in east central Minnesota. Oecologia 72:178-184.

8. Inouye, R.S. and D. Tilman. 1988. Convergence and divergence along experimental nutrient gradients. Ecology, in press.

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

10. McKone, M.J. and D.D. Biesboer. 1986. Nitrogen fixation in association with the roots of goldenrods (*Solidago* L.). Soil Biology and Biochemistry 18:543-545.

11. McKone, M.J. and D. Tonkyn. 1986. Intrapopulation gender variation in common ragweed (*Ambrosia artemisiifolia*), a monoecious annual herb. Oecologia 70:63-67.

12. Palmer, M. W. 1987. Variability in species richness within Minnesota oldfields: A use of the variance test. Vegetatio 70: 61-64.

13. Pastor, J., M.A. Stillwell, and D. Tilman. 1987. Nitrogen mineralization and nitrification in Minnesota old fields. Oecologia 71:481-485.

14. Pastor, J., M.A. Stillwell, and D. Tilman. 1987. Little bluestems litter dynamics

in Minnesota old fields. Oecologia 72:327-330.

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

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

17. Strauss, S. 1987. Direct and indirect effects of host plant fertilization on an insect herbivore community. Ecology 68: 1670-1678.

18. Tester, J.R. 1986. Seasonal changes in activity rhythms of some free-ranging animals. Canadian Field Naturalist 101: 13-21.

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

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

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

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

23. Tilman, D. 1986. A consumer-resource approach to community structure. American Zoologist 26:5-22.

24. Tilman, D. 1986. Nitrogen-limited growth in plants from different successional stages. Ecology 67:555-563.

25. Tilman, D. 1986. Resources, competition and the dynamics of plant communities. Pages 51-75. In M. Crawley, ed., Plant Ecology. Blackwell Scientific Publications, Oxford.

26. Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecological Monographs 57: 189-214.

27. Tilman, D. 1987. Further thoughts on competition for essential resources. Theoretical Population Biology, in press.

28. Tilman, D. 1987. The importance of mechanisms of interspecific interaction. American Naturalist 129:769-774.

29. Tilman, D. 1987. On the meaning of competition and the mechanisms of competitive-superiority. Functional Ecology 1: in press.

30. Tilman, D. 1988. Ecological Experimentation: strengths and conceptual problems. To appear in Long-Term Studies in Ecology: Approaches and Alternatives, G.E. Likens, Editor (Proceeding of the Cary Conference of the same title).

31. Tilman, D., R. Kiesling, R. Sterner, S. Kilham, and F. Johnson. 1986. Green, bluegreen and diatom algae: taxonomic differences in competition ability for P,

Si, and N. Archiv fur Hydrobiologie 106:473-485.

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

Theses

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

34. Cowan, M.L. 1986. Growth responses of old-field plants to a nitrogen gradient. M.S. Thesis, University of Minnesota.

34. Goldburg, R. 1986. Goldenrod, grasshoppers, and the distribution of Epicauta pennsylvanica (Coleoptera:Meloidae). Ph.D. Thesis, University of Minnesota.

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

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

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

Manuscripts in Review in Major Refereed Journals

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

40. Grover, J.P. The dynamics of phytoplankton competition in a variable environment. Ecology, in press.

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

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

43. Sterner, R.W. Experimental studies of phytoplankton succession.

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

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

Manuscripts in Preparation

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

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

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

48. Gleeson, S. and D. Tilman. A re-evaluation of the equal limitation hypothesis.

49. Gleeson, S. and D. Tilman. Patterns of allocation to roots, leaves and stems during secondary succession.

50. Gleeson, S. and D. Tilman. Allocation, competition, and the dynamics of secondary succession.

51. Grace, J. and D. Tilman, Editors. Perspective on Plant Competition. (Proceedings of a University sponsored symposium of the same title held at Cedar Creek, October, 1987.)

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

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

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

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

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

57. Huntly, N.J., and R.S. Inouye. The dynamics of grasshoppers during old field succession.

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

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

60. McKane, R. and D. Tilman. Neighborhood competition for nitrogen among prairie plant species.

61. Norland, M. and D. Grigal. The cations exchange capacity of roots of some old field successional plant species.

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

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

64. Norland, M., B. McKane and D. Grigal. Interactions among nitrogen, water, and primary production in an old field chronosequence.

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

66. Tilman, D., and M.L. Cowan. Nitrogen-dependent growth and allocation in successional plants.

67. Tilman, D. Transient dynamics and the interpretation of field experiments.

68. Tilman, D. Disturbance frequency and nitrogen availability in old fields.

69. Tester, J. and D. Tilman. Effects of fire frequency and nitrogen on the species composition of an oak savanna grassland.

70. Zak, D., D. Grigal and D. Tilman. Patterns of C and N cycling during secondary succession: constraints limiting plant and microbial.

71. Zak, D., D. Grigal and D. Tilman. Spatial and temporal dynamics of nitrogen cycling in a forest-prairie landscape.

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

SUCCESSIONAL DYNAMICS AND SPATIAL PATTERNING IN ECOSYSTEMS AT THE PRAIRIE-FOREST BORDER

I. INTRODUCTION

Ecology deals with the causes of patterns in nature. The simplicity of this definition belies the complexity that ecologists face. The ecological world is a multi-causal system in which patterns arise from direct effects of physical factors, from biotic interactions, and from feedbacks of one species or system element on another. Some effects cascade from the top of the trophic chain downward (e.g., Carpenter, Kitchell and Hodgson 1985; Carpenter et al. 1988). Others come from the bottom and move upward (e.g., Tilman 1977, 1982). Still others start in the middle and move both up and down.

Despite the complexity of causality in natural systems, some general patterns are common to most ecosystems. Two of these patterns -- dynamics of succession and changes in ecosystem structure along productivity gradients -- have been major themes in American ecology for the 8 decades since the pioneering work of Cowles (1899), Cooper (1913) and Clements (1916). MacMahon (1981; p. 277) reviewed this work and concluded "there is a surprising degree of pattern to the successional processes in various parts of the world." What causes different ecosystems to have similar successional patterns? Similarly, on a wide range of spatial scales, ecosystems with different species compositions and evolutionary pasts have qualitatively similar properties along productivity gradients (Whittaker 1975). On global and regional scales in temperate, tropical, and mediterranean biomes, the life history, morphology, physiology, diversity, tissue chemistry, and nutrient cycling characteristics of primary producers change in similar ways along productivity gradients (e.g., Beard 1944, 1955, 1983, Whittaker 1975, Mooney 1977, Cody and Mooney 1978, Vitousek et al. 1982, Tilman 1982, 1988a, Flanagan and Van Cleve 1983). Qualitatively similar patterns are repeated on virtually every other spatial scale, from within-biome differences caused by soil parent materials, to soil catenas within landscapes, to small-scale heterogeneity within fields. What factors cause these similar ecosystem behaviors across this range of scales? At Cedar Creek Natural History Area

(CCNHA), we are using long-term observations and experiments, and a variety of models, to address these questions. The major theme of our work is the cause of temporal (successional) and spatial patterns, both with the ecosystem of Cedar Creek, and across the biomes of North America.

We believe that we must understand the causes of broad, general patterns, such as successional dynamics and spatial patterning along productivity gradients, if we are to put other patterns in perspective. Broad, general, and repeatable patterns are likely to result from a common set of environmental constraints and organismal tradeoffs (Tilman 1986, 1988a, Huston and Smith 1987). The major environmental constraints to organisms come from the ecosystem-level processes of energy flow and nutrient cycling. The organismal tradeoffs come from the "jack of all trades, master of none" principle: an organism with a morphology, physiology, and/or life history to overcome one type of environmental constraint cannot have an alternative morphology, physiology, and/or life history helpful in overcoming other constraints. For plants, major tradeoffs come from carbon allocation to leaves, stems, roots, and seeds and from protein (nitrogen) allocation to different physiological systems and defensive compounds (Tilman 1988a). Decomposers, herbivores, and carnivores face similar tradeoffs. These allocation tradeoffs in turn affect ecosystem processes through the types, amounts, placement, and phenology of litter return and nutrient uptake. A premise of our approach is that the spatial and temporal patterns of ecosystems arise, in part, from the interactions between the constraints imposed by ecosystem processes and the tradeoffs that organisms face in dealing with these constraints.

At one level, plant community dynamics might be explained as resulting from the constraints of the inverse relation between the supply of a limiting soil resource and light, and the allocation-based tradeoffs plants have to these resources (Pastor et al. 1982, 1984, Tilman 1982, 1985, 1987, 1988a, Huston and Smith 1987). We hypothesize that this constraint arises partly from a positive feedback between vegetation and soil through litter decay and plant uptake, which is in turn bounded by negative feedbacks between plant biomass and light extinction, mineral N concentration and leaching loss, and the constraints of temperature and soil water availability (Pastor and Post 1986, Tilman 1985, 1987, 1988a, DeAngelis et al. 1986). Herbivory, fire, and other disturbances alter these feedbacks, form additional feedback loops, and modify the ecosystem constraints. Furthermore, our understanding of the nature of these feedbacks and constraints depends on the temporal and spatial scales over which they are measured. For example, at microsite and annual scales, soil nutrient availability constrains plant growth and competition, but over decadal and landscape scales, there is a litter return, decomposition and nutrient release feedback loop. The interactions among feedbacks and constraints and the different temporal and spatial scales over which they work are predicted by theory to produce complex ecosystem dynamics that can only be demonstrated through long-term experiments and observations and explained through the rigorous distillation of hypotheses into dynamic ecosystem models.

Most ecological research - both observational and experimental - has been short term (Fig. 1). The "observational" studies shown in Figure 1A as being longer than 50 years are not based on direct observation, but are reconstructions from chronosequences or paleoecological records (Tilman 1988b). Fewer than 7% of field experiments have lasted even 5 years (Fig. 1B). However, many short-term experiments have produced statistically significant results that often have been interpreted as the long-term equilibrial effect of the treatments. In striking contrast, the CCNHA LTER experiments have demonstrated that the "result" of an experimental manipulation is a succession of peaks of transient dominance by various species, which in turn affect and are affected by ecosystem properties (Tilman 1988). The immediate effect of our manipulations has often been the opposite of that observed after 6 years (Fig. 2; Tilman 1987a, 1988a, 1988b). Several theories suggest that such transient dynamics should be general features of complex systems (e.g., DeAngelis et al. 1986, Tilman 1985, 1988a). If this is true, short-term experiments must be interpreted as having transient dynamics that can be the exact

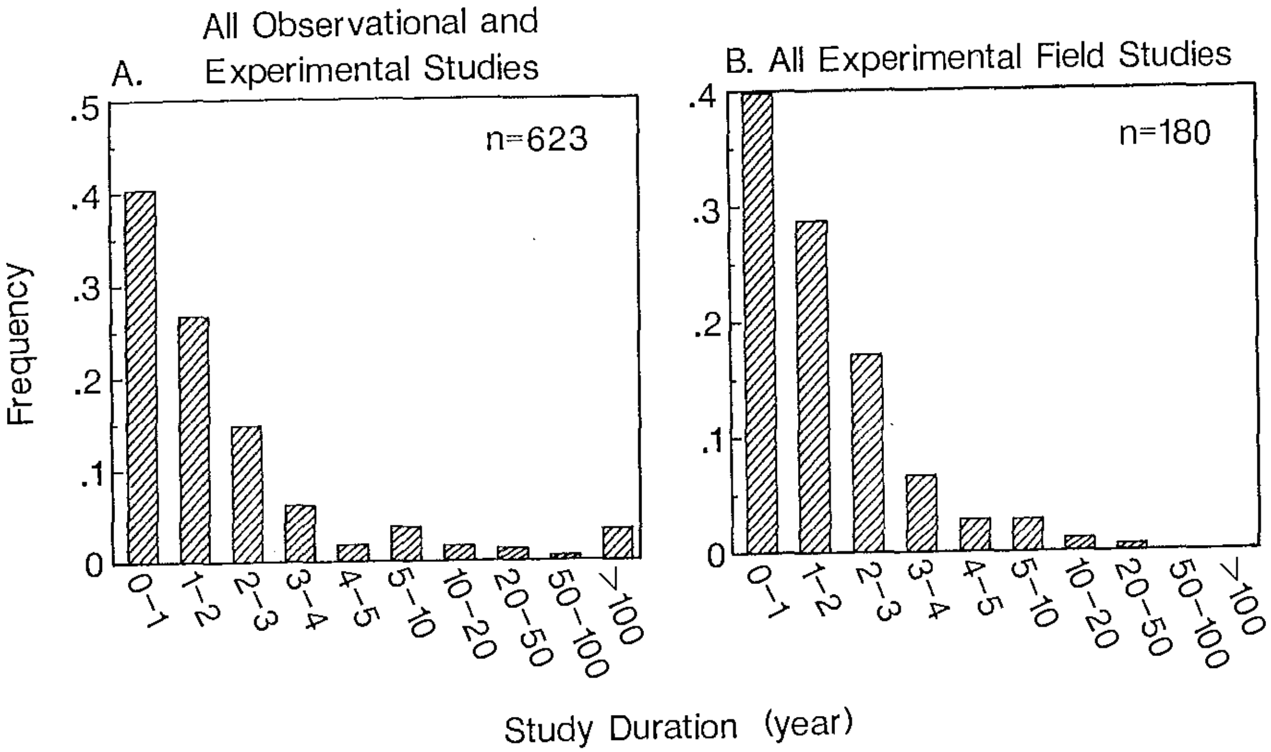

Figure 1. In order to estimate the average durations of ecological research projects, issues of Ecology published during 1977 - 1987 were randomly selected, and all papers in each issue were classified as to the type of study and its duration. A total of 749 papers were included in the sample.

A. Of these 749 papers, 623 were based mainly on field observations or field experiments. The histograms show the proportion of these 623 papers that reported a data record with a duration of less than one year (study duration of 0 - 1), from 1 up to, but not including, 2 years, etc. The data shown are based on the actual or inferred duration of a study. Studies based on chronosequences and paleoecological reconstructions were assigned a duration equal to the length of the chronosequence or of the paleoecological record. Most studies shown as longer than 10 years, and all studies shown as longer than 50 years, were based not on direct observation, but on chronosequences or paleoecology. Note that 80% of all studies in this sample had a duration of 3 field seasons or less.

B. Of the 623 studies, 180 reported results of field experiments. Long-term field experiments are rare, with 85% of field experiments lasting less than 3 years. Phenomena that occur on longer time scales, such as succession and various ecosystem feedback effects, cannot be understood until they are addressed with observational and experimental studies that are sufficiently long to encompass the underlying processes and responses.

(from Tilman 1988b)

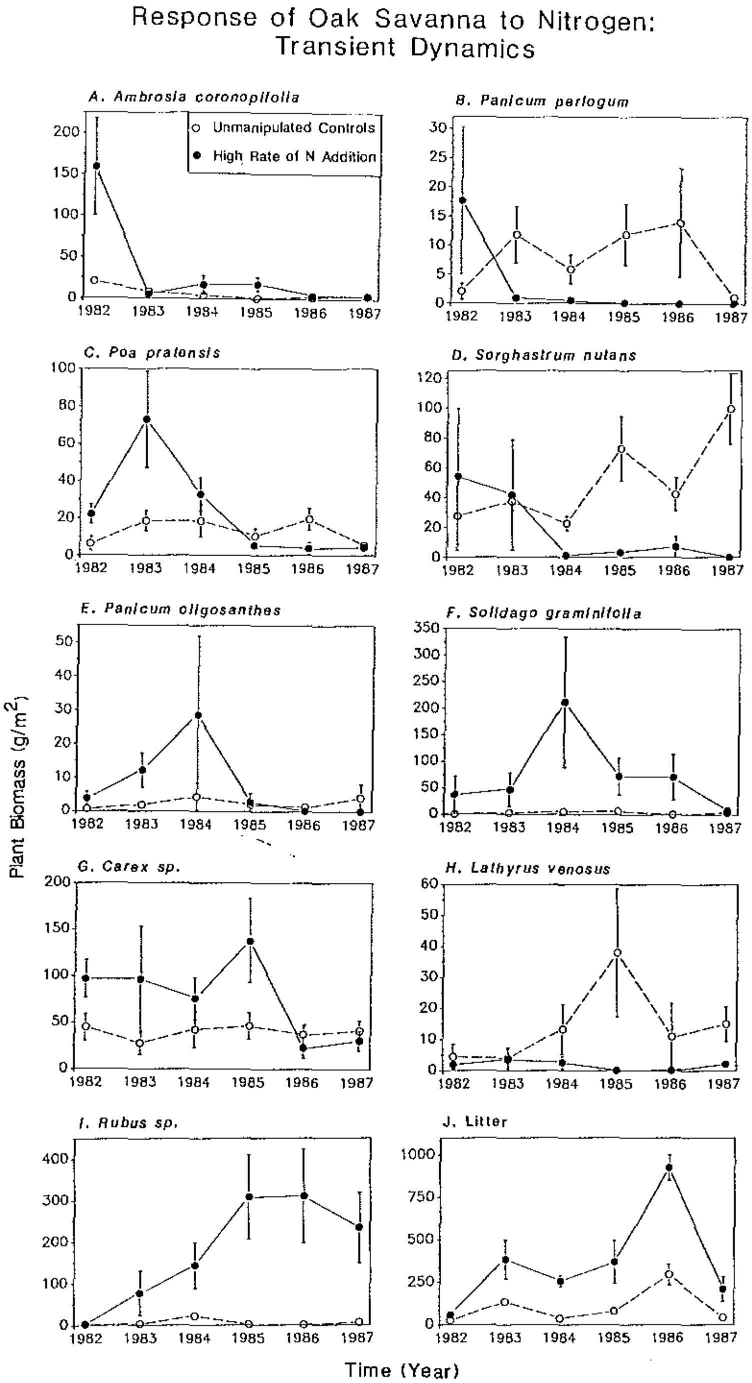

Figure 2. Transient responses to N addition. The mean (as an open circle or solid dot) and the standard error (as vertical bars) of a species' abundance in unmanipulated control plots (open circles, broken lines) or in plots with a high rate of nitrogen addition (solid dots, solid lines) in Field D, a prairie opening in native oak savanna (Tilman 1987a, 1988a). Some species (e.g., *Ambrosia*) responded significantly to N addition the first year, but not later. Others responded significantly the 2nd or 3rd year (*Poa*, *Solidago*), but not later. Others (*Rubus*) did not respond initially, but did for the next 5 years. This experiment shows that the qualitative nature of significant treatment effects can change from year to year, giving an "outcome" that is time dependent.

opposite of their long-term outcome. Therefore, if we are to understand the causes of ecosystem patterns, it is imperative that experiments be allowed to proceed for a sufficiently long time to be correctly interpreted. This, unfortunately, has not often been the case in ecology, a situation that the LTER program is designed to correct.

CCNHA is a mosaic of landscape elements that differ in their disturbance history, their productivity, and their landscape position. Almost 40% of CCNHA's 2185 hectares are now undergoing secondary succession after abandonment from agriculture. A series of 78 old fields of documented past history, ranging from newly abandoned to 61 years old, are available for comparative and experimental research. Because most of the remaining 60% of CCNHA has never been farmed or clearcut, it provides excellent sites for observational and experimental studies of patterns of variation in non-successional ecosystems.

There are two striking features of succession at CCNHA. First, secondary succession yields a temporal productivity gradient. When we began our research, we hypothesized that species would separate out in the same order along this temporal gradient as they do along spatial or experimental productivity gradients (Tilman 1982, 1985). However, our results have refuted this hypothesis (Tilman 1988a; compare Figs. 4 and 8). Why don't species occur in the same order along successional productivity gradients as along experimental productivity gradients? How does the superposition of these two types of productivity gradients cause the spatial patterning of the CCNHA landscape? Second, although open canopied oak forest is common in post-successional vegetation at CCNHA (without frequent fires), it has never established in forest-surrounded fields as old as 60 years. Why is succession so slow? Why, after 60 years, have old fields become prairie, not oak savanna? What determines whether herbaceous or woody species will become dominant - i.e., what causes prairie versus savanna or forest? Have disturbances such as fire or farming altered soils so that trees can no longer grow on old fields, even in the absence of fire, or can herbaceous vegetation prevent successful invasion of woody plants, or does herbivory prevent woody plant establishment? Does the answer depend on the scale and intensity of disturbance? What are the consequences at the ecosystem level?

At CCNHA and elsewhere, disturbance, productivity, herbivory, nutrient dynamics, and landscape position covary, and their separation is difficult. The interactions among these elements may propagate through both population and ecosystem levels, resulting in various patterns across the landscape and through time. Within CCNHA old fields, more productive areas are more likely to be grazed or browsed by deer, grasshoppers, and gophers and to burn more frequently, and fertile soils are more likely to be disturbed by gophers or farmed by settlers. However, frequent disturbances decrease soil fertility and thus act as a negative feedback on the increase in soil fertility we find during old field succession. Just as all of CCNHA is a mosaic, so are individual fields and forests, for soils are spatially heterogeneous in fertility and disturbance history. Some of the heterogeneity results from landscape position as materials are moved downslope, but a great deal is still unexplained. In order to understand the causes of spatial and temporal patterning at CCNHA and elsewhere, it is necessary to consider the direct and indirect effects and interactions of landscape position, disturbance, productivity, herbivory and nutrient cycling on several spatial and temporal scales. To do this, we have established experimental manipulations, because only experiments can separate causation from spurious correlation. We have also established long-term observations to document the natural correlational relationships among these variables.

The temporal patterns of CCNHA ecosystems are mainly successional, for most result from disturbance. The disturbance could be global, such as climate change, regional, such as farming or fire, or local, such as treefall gaps or gopher mounds. Whatever the source of a disturbance, it is likely to have a long-term effect on the dynamics and structure of the area disturbed. The spatial patterns of ecosystems have two main components: one from the successional status of a site and one from its productivity and landscape position. At CCNHA, as in many other habitats, productivity and landscape position are linked. The linkage, though, may be tighter at CCNHA than elsewhere because of the uniformity of parent materials from which the soils have developed.

Successional dynamics and spatial patterning both result from interactions among evolutionary and population processes (e.g., life history differentiation, competition, herbivory, colonization), ecosystem processes (nutrient cycling, accumulation, and downslope movement), top-down and feedback effects of plants and herbivores on soils, and bottom-up effects of soils on plants and herbivores. Thus, an understanding of temporal and spatial patterns requires a synthesis of causal mechanisms at population, community, and ecosystem levels, heretofore disparately considered by most ecologists. Furthermore, a study of temporal and spatial patterning at CCNHA meshes well with the five core areas for the LTER Program, since these patterns involve disturbances as well as changes in productivity, in the spatial and temporal distributions of plant and animal populations, in soil organic matter, and in nutrient pools and cycles.

These, then, are the premises, themes and questions that guide the CCNHA LTER project. Our research focuses on soil processes, primary producers, herbivores, and disturbances. We are interested in the details of each of these, but even more interested in the indirect effects and feedbacks of each of these elements on the others. Because of the greater rapidity of change in recently disturbed areas than in non-disturbed areas, we began our LTER work focusing on successional dynamics, especially in our diverse array of abandoned fields. The long-term experimental and observational studies we established have been fruitful and hold the promise of significant insights in the future. However, we now need to expand our work into a broader cross-section of the native, post-successional ecosystems that constitute a majority of the CCNHA landscape, including oak savanna, old growth oak, sugar maple, and white pine upland forests, and lowland black ash swamp and cedar fen. These post-successional areas differ in productivity and fall at different points along an elevational gradient with respect to the regional water table. They represent a gradient of constraints and endpoints to succession, and thus complement our studies of successional dynamics and spatial structure at CCNHA.

Our work has advanced to the stage where it is critical to compare our results with those generated at other LTER sites. Such cross-site comparisons and syntheses provide alternative tests of our findings, increase the breadth of environments to which they may apply, and determine the generality of the ecosystem constraints and organismal tradeoffs studied at CCNHA. CCNHA is ideally situated within the LTER network and the biomes of North America for such a synthetic approach. It lies within the transition zone between the grassland biomes to the west and the forest biomes to the east and north (Fig. 3). It is the only LTER site at this climatic transition zone between herbaceous and woody life forms. Moreover, 7 sites within the LTER network span the North American trans-biome productivity (moisture) gradient described by Whittaker (1975): Jornada (desert); CPER (shortgrass prairie); Konza (tallgrass prairie); Cedar Creek (oak savanna); Kellogg (oak forests); Hubbard Brook (northern hardwoods); and Coweeta (cove forests). We will use data collected along this trans-biome gradient for cross-site comparisons and syntheses that are directly relevant to the main focus of the CCNHA LTER project, including our studies of the successional transition from herbaceous to woody species at CCNHA (p. 48).

CCNHA makes unique and important contributions to the LTER network not only through our highly experimental approach, our location at a major biome transition, and our cross-biome comparisons, but also because we attempt to synthesize disparate approaches to ecological research. During the last 20 years, advances in understanding of primary production, population growth, competition, evolutionary ecology, optimal foraging, energy flow, and nutrient cycles have been gained by ignoring or greatly simplifying higher or lower level phenomena. One portion of an ecosystem has been studied in great depth while other portions impinging on it have been treated as constant or have been ignored. We believe that major advances in ecological understanding will now come from a synthesis of the principles, processes, and mechanisms of population and community ecology into the framework of the entire ecosystem. However, this synthesis requires coordinated, simultaneous, long-term experimental and observational studies of major processes on all these levels. Our studies of the mechanisms of interspecific interactions and feedbacks of various species on each other and on ecosystem processes is contributing to this synthesis. By performing our research in a balanced manner across the disciplines of population, community, and ecosystem ecology, and by encouraging communication and cooperation within our group and among LTER sites, we are adding this element of cross-disciplinary synthesis to the LTER network.

The CCNHA LTER project is designed to determine the causes of successional dynamics and spatial patterning in CCNHA ecosystems. We have already gathered a rich data set that describes the interrelations among soil processes, primary producers, herbivores and disturbance in old fields and oak savanna. We have established long-term observational and experimental studies in these habitats that will become increasingly powerful with each additional year of data. We now wish to continue our present, on-going research and expand it to encompass a broader range of the ecosystem types within CCNHA. It is especially important that we add studies of "post-successional" areas within CCNHA, for these can help us elucidate the causes of the spatial patterning we observe, as well as provide us with the endpoints of the successional process at CCNHA.

II. RESEARCH PLAN

Our plan for the next five years is (1) to continue our experimental and observational studies in successional fields and oak savanna, (2) to establish new long-term experiments and observational studies in post-successional habitats, (3) to add research in ecosystem modelling, and (4) to perform cross-site comparisons and syntheses. These activities are interdependent, each providing data and insights useful to the other. Our studies in post-successional habitats, for instance, will establish the relationships between ecosystem type and environmental constraints, including productivity, at CCNHA. Our comparisons across North American biomes will explore these same relationships on a much broader spatial scale. Both of these provide important comparisons with our studies of the factors controlling the transition from herbaceous to woody vegetation during succession and from prairie to oak savanna to forest in non-successional ecosystems. Our Research Plan has five categories: A. Long-Term Observations;

B. Long-Term Experiments; C. Ecosystem Models; D. Cross-Site Syntheses; and E. the Five Core Topics. The Five Core Topics form an important focus and a source of breadth for our work. They are imbedded in the discussion that follows and summarized in section E.

A. LONG-TERM OBSERVATIONAL RESEARCH AT CCNHA

Long-term observational data sets are rare in ecology (Figure 1) but of central importance (e.g., Franklin 1988). Only such data can document the dynamic nature of population, community, and ecosystem processes and parameters. Static views can give misleading pictures of interactions among the parts of ecosystems. We have established a set of permanent, unmanipulated, long-term observational plots in a successional chronosequence, and will establish similar plots in the major post-successional types of CCNHA. The latter areas occur along a spatial gradient from upland to lowland. For both the successional gradient and the post-successional ecosystems, observational data cover the five core LTER topics and address the specific hypotheses that guide our project. The other component of our long-term observational work comes from regular measurements of chemical and physical environmental variables at CCNHA.

1. Observations in the old-field successional chronosequence

At the time of European settlement in the 1880's, upland areas of CCNHA were a mosaic of oak savanna and prairie, with scattered stands of jack pine, white pine or sugar maple. By 1910, about 40% of CCNHA had been clearcut and cultivated (Pierce 1954). The well-sorted, extremely well-drained fine sands of CCNHA were initially low in nitrogen, and were easily depleted by cropping practices. By the late 1920's farmers began abandoning fields and secondary succession began under conditions of significant nitrogen limitation. Seventy-eight fields of known past history (Pierce 1954), ranging in size from 2 to more than 40 ha, have been abandoned on land that is now CCNHA. Additional fields are still farmed, and will be abandoned over the next 50 years. These fields are a valuable resource for studies of succession.

After preliminary sampling in 1982, we selected 22 fields, based on soil parent material, topography and age, to form a successional chronosequence. Of these, 18 are reserved for observations that impose minimal disturbance; portions of 4 additional fields (A B, C, and E) are used for experimentation. In all 22 fields, soils and vegetation (Inouye, et al. 1987b, Tilman 1987a, 1988a), rates of nutrient loss (via 10 lysimeters per field), gopher mounds and disturbance (Inouye et al. 1987a), small mammals (Huntly and Inouye 1987) and foliage-feeding insects (Huntly and Inouye 1988b) will be monitored annually in permanent plots. We will also install a piezometer (sandpoint well) in each old field for monitoring depth to water table each month. This will determine where each field falls on an elevational gradient from lowlands to uplands (p. 19). In addition, areas within each field have been designated for periodic small-scale destructive sampling (e.g. above- and below-ground plant biomass). All plots were established such that sampling of one would have minimal impact on the others.

Soils and Life Forms: Sampling has revealed a rich array of statistically significant, interrelated successional patterns. Total soil N and mineral N (KCl-extractable NH_4 and NO_3) increased significantly with field age (Fig. 4A, 4B). Leaching loss of N is low throughout succession. N mineralization increased steadily with field age, but the relative rate of N mineralization per gram of total N decreased with field age, suggesting a decline in organic matter quality (Pastor et al. 1987b). Cover by annual plants (Fig. 4C) decreased, but perennial plants (Fig. 4D) and litter increased with soil N and age. Total plant biomass (**belowground** plus **aboveground**) increased with field age (Fig. 4G). Unlike other successions, this was not caused by increased stem biomass (Fig. 4J), but by increases in root biomass (Fig. 4I) and leaf biomass (Fig. 4H). Root biomass increased more rapidly than did leaf biomass, causing root:shoot ratios to increase with field age (Fig. 4K). Woody plants (Fig. 4F) increased with age and N but, despite their abundance in nearby uncut forests, were less than 15% of vegetative cover in the 60-yr fields. We are now performing experimental work and collecting additional observational data to test various hypotheses that may explain these patterns.

Species Richness: Total species richness (Fig. 4L), and quadrat-to-quadrat heterogeneity in species composition within a field, increased with field age. In contrast, species richness of individual quadrats **decreased** with increasing soil N. Species richness per quadrat also decreased following experimental N addition (Tilman 1987a). Thus, the greater species richness of older fields was not caused by an increased number of species within individual quadrats, but by increased quadrat-to-quadrat soil heterogeneity within older fields, probably related to gopher mounds. Even though gopher mounds, the major source of disturbance, are more common in younger fields, they have a greater effect on soil heterogeneity in older fields (Inouye, et al. 1987a) because gophers deposit subsurface soil low in N upon N enriched surface horizons.

Species Responses: Most common plant species separate clearly along the chronosequence (Tilman 1988a; Fig. 5), and in relation to total soil N (Tilman 1987a; Fig. 6). Comparison of Figure 5 and 6 reveals that many early successional species (*Ambrosia artemisiifolia*, *Agrostis scabra*, and *Crepis tectorum*) reach peak abundance at low soil N (<400 mg/kg). Similarly, many late successional species (*Schizachyrium scoparium*, *Sorghastrum nutans*, *Rubus* sp. and *Artemisia ludoviciana*) reach peak abundance at high soil N within individual fields and for all fields combined. Some species, however, have patterns inconsistent with this generalization. Our future experimental and observational work is designed to determine the causes of such patterns.

Herbivores: We are observing dramatic changes in herbivore and carnivore densities in the 18 minimally disturbed old fields. *Microtus pennsylvanicus*, an herbivore, was extremely rare in all old fields in 1983, increased almost 100-fold by 1986, and declined 4-fold in 1987 (Fig. 7A). *Peromyscus leucopus* was fairly stable from 1983 to 1985, increased 4-fold in 1987, and declined 50% in 1987 (Fig. 7B). The insectivorous shrew, *Sorex cinereus*, increased during this period (Fig. 7C). As mammalian herbivores were increasing, grasshoppers were decreasing, with densities in 1987 less than 1/10 of 1984 (Fig. 7D). Year-to-year changes in grasshopper and small mammal densities occurred simultaneously in all 18 fields, independent of successional age. We have a longer-term record for deer densities in the CCNHA region (Fig. 7E), which increased almost 10-fold in

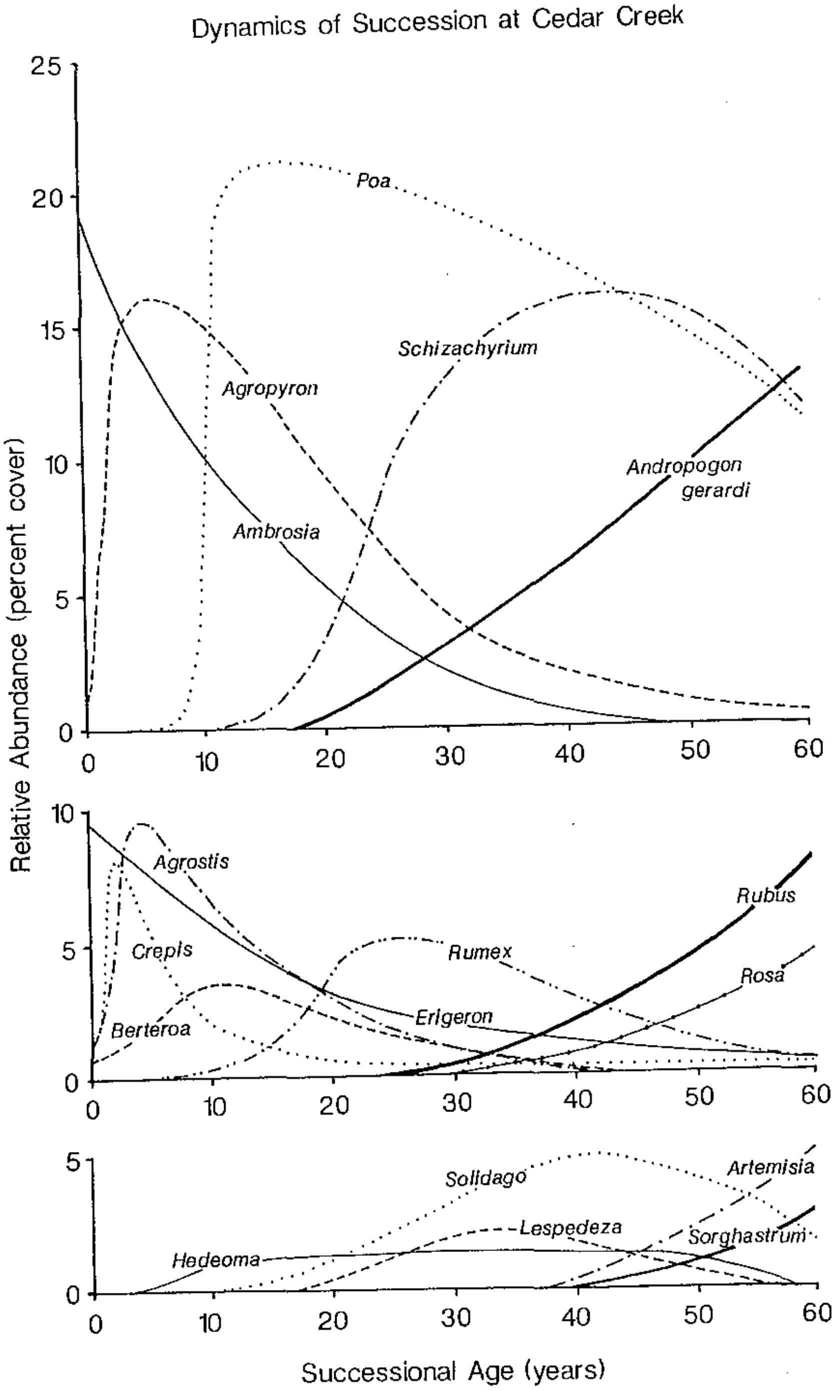

Figure 5. Dynamics of old field succession at CCNHA. In our survey of the successional chronosequence, we recorded the percent cover of all species within a total of 2300 permanent quadrats. (There are 100 quadrats per field in 20 fields, and 150 quadrats per field in 2 fields). Similarly, we have 40 permanent quadrats per successional field in each of the 11 sequentially abandoned 20 x 100 m plots of the "Lawrence Successional Plots" at CCNHA. For most of these, we have estimates of plant abundance in each quadrat each year since abandonment. We calculated the average abundance per field or successional plot for each species, and used these to infer the successional dynamics of the common species. Thus, the figure above is based on a total of 33 fields or plots of known successional age. Figure from Tilman (1988a).

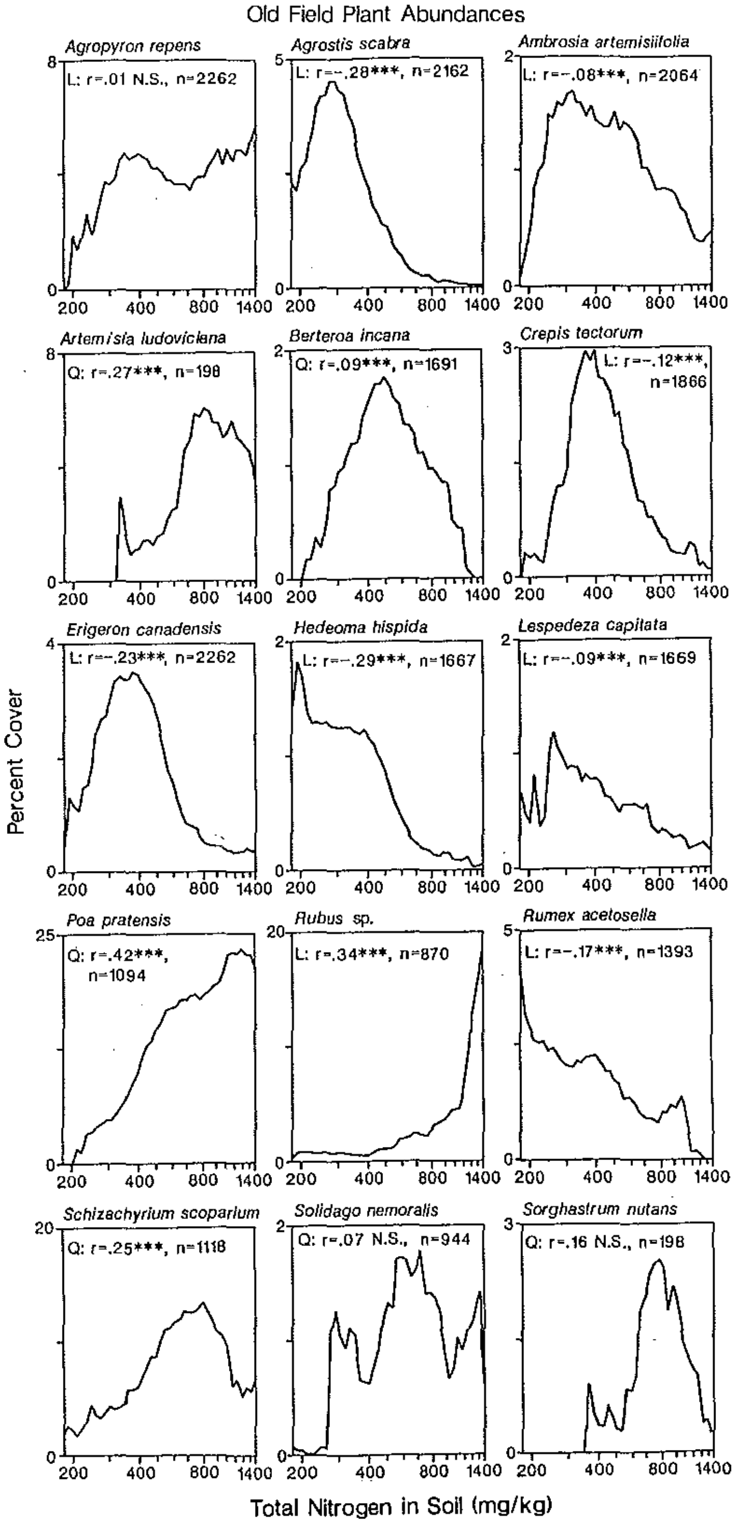

Figure 6. Each part of this figure shows the dependence of the percent cover of a common successional species on total soil nitrogen. The curves shown are histograms of percent cover versus total soil nitrogen, on a quadrat-by-quadrat basis, using all quadrats in all fields in which a species occurred. Data are from our survey of 2300 permanent quadrats in 22 old fields. Actual data (not histograms) were fit with both linear (L) and quadratic (Q) models. The best fit, and its correlation coefficient (r) are indicated, as well as the number of data points (n). Figure from Tilman (1987a).

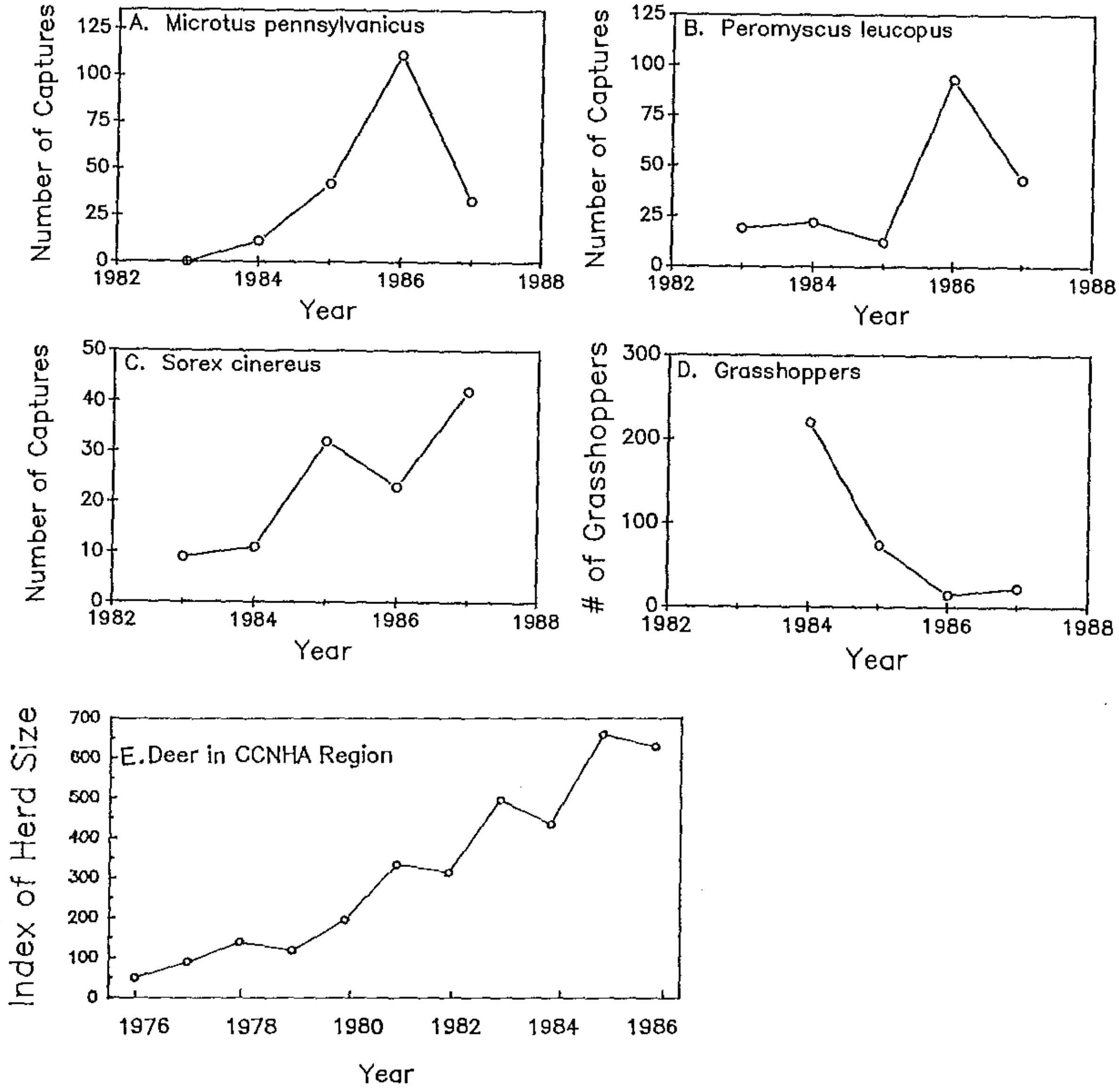

Figure 7. Herbivore population dynamics at CCNHA.

A. Microtus pennsylvanicus, a vole, can be a major herbivore in CCNHA old fields, but has dramatic changes in its densities from year to year. Each point shown is an average based on trapping data from 18 old fields each year.

B. Peromyscus leucopus is a seed-eating mouse that also displays great changes in its density, based on annual trapping data from 18 old fields.

C. Sorex cinereus, an insectivore, has also has large changes in its density in these 18 fields.

D. Grasshoppers are the major insect herbivore at CCNHA. Based on monthly sampling of grasshopper densities, identified to species, in these 18 old fields, grasshopper densities declined significantly while small mammal densities increased.

E. White-tailed deer are common at CCNHA, especially during winter, when they yard in the white cedar swamps, and feed on woody plants. They disperse from CCNHA during the summer. The Minnesota Department of Natural Resources performs annual surveys for the CCNHA region, including winter counts from helicopters. The DNR data provide an index of deer densities. This index shows a rapid increase in deer density since 1976.

the past decade, apparently caused by changes in hunting regulations. However, as yet, we have no explanation for small mammal or grasshopper dynamics. Our further observational work, and experiments, will address this question.

Because sampling in 1982 and 1983 showed that vegetation change in old fields was quite slow, we decided that resources would be best spent if we resampled the 22 old fields only every 5 to 7 years. However, we established permanent plots for annual sampling of plant species biomass in 3 old fields and in oak savanna. These reveal more dynamic change than expected (Fig. 8) and surprising differences among fields. We thought old fields would have slow, long-term successional trends on which would be superimposed effects of climatic variation, but that savanna would show only climatic effects. However, some of the greatest changes are occurring in savanna. These results raise numerous questions. If climate is responsible for some of this variation, why did grasses peak in one field in the same year that they were near their lowest level in another? Why are grasses and forbs negatively correlated in some fields, but not others? What role might herbivores such as grasshoppers and voles play in causing these dynamics? Could herbivores, which have synchronous increases and decreases in all fields, cause such divergent patterns? Could these changes, in turn, cause small mammal cycles?

We will not answer these questions until we have a longer-term record from a larger set of fields. Starting next field season (1988) we will expand annual vegetation sampling to include all 22 old fields and sample vegetation in 12 permanent quadrats per field, using methods described by Inouye et al. (1987b). This will allow us to relate dynamics of herbivore species in each field to dynamics of plant species in the same field. These long-term observational data, in combination with experiments described later will provide a detailed record from which to infer potential causes of these patterns.

The old field chronosequence has provided strong correlations, but these need not indicate causation. Is the apparent increase in total and mineralized soil N really an increase of N through time, or were fields abandoned 50 years ago different in N-status

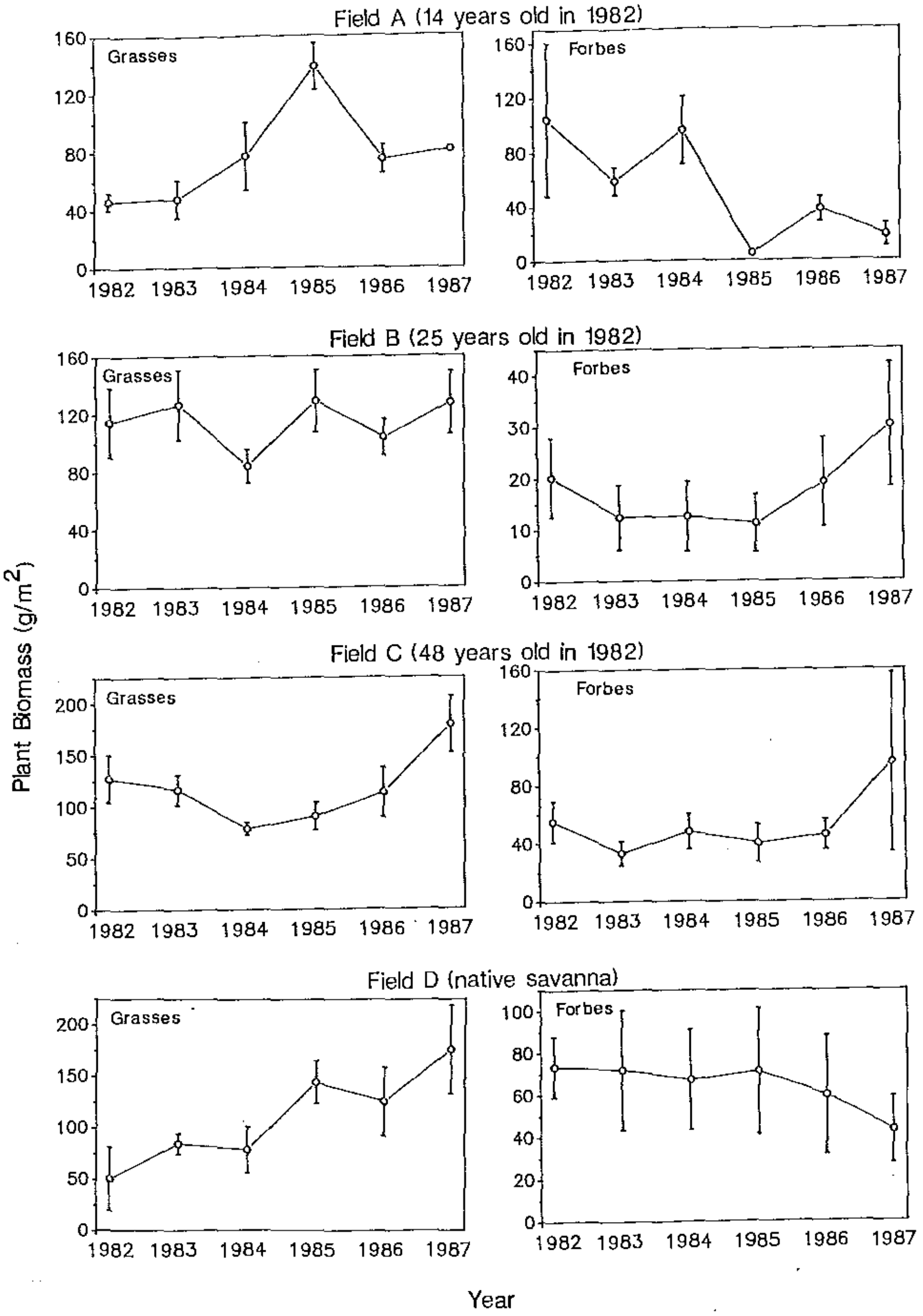

Figure 8. Biomass of grasses and forbs in permanent, unmanipulated control plots that are sampled annually. Note that the pattern of change is quite different in each of these four different fields. Each point shows the mean and standard error for a given year, based on 6 replicate plots per field. Data collected each year by clipping one 10 cm x 300 cm strip of vegetation per plot, sorting this to species, and then drying and weighing it.

from those abandoned recently? Similarly, are plant dynamics inferred from the chronosequence (Fig. 5) indicative of the dynamics that would be observed through time in an abandoned field? If N does increase during succession, we should be able to detect it when we re-sample the 2300 permanent old-field quadrats after 7 years in 1990. The slope of the 1983 regression (Fig. 4A) predicts an average increase of 6.8 mg of N kg^{-1} of soil yr^{-1}. After 7 years this should give an increase of almost 50 mg/kg. Because we have archived dried soil samples, upon resampling in 1990 we shall be able to calculate the differences in total soil N for each quadrat without having to allow for changes in chemical technique. Similarly, by resampling the vegetation we shall determine whether the dynamics of vegetation change **on individual quadrats** are correctly inferred from the chronosequence. This a critically important test of the validity of chronosequences. We know of no other resampling of a chronosequence to determine the validity of the dynamics inferred from a chronosequence. Assuming that soil N does increase during secondary succession, what is the cause? Is it N fixation by legumes, blue-green soil algae, or various associative or free-living N-fixing bacteria in the rhizosphere? Or is it an accumulation of fixed N via wet and dry fall, which is not lost from the soil? Can accrual of soil N be explained by a simple model of atmospheric inputs and atmospheric and soil-leaching losses? How do litter accumulation and decomposition influence soil during succession? When and why does the increase in total and mineralizable N cease? Do later successional species produce low-quality litter (high C:N ratio, high lignin content) that inhibits N accumulation at a point favoring those species? Do periodic droughts set bounds on soil development? These questions, raised by our work to date, will be addressed during the next 5 years.

Microbial Community: Soil microorganisms play an integral role regulating the flow of nitrogen within terrestrial ecosystems. However, we know little of the changes occuring in the structure and function of the microbial community during secondary succession. Nitrogen availability is an important factor directing the composition, structure and productivity of both plant and small mammal communities during old field succession at Cedar Creek (Tilman 1987a, 1988a, Huntly and Inouye 1987). In turn, microbial growth within the soil is constrained by the quantity of labile C supplied through plant litter production (Grey and Williams 1971). Thus, plant and microbial activities may limit and balance one another. Does the gradual increase in N mineralization during secondary succession correspond to changes in the structure and function of the microbial community? What influence do changes in litter chemistry have on the microbial community? Are microbial populations more efficient at utilizing recalcitrant C late in secondary succession? Do patterns of plant and microbial biomass production exhibit concomitant patterns during old field succession because they are linked through C and N availability?

We will address these questions by determining changes in the composition, structure and function of the microbial community during old field succession at CCNHA. Our aim is to directly link differences in species composition with functional changes in the microbial community (e.g. C and N mineralization). We have recently determined that microbial biomass increases during secondary succession according to first order kinetics (Zak et al., unpublished data). Organic C, H_2O soluble C, mineral N, and total N also change with succession. In addition, laboratory experiments have been initiated to simultaneously determine rate constants (k) for C and N mineralization in the old field chronosequence. Upon termination of this experiment, soil fungi will be cultured and identified to species for each soil incubation; additional fresh samples were collected to determine the correspondence in species composition between incubated and fresh soil. The xeric, acidic soils of CCNHA suggest that fungi may be dominant decomposing organisms; we will initially concentrate our effort on these organisms. This work will be conducted and analyzed in cooperation with Dr. Martha Christensen (Dept. of Botany, University of Wyoming) currently on sabbatical at Iowa State University, who has separate NSF funding for this work at CCNHA. In addition to changes in the heterotrophic community, mycorrhizal symbionts may change in abundance during succession. This will be addressed by Nancy Johnson, a doctoral student of Dave Tilman. She will use a bioassay to determine differences in the relative mycorrhizal activity for the successional chronosequence, and identify and count endomycorrhizal spores at these sites.

Our work on microbial dynamics during old field succession will complement and integrate with other ongoing studies at CCNHA. Information regarding patterns of plant biomass production and species composition across the chronosequence will be directly related to the studies outlined above. Therefore, we will directly link changes in the plant and microbial communities to patterns of C and N cycling during succession.

2. Productivity Gradients in Post-Successional Ecosystems

As discussed above, we use the old-field chronosequence to describe both the patterns of secondary succession at CCNHA and the inter-relations of various environmental variables, species, and ecosystem processes that may cause successional patterns. Upon renewal, we will establish comparably-detailed studies of the causes of spatial variation in "post-successional" vegetation at CCNHA, i.e., in ecosystems that have not been subject to major anthropogenic disturbances. These ecosystems represent the approximate "endpoints" of succession at CCNHA, and thus will provide valuable information on the ecosystem processes, species, and environmental factors that influence the long-term outcome of the successional process. Our research in these post-successional habitats will have two components: a survey of a wide range of post-successional upland habitats, and a more intensive study of an upland to lowland productivity gradient.

<u>Survey of Post-Successional Upland Stands</u>: We will choose 40 to 50 stands that are representative of the range of variation in upland, post-successional ecosystems of CCNHA. Stands to be chosen will range from sugar maple and basswood forest (such as on Crone's Knoll, a former island in Cedar Bog Lake that has been protected from fire, first by open water and now by wetlands), to red maple stands, red oak stands, black oak stands, white pine stands, aspen stands, hazel shrub thickets, bur oak stands, stands of ericaceous shrubs, and prairie openings. Our present work at CCNHA leads us to hypothesize that this range of variation is mainly caused by two variables: (1) the position of a

stand along a complex elevational, productivity and original parent material gradient from dry, eroded hilltops to low, moist swales; and (2) the disturbance history of an area, especially its fire frequency. In each stand, we will perform a broad survey of soils and other physical factors (e.g., total and mineral N; pH; vertical light profiles from canopy to soil surface; sand, silt and clay; cation exchange capacity; percent organic matter; extractable cations and anions), vegetation (biomass and cover estimates, to species; leaf, root, and stem mass per unit area), herbivores (extent of deer browsing; gopher activity; small mammal densities; foliage-feeding insects to species), types and frequency of present and past disturbances (determined from tree falls, tip up mounds, gopher mounds, fire scars, presence of local natural fire breaks, etc.) and height above water table and landscape position (from aerial photographs and topographic maps). We will perform our sampling in permanently marked quadrats, of sizes appropriate to the stand type, so that we may resample them at a future date. By analyzing these data much as we have analyzed our old field survey, and by comparing them with the data we have collected in the oak savanna prescribed burning experiments (p. 37), we will determine the interrelations of soils, plants, herbivores and disturbances in these areas. By comparing these patterns with those we are observing during secondary succession, we should gain a better understanding of the causes of patterns in both successional and post-successional ecosystems. Although this sampling will be labor-intensive, we have considerable experience accomplishing such surveys, and are sure of our ability to do this work within the bounds of our resources. We will resample these stands every 5 years to document the dynamics of change in them.

An Upland to Lowland Elevational Gradient: In addition to performing this broad survey of post-successional upland ecosystems of CCNHA, we will choose sites in which to perform more frequent monitoring of and more intensive studies of nutrient and soil dynamics and processes, vegetation, herbivores and disturbance (i.e., the Five Core Topics). The main area for this work will be an elevational gradient along a 250 m transect from the top of a hill NW of Cedar Bog Lake to the shore of the lake. This gradient, which encompasses a range of post-successional vegetation, is of particular interest to us because Lindeman (1941) established much of the transect. With the help of Dr. Don Lawrence, Lindeman's original plot markers have been relocated, and we can now extend Lindeman's observations and determine the dynamic changes that have occurred during the past 50 years. Because this transect includes wetlands, it will allow us to extend the scope of our project to ecosystems that may be highly susceptible to a potentially major future global disturbance -- climatic change caused by the accumulation of greenhouse gases. We admit that wetlands do not fit neatly into our studies of successional dynamics, but they are an important element of spatial (elevational) gradients at CCNHA. Moreover, they are a major sink for nutrients and organic matter that have been moved downslope. The wetland studies that we propose are an important source of breadth to the LTER project.

The upland to lowland transect crosses five distinguishable ecosystem types: (1) upland mixed oak forest, (2) marginal hardwood swamp, (3) white cedar swamp, (4) tamarack swamp, and (5) a sedge mat. Each differs in depth to water table, which may be a driving or governing variable. They differ widely in productivity, organic-matter accumulation, and litter quality, which may be determined partly by down-slope transport of organic matter and nitrogen. In addition, within CCNHA we have located and will study two other replicates of each ecosystem type, giving us a total of 15 sites for intensive study along this elevational (soil moisture, water table depth, productivity) gradient.

Our observations along this gradient will be used to describe these ecosystems, and to test these hypotheses:

(1) Primary productivity at different points along this gradient increases with N availability but decreases the longer the seasonal duration of anaerobic soils. Anaerobic soils are a major factor determining plant physiognomy; the relationship between primary productivity and plant physiognony will change depending on the seasonal duration of anaerobic soils, and thus will differ from wetland to upland forest.

(2) Water-table is an important factor governing (a) floristic composition; (b) productivity, (c) decomposition; (d) accumulation of organic matter, and (e) other soil processes such as N-mineralization and trace-gas (CO_2, CH_4) emission, only where it is (on average) within 30-50 cm of the soil/peat surface.

(3) Fluctuations in water table caused by seasonal and annual climatic variation will cause substantial alterations only when the water table is (on average) within 30-50 cm of the soil/peat surface.

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To do this, we will work with Dr. Kenneth Brooks, a professor of hydrology at the University, to modify an existing simulation model of upland-wetland systems (the Peatland Hydrologic Impact Model - PHIM). PHIM has been tested and validated on three separate Minnesota peatland and upland systems (Guertin 1984; Guertin and Brooks 1985; Guertin et al., 1987). PHIM is a deterministic, mechanism-based model that accommodates different soil-vegetation systems by characterizing landscape units in terms of vegetation type, rooting depth, soil characteristics, and meteorology. We will collect detailed field data to calibrate PHIM for CCNHA, including: continuously measured streamflow; infiltration and subsurface flow using infiltrometers and tracing techniques (see Gafni, 1986); measurements of hydraulic gradients and organic soil properties (Gafni, 1986); and water table levels both in already-established USGS wells at CCNHA and in additional wells (piezometers) we will install in old fields and along the upland to lowland gradient. The model will be integrated into our study of nutrient dynamics and control and of climatic charge as a source of ecosystem disturbance. The model will help us explore the possibility of "uphill" transport of nitrogen through the water table. Alder (Alnus rugosa) is a source of nitrate to groundwaters. If the water table is a significant source of water for upland vegetation, it could also be a source of N for that vegetation. We shall study N fixation by alder, nitrification and nitrate movement to and in groundwater, aided by PHIM and perhaps by natural isotopes of N and O.

Precipitation chemistry: Inorganic inputs to CCNHA via the atmosphere are monitored in cooperation with the Minnesota Pollution Control agency as part of their Acid Deposition Sampling Network. This sampling includes continuous monitoring of ozone as well as wetfall and atmospheric concentrations of particles and gases on a weekly basis. Atmospheric concentrations are determined using a Sierra-Andersen Series 100 constant flow air sampler and a three-stage Nucleopore membrane filter pack, with sulfur dioxide collected on an alkaline-impregnated filter. Filters are analyzed for 21 anions and cations. Wetfall is collected with a Aerochem Metrics Model 301 wet/dry precipitation collector. A recording raingauge verifies collection efficiency and determine loadings. Samples of precipitation are analyzed for pH, conductivity, and acidity, and 16 major cations and anions. After QA/QC validation, these data are added to the LTER data set.

Lysimetry: Leaching movement of elements is important in determining both losses from upland systems and gains to groundwater and peatland systems. To date, we have used two different methods to measure these: isolated soil columns (15 cm diameter) with ceramic-cup lysimeters to quantitatively sample soil solution; and porous ceramic cups to monitor soil solution chemistry at different depths. The former suffered from a number of problems, especially leakage caused by frequent gnawing by gophers on tubing. Thus, we plan to concentrate on the latter method (monitoring soil solution chemistry) in the future. Although the ceramic cups lack a quantitative estimate of volume of flow, this will be provided by the calibrated PHIM model. Ceramic-cup lysimeters are durable, inexpensive and easily sampled. We will install lysimeters in 49 different sites (22 old fields, 12 stands of oak savanna subject to different burn frequencies, and the 15 sites along the elevational gradient). There will be 10 lysimeters per site, with 5 of these at 10 cm depth and 5 at 100 cm depth. This will provide an excellent description of nutrient concentration, movement and loss across the full range of CCNHA ecosystem types.

Soil water: Soil moisture is monitored with a Troexler neutron probe both in the old field chronosequence and along a number of slope position/aspect combinations in the oak forests. We have already found correlations among soil water content, slope positions in upland forests, soil organic matter content, and N mineralization and nitrification within structurally and floristically similar oak forests. Water table depth will be determined by piezometers in the 22 old fields and along the upland to lowland gradient.

B. LONG-TERM EXPERIMENTAL STUDIES

We established 4 types of interrelated experiments, each designed to determine the role of particular processes on temporal and/or spatial patterns in CCNHA ecosystems and to elucidate the causes of correlations in the observational data. Because a change in any one ecosystem element has ramifications for all others, we determine (as much as possible with our resources) the effect of each treatment on several trophic levels and/or ecosystem processes. The four classes of experiments are manipulations (with controls) of (1) carbon and nitrogen dynamics, (2) productivity, (3) herbivores, and (4) disturbance. We started most experiments in old fields or oak savanna, but are now broadening our work to include post-successional elements of the CCNHA landscape.

1. Carbon and Nitrogen Dynamics and Controls

Studies of C and N dynamics include (1) litter-decomposition experiments; (2) effects of different rates of N addition on nitrification and leaching losses; (3) experimental studies of N fixation by soil algae, legumes, free-living soil bacteria, and associative N-fixers; (4) studies of denitrification; and (5) studies of microbial biomass, dissolved organic C, total organic C, and N dynamics.

CCNHA offers a unique opportunity to investigate N dynamics at a range of spatial and temporal scales. Temporal scales range from brief pulses of microbial activity following rainfall to long-term N accrual during secondary succession. Spatial scales go from micro-gradients of anaerobiosis and denitrification within soil aggregates to regional N availability and loss.

The old-field chronosequence is providing information on biological and environmental variables that regulate the distribution and accumulation of N during succession. Plant productivity is linked to and constrained by N availability, and it feeds back on N dynamics. Our current data suggest that soil N accrues at a rate of 9.7 kg ha^{-1} yr^{-1} (6.8 mg of N kg^{-1} of soil yr^{-1}) during succession at CCNHA. Annual additions of atmospheric N, totaling 9.0 kg ha^{-1} yr^{-1}, account for most N entering old fields (Table 1). Biological inputs through free-living, associative and symbiotic fixation are small (McKone and Biesboer 1986, Zak and Johnson unpublished data). Export of N during succession is small in comparison to annual rates of addition. Atmospheric additions are two orders of magnitude greater than leaching losses measured with lysimeters. Thus, N accrual is mainly determined by the difference between atmospheric loading and leaching loss, much as

Table 1. Patterns of nitrogen cycling during old field succession at CCNHA. The distribution, reallocation, input and export of nitrogen are summarized for three old fields of different successional stages.

	Field Age 17 years	 27 years	 51 years
	kg/ha		
I. Nitrogen Pools			
Aboveground Biomass	11	13	20
Belowground Biomass	30	57	100
Plant Litter	9	18	23
Microbial Biomass	4	6	9
Soil Total N	829	749	1123
II. Nitrogen Fluxes			
	$kg\ ha^{-1}\ yr^{-1}$		
Atmospheric Additions	9	9	9
Free Living[1] Fixation	ud	ud	ud
NO_3^- Leaching	0.07	0.04	0.01
Denitrification[2]	ud	ud	ud
Mineralization	42	47	53

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[1] Undetectable levels of C_2H_2 reduction (Zak and Johnson, unpublished data)

[2] Undetectably low rates of dentrification during period of measurement.

Olson (1958) found for the sand dunes of southern Lake Michigan.

Although our work to date may explain N accrual in old fields, it does not explain the quasi-equilibrium levels we see in oak savanna and in post-successional ecosystems. N accumulation can cease only when loss rates increase to equal input rates. Does dentrification become a more substantial sink for N as soil organic matter increases during secondary succession? What are the seasonal patterns of denitrification in the old-field chronosequence? In oak savanna? In forest? Can large, brief temporal fluxes cause total soil N to equilibrate late in secondary succession? These are some of the central questions we will pursue with regard to soil N dynamics in the future.

We will also investigate N cycling at several spatial scales. CCNHA is a mosaic of ecosystems linked through energy and matter flow. Upland ecosystems export moisture, nutrients and organic matter downslope. This spatial stratification significantly influences ecosystem processes. For example, denitrification is influenced by topographic position, drainage and soil texture (Davidson and Swank 1986, Groffman and Tiedje 1987). We hypothesize that topographic position and soil moisture are the physical variables that give rise to spatial and temporal patterns of N availability and loss at CCNHA. Do ecosystems occurring on similar landforms have similar soil development and cycle N in similar patterns? To what extent does landform complexity within individual ecosystems regulate small-scale spatial variation in N availability and loss?

Few studies have characterized spatial patterns of nutrient cycling and extrapolated them across large areas (Pastor et al. 1984, Schimel et al. 1985, Zak et al. 1986, 1987, Zak and Pregitzer 1988). Pastor et al. (1984) observed that patterns of N mineralization were related to the overstory species, which in turn were a function of the soil-moisture gradient. In a preliminary study we measured N mineralization, nitrification, dentrification, and microbial biomass N within 4 major ecosystems of CCNHA (Table 2). Each of 3 upland and 1 lowland ecosystem were replicated twice. Nitrogen cycling was most dynamic within the black ash swamp, where the water table is frequently near the soil surface. Our future work will use these approaches in studying the upland to wetland

Table 2. Early-growing season N dynamics of 4 ecosystems in CCNHA. Values are the mean of 2 sites in each ecosystem type. Production of mineral N and NO_c are means for May 1987.

ECOSYSTEM	Microbial N	Mineralization	Nitrification	N_2O-N
	ug N/g			ng g^{-1} hr^{-1}
Old Field	2.49 a	0.74 a	0.32 a	2.83 a
Oak Savanna	2.52 a	0.89 a	0.49 a	2.95 a
Red Oak Forest	5.89 a	1.05 a	0.28 a	4.07 a
Black Ash Swamp	28.52 b	3.57 b	1.02 a	21.49 b
LSD	4.92	0.34	n/s	8.26

Note: Means within a column that have the same letter are not significantly different at alpha = 0.05 using Fisher's protected LSD.

gradient and the old fields.

Litter Feedback and N Mineralization: Although litter produced by different tree species is known to have differential decay and N mineralization rates (e.g., Melillo et al. 1983, Flanagan and Van Cleve 1983, Pastor et al. 1984), such differences are sparsely documented for forb and grass species (Koelling and Kucera 1965, Holland and Coleman 1987, Pastor et al. 1987c). The first two years of a long-term monoculture experiment at CCNHA has shown that different species can have rapid and large effects on in situ N mineralization (Fig. 9). This suggests that the ability of plants to alter the supply of limiting soil resources could be a major, and heretofore unrecognized, mechanism of competition and supports our view that population ecology must be placed in an ecosystem-level context. We propose to begin a long-term litterbag experiment to determine the decay rates and C and N dynamics of major grass and forb species. For aboveground litters, bags will be placed both on the soil surface and held vertically in frames to distinguish between decay of standing dead and downed litter. We will use both fine-mesh nylon cloth and coarse-mesh screen bags to exclude and include soil arthropods. Enough bags and material in each will be employed to allow the experiment to continue for 10 years. Bags will be periodically sampled and analyzed for mass loss and changes in C, N, sugars, cellulose, and lignin. This experiment will provide much of the required decomposition data for ecosystem model construction (p. 43).

Nitrogen Saturation: A current issue in ecosystem research is whether systems can become "N-saturated" and have significant NO_3^- export (Van Miegroet and Cole 1984). SO_4 and small amounts of NO_3 pass through CCNHA soils, carrying various bases (K, Mg, Ca, etc.) with them. We have developed a model of base loss for Minnesota soils as a function of precipitation chemistry (Bloom and Grigal 1985). Based on this model, the CCNHA soils are highly susceptible to base loss from addition of strong acid anions (i.e., acid rain). We will study N-saturation in an old field, in oak savanna, and in oak forest by determining the compartments (e.g., microbial biomass, plant biomass) in which added ^{15}N

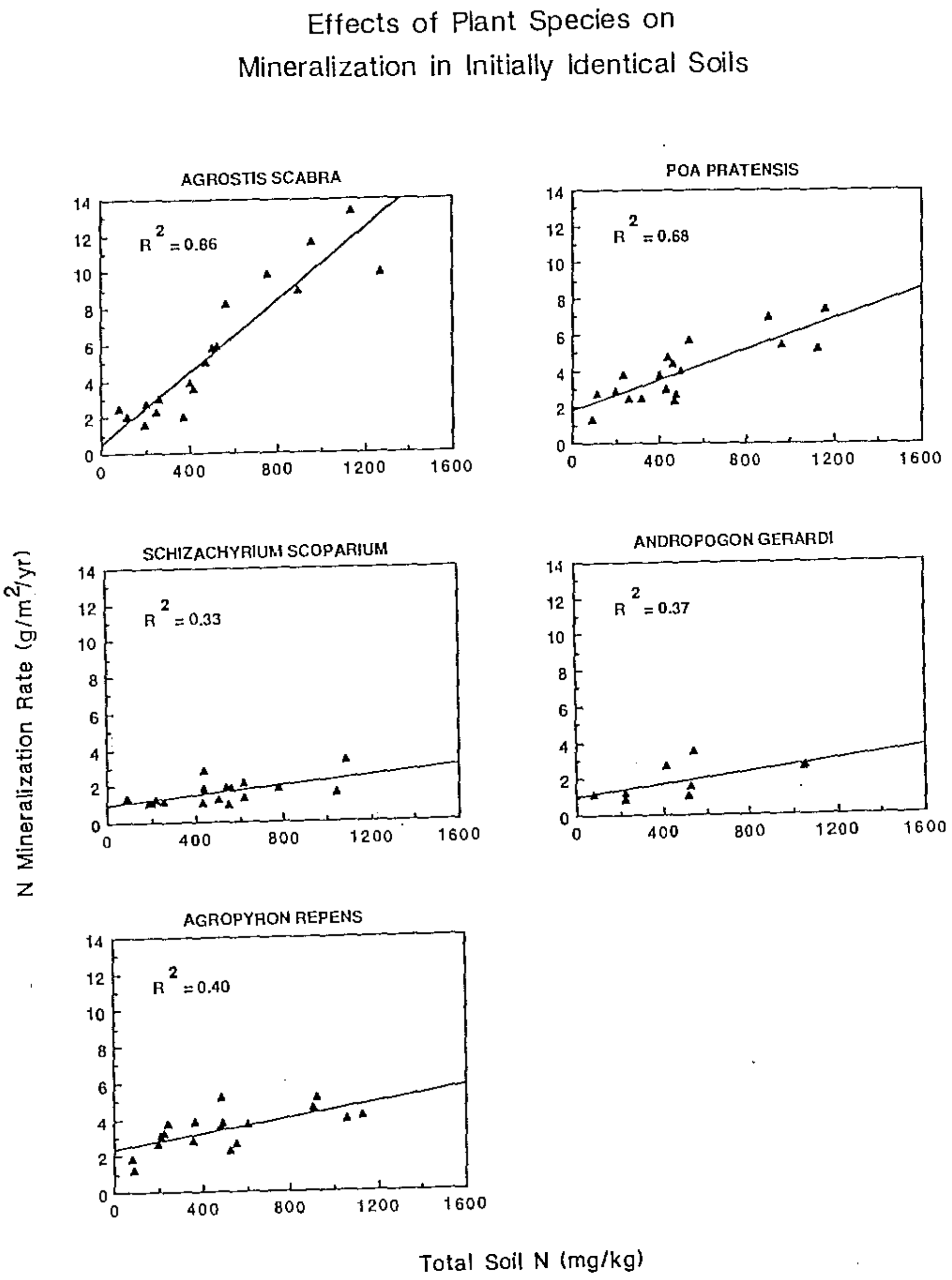

Figure 9. The in situ rate of N mineralization, for initially identical soils, diverged significantly, dependent on the species growing on a plot. Each point in each part of this figure shows the growing-season total rate of N mineralization, as measured using the buried bag technique (Eno 1960; Pastor et al. 1984). Monocultures of these 5 major CCNHA grass species were started on a range of soil mixtures that differed in their total N. Species were randomly assigned to the plots. The results shown above are for the second year of the experiment (1987). There were no significant differences in N mineralization rates the first year, but, by the second year, Agrostis scabra monocultures had a highly significantly (F=33.7, df=8,71, $P < .005$) steeper slope than the other 4 species. The steeper slope means that, for any given soil, the soil N mineralization rate is higher in Agrostis plots than in monocultures of other species. We are now analyzing plant tissue, litter, and root samples from all monocultures to determine C:N ratios, N:lignin ratios, etc., and will initiate litter bag studies to see what causes this divergence. Our current hypothesis is that species-specific differences in litter quality cause monocultures of different species to diverge because of a feedback effect of litter quality on N mineralization rates. We have also established competition plots to determine if this effects occurs in mixed-species plots and its effect on competition.

first accumulates, and the rate at which they become saturated. We will set up 12 large fiberglass lysimeters per region, each 1 m in diameter by 1 m deep. Ceramic cups at the bottom of each lysimeter will sample soil solution. There will be a control plus 3 rates of $^{15}NH_4{}^{15}NO_3$ addition (added once a month) with 3 replicates per treatment. We will measure soil solution chemistry and microbial biomass monthly, both for 1 year before N addition and indefinitely afterward. Once a year we will pull a soil core for root biomass and other analyses. Non-destructive methods (percent cover, light penetration) will be used for above-ground biomass. This manipulation of the N cycle will help determine the forces that cause N levels to equilibrate and that determine soil fertility.

2. Experimental Manipulations of Productivity

These determine the role of soil resources in controlling spatial heterogeneity, productivity, composition, diversity and successional dynamics of primary producers, and the feedback effects of plants on soil properties. The main experiments, are (1) addition of nutrients one at a time to determine which limit production; and 2) experimental productivity gradients of natural vegetation within deer and gopher exclosures.

From the 22 fields of the chronosequence we chose 3 fields and a prairie opening in native oak savanna for these experiments (Tilman 1987a). These 4 fields, described in detail in Tilman (1987a), were, in 1982, 14-years old (called Field A), 25-yr old (Field B), 48-yr old (Field C) and native oak savanna (Field D). By restricting most old field experiments to these localities, we obtain detailed information on several ecosystem processes and underlying mechanisms in one set of localities, so that they may be directly compared. This keeps other fields free of any inadvertent experimental effects.

Single-nutrient addition experiments: In 1982 in each of the 4 experimental fields, we established 36 plots, randomly assigned to receive one of 9 treatments. Treatments consist of single additions of potentially limiting soil resources, with a control. The nutrients, added twice a year, are N, P, K, Ca, Mg, S, a trace metal mixture, or water (2.5 cm/wk through the growing season). Harvests of above-ground plant biomass, analyzed by ANOVA with contrasts using Dunnett's **t** (Steel and Torrie 1980), show that N addition

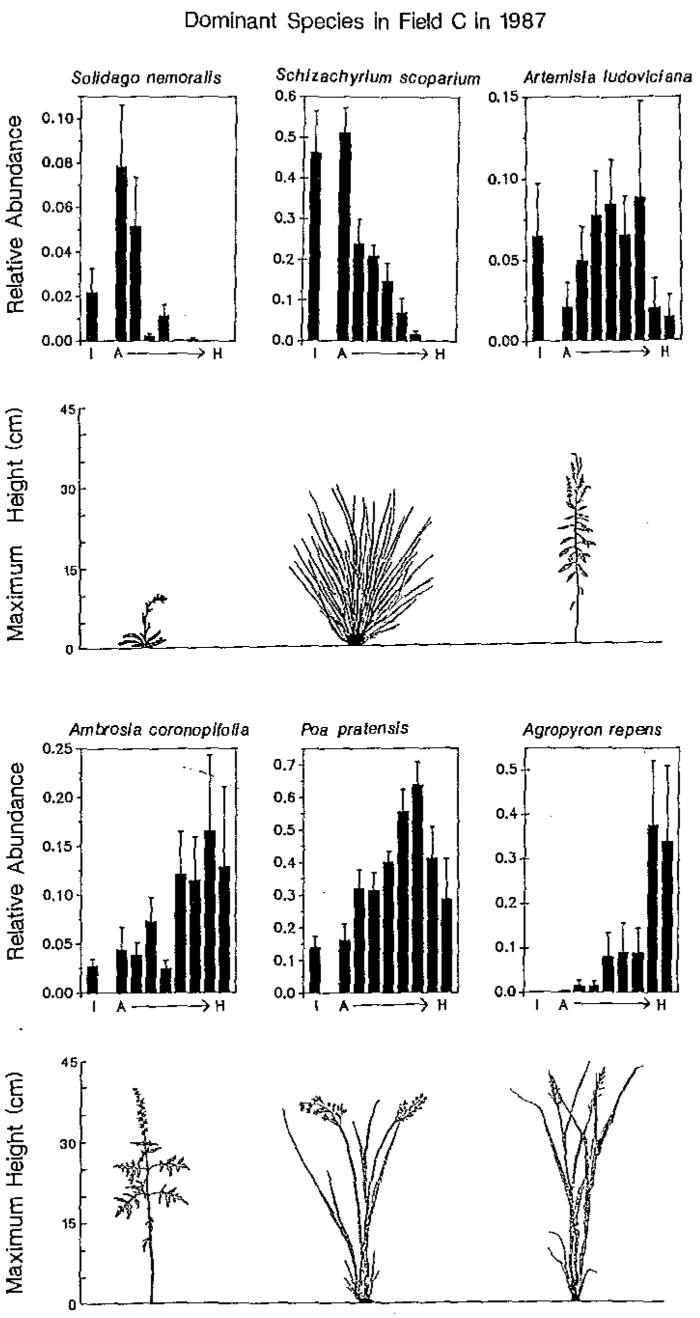

Figure 10. Species separation along an experimental nitrogen gradient. This figure shows the dependence of the relative abundance of the 6 most common species of Field C on the rate of nitrogen addition. Each of the 9 histogram bars shows a different rate of nitrogen addition, from no addition (Treatments I and A), to the highest rate (Treatment H). Note that no added N is at the left and the highest rate of N addition is at the right in each figure. The drawings below each species shown its physiognomy, with the height used being the maximal treatment-average height for the species in that field in 1987. The actual rates of N addition used, and other details of the experiment, are in Tilman (1987). Rates of N addition were chosen to give above-ground plant biomasses that span the range observed in CCNHA old fields. Except for the highest rate of N addition (Treatment H, which was chosen to be supra-normal), the other 8 treatments are representative of mineralization rates in soils in the region.

consistently led to significant increases in above-ground plant biomass. Other nutrients were never significant in more than 1 of 16 ANOVA's (Tilman 1987a; Inouye, Huntly, Tilman and Tester 1987; Tilman 1988a). The consistency of results from year-to-year and across fields of different ages, and their agreement with previous work (Tilman 1983, 1984), led us to focus on N as the soil factor most likely to influence primary productivity, plant community composition, and successional dynamics. However, they have raised a major question. Theory has predicted that a plant should adjust its morphology and physiology so as to be equally limited by all resources (Bloom, Chapin and Mooney 1985; Tilman 1982). Even when viewed on a species-by-species basis, CCNHA results suggest that plants are limited by two resources at most (N and light), and that P, K, Ca and trace metals are never limiting. Does this mean that plants are not as plastic (physiologically and morphologically) as theories have assumed? Could these ecosystems be invaded by species with higher requirements for P, K, Ca, and trace metals but lower requirements for N (i.e., legumes; Tilman 1982)? If so, why are legumes so rare at CCNHA? We have recently begun similar nutrient additions in a small, visibly zoned wetland, using 3 replicate plots per treatment in each of 4 zones. After 1 year, the 2 upslope zones showed significant N responses, but the 2 downslope zones did not respond to any nutrients.

Experimental Productivity Gradients Without Herbivores: Strong and consistent patterns of N limitation at CCNHA, correlations between successional dynamics and soil N (Figs. 4, 5), and separation of species along spatial or temporal N gradients (Fig. 6), raise questions that can only be tested using experimental N gradients:

1. Is the primary cause of secondary succession at Cedar Creek the slow increase in soil N, and the effects of this on plant competition for nitrogen and light (as hypothesized in the resource ratio hypothesis of Tilman 1982, 1985)?

2. How does the pattern of succession depend on the rate of N addition? Does N addition increase the rate of succession, but not the order in which species attain dominance, as predicted by the resource ratio hypothesis? Or, do different rates of N addition lead to distinctly different patterns of succession, as predicted by models of succession as transient dynamics (Tilman 1985, 1988a; Huston and Smith 1987)?

3. Can a high rate of N addition cause a temporary "retrogression," as predicted by models of succession as transient dynamics (Tilman 1988a), i.e., can a high rate of N

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Meteorological measurements: A variety of meteorological variables are continuously monitored and recorded at CCNHA, adding to a data record that is over 30 years old. The CR10 weather station, located near the headquarters of CCNHA, is integrated into a University of Minnesota network managed by Dr. Mark Seeley, Dept. of Soil Science. Stations automatically transmit data (daily, by telephone) to a central university facility, with data available within 24 hours of collection. These data are a necessary input to the hydrologic modeling, and to many other activities at CCNHA.

Hydrology: Knowledge of water flow into, through, and out of soils is fundamental to understanding nutrient cycling, the dynamics of soil development, the residence time of chemical constituents in the soil, and the effects of disturbance on soils and vegetation. Water provides the physical link among landscape units, particularly between upland and wetland components, and is the transport mechanism and medium for both nutritive and non-nutritive elements. Water carries elements from surface to subsurface soils, from upland to lowland, and to shallow groundwater. However, the pathways and timing of water flow through terrestrial ecosystems in the glaciated mid-continent are poorly understood. Here watersheds are not the discrete, physically bounded entities that occur at Hubbard Brook or Coweeta. To characterize water movement on the 30 m deep sands of CCNHA requires that we develop and verify a hydrologic model for our site.

To do this, we will work with Dr. Kenneth Brooks, a professor of hydrology at the University, to modify an existing simulation model of upland-wetland systems (the Peatland Hydrologic Impact Model - PHIM). PHIM has been tested and validated on three separate Minnesota peatland and upland systems (Guertin 1984; Guertin and Brooks 1985; Guertin et al., 1987). PHIM is a deterministic, mechanism-based model that accommodates different soil-vegetation systems by characterizing landscape units in terms of vegetation type, rooting depth, soil characteristics, and meteorology. We will collect detailed field data to calibrate PHIM for CCNHA, including: continuously measured streamflow; infiltration and subsurface flow using infiltrometers and tracing techniques (see Gafni, 1986); measurements of hydraulic gradients and organic soil properties (Gafni, 1986); and water table levels both in already-established USGS wells at CCNHA and in additional wells (piezometers) we will install in old fields and along the upland to lowland gradient. The model will be integrated into our study of nutrient dynamics and control and of climatic charge as a source of ecosystem disturbance. The model will help us explore the possibility of "uphill" transport of nitrogen through the water table. Alder (Alnus rugosa) is a source of nitrate to groundwaters. If the water table is a significant source of water for upland vegetation, it could also be a source of N for that vegetation. We shall study N fixation by alder, nitrification and nitrate movement to and in groundwater, aided by PHIM and perhaps by natural isotopes of N and O.

Precipitation chemistry: Inorganic inputs to CCNHA via the atmosphere are monitored in cooperation with the Minnesota Pollution Control agency as part of their Acid Deposition Sampling Network. This sampling includes continuous monitoring of ozone as well as wetfall and atmospheric concentrations of particles and gases on a weekly basis. Atmospheric concentrations are determined using a Sierra-Andersen Series 100 constant flow air sampler and a three-stage Nucleopore membrane filter pack, with sulfur dioxide collected on an alkaline-impregnated filter. Filters are analyzed for 21 anions and cations. Wetfall is collected with a Aerochem Metrics Model 301 wet/dry precipitation collector. A recording raingauge verifies collection efficiency and determine loadings. Samples of precipitation are analyzed for pH, conductivity, and acidity, and 16 major cations and anions. After QA/QC validation, these data are added to the LTER data set.

Lysimetry: Leaching movement of elements is important in determining both losses from upland systems and gains to groundwater and peatland systems. To date, we have used two different methods to measure these: isolated soil columns (15 cm diameter) with ceramic-cup lysimeters to quantitatively sample soil solution; and porous ceramic cups to monitor soil solution chemistry at different depths. The former suffered from a number of problems, especially leakage caused by frequent gnawing by gophers on tubing. Thus, we plan to concentrate on the latter method (monitoring soil solution chemistry) in the future. Although the ceramic cups lack a quantitative estimate of volume of flow, this will be provided by the calibrated PHIM model. Ceramic-cup lysimeters are durable, inexpensive and easily sampled. We will install lysimeters in 49 different sites (22 old fields, 12 stands of oak savanna subject to different burn frequencies, and the 15 sites along the elevational gradient). There will be 10 lysimeters per site, with 5 of these at 10 cm depth and 5 at 100 cm depth. This will provide an excellent description of nutrient concentration, movement and loss across the full range of CCNHA ecosystem types.

Soil water: Soil moisture is monitored with a Troexler neutron probe both in the old field chronosequence and along a number of slope position/aspect combinations in the oak forests. We have already found correlations among soil water content, slope positions in upland forests, soil organic matter content, and N mineralization and nitrification within structurally and floristically similar oak forests. Water table depth will be determined by piezometers in the 22 old fields and along the upland to lowland gradient.

B. LONG-TERM EXPERIMENTAL STUDIES

We established 4 types of interrelated experiments, each designed to determine the role of particular processes on temporal and/or spatial patterns in CCNHA ecosystems and to elucidate the causes of correlations in the observational data. Because a change in any one ecosystem element has ramifications for all others, we determine (as much as possible with our resources) the effect of each treatment on several trophic levels and/or ecosystem processes. The four classes of experiments are manipulations (with controls) of (1) carbon and nitrogen dynamics, (2) productivity, (3) herbivores, and (4) disturbance. We started most experiments in old fields or oak savanna, but are now broadening our work to include post-successional elements of the CCNHA landscape.

1. Carbon and Nitrogen Dynamics and Controls

Studies of C and N dynamics include (1) litter-decomposition experiments; (2) effects of different rates of N addition on nitrification and leaching losses; (3) experimental studies of N fixation by soil algae, legumes, free-living soil bacteria, and associative N-fixers; (4) studies of denitrification; and (5) studies of microbial biomass, dissolved organic C, total organic C, and N dynamics.

CCNHA offers a unique opportunity to investigate N dynamics at a range of spatial and temporal scales. Temporal scales range from brief pulses of microbial activity following rainfall to long-term N accrual during secondary succession. Spatial scales go from micro-gradients of anaerobiosis and denitrification within soil aggregates to regional N availability and loss.

The old-field chronosequence is providing information on biological and environmental variables that regulate the distribution and accumulation of N during succession. Plant productivity is linked to and constrained by N availability, and it feeds back on N dynamics. Our current data suggest that soil N accrues at a rate of 9.7 kg ha^{-1} yr^{-1} (6.8 mg of N kg^{-1} of soil yr^{-1}) during succession at CCNHA. Annual additions of atmospheric N, totaling 9.0 kg ha^{-1} yr^{-1}, account for most N entering old fields (Table 1). Biological inputs through free-living, associative and symbiotic fixation are small (McKone and Biesboer 1986, Zak and Johnson unpublished data). Export of N during succession is small in comparison to annual rates of addition. Atmospheric additions are two orders of magnitude greater than leaching losses measured with lysimeters. Thus, N accrual is mainly determined by the difference between atmospheric loading and leaching loss, much as

Table 1. Patterns of nitrogen cycling during old field succession at CCNHA. The distribution, reallocation, input and export of nitrogen are summarized for three old fields of different successional stages.

	Field Age		
	17 years	27 years	51 years
	kg/ha		
I. Nitrogen Pools			
Aboveground Biomass	11	13	20
Belowground Biomass	30	57	100
Plant Litter	9	18	23
Microbial Biomass	4	6	9
Soil Total N	829	749	1123
II. Nitrogen Fluxes			
	kg ha^{-1} yr^{-1}		
Atmospheric Additions	9	9	9
Free Living[1] Fixation	ud	ud	ud
NO_3^- Leaching	0.07	0.04	0.01
Denitrification[2]	ud	ud	ud
Mineralization	42	47	53

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[1] Undetectable levels of C_2H_2 reduction (Zak and Johnson, unpublished data)

[2] Undetectably low rates of dentrification during period of measurement.

Olson (1958) found for the sand dunes of southern Lake Michigan.

Although our work to date may explain N accrual in old fields, it does not explain the quasi-equilibrium levels we see in oak savanna and in post-successional ecosystems. N accumulation can cease only when loss rates increase to equal input rates. Does dentrification become a more substantial sink for N as soil organic matter increases during secondary succession? What are the seasonal patterns of denitrification in the old-field chronosequence? In oak savanna? In forest? Can large, brief temporal fluxes cause total soil N to equilibrate late in secondary succession? These are some of the central questions we will pursue with regard to soil N dynamics in the future.

We will also investigate N cycling at several spatial scales. CCNHA is a mosaic of ecosystems linked through energy and matter flow. Upland ecosystems export moisture, nutrients and organic matter downslope. This spatial stratification significantly influences ecosystem processes. For example, denitrification is influenced by topographic position, drainage and soil texture (Davidson and Swank 1986, Groffman and Tiedje 1987). We hypothesize that topographic position and soil moisture are the physical variables that give rise to spatial and temporal patterns of N availability and loss at CCNHA. Do ecosystems occurring on similar landforms have similar soil development and cycle N in similar patterns? To what extent does landform complexity within individual ecosystems regulate small-scale spatial variation in N availability and loss?

Few studies have characterized spatial patterns of nutrient cycling and extrapolated them across large areas (Pastor et al. 1984, Schimel et al. 1985, Zak et al. 1986, 1987, Zak and Pregitzer 1988). Pastor et al. (1984) observed that patterns of N mineralization were related to the overstory species, which in turn were a function of the soil-moisture gradient. In a preliminary study we measured N mineralization, nitrification, dentrification, and microbial biomass N within 4 major ecosystems of CCNHA (Table 2). Each of 3 upland and 1 lowland ecosystem were replicated twice. Nitrogen cycling was most dynamic within the black ash swamp, where the water table is frequently near the soil surface. Our future work will use these approaches in studying the upland to wetland

Table 2. Early-growing season N dynamics of 4 ecosystems in CCNHA. Values are the mean of 2 sites in each ecosystem type. Production of mineral N and NO_c are means for May 1987.

ECOSYSTEM	Microbial N	Mineralization	Nitrification	N_2O-N
	----------------	ug N/g	------------------	ng g^{-1} hr^{-1}
Old Field	2.49 a	0.74 a	0.32 a	2.83 a
Oak Savanna	2.52 a	0.89 a	0.49 a	2.95 a
Red Oak Forest	5.89 a	1.05 a	0.28 a	4.07 a
Black Ash Swamp	28.52 b	3.57 b	1.02 a	21.49 b
LSD	4.92	0.34	n/s	8.26

Note: Means within a column that have the same letter are not significantly different at alpha = 0.05 using Fisher's protected LSD.

gradient and the old fields.

Litter Feedback and N Mineralization: Although litter produced by different tree species is known to have differential decay and N mineralization rates (e.g., Melillo et al. 1983, Flanagan and Van Cleve 1983, Pastor et al. 1984), such differences are sparsely documented for forb and grass species (Koelling and Kucera 1965, Holland and Coleman 1987, Pastor et al. 1987c). The first two years of a long-term monoculture experiment at CCNHA has shown that different species can have rapid and large effects on in situ N mineralization (Fig. 9). This suggests that the ability of plants to alter the supply of limiting soil resources could be a major, and heretofore unrecognized, mechanism of competition and supports our view that population ecology must be placed in an ecosystem-level context. We propose to begin a long-term litterbag experiment to determine the decay rates and C and N dynamics of major grass and forb species. For aboveground litters, bags will be placed both on the soil surface and held vertically in frames to distinguish between decay of standing dead and downed litter. We will use both fine-mesh nylon cloth and coarse-mesh screen bags to exclude and include soil arthropods. Enough bags and material in each will be employed to allow the experiment to continue for 10 years. Bags will be periodically sampled and analyzed for mass loss and changes in C, N, sugars, cellulose, and lignin. This experiment will provide much of the required decomposition data for ecosystem model construction (p. 43).

Nitrogen Saturation: A current issue in ecosystem research is whether systems can become "N-saturated" and have significant NO_3^- export (Van Miegroet and Cole 1984). SO_4 and small amounts of NO_3 pass through CCNHA soils, carrying various bases (K, Mg, Ca, etc.) with them. We have developed a model of base loss for Minnesota soils as a function of precipitation chemistry (Bloom and Grigal 1985). Based on this model, the CCNHA soils are highly susceptible to base loss from addition of strong acid anions (i.e., acid rain). We will study N-saturation in an old field, in oak savanna, and in oak forest by determining the compartments (e.g., microbial biomass, plant biomass) in which added ^{15}N

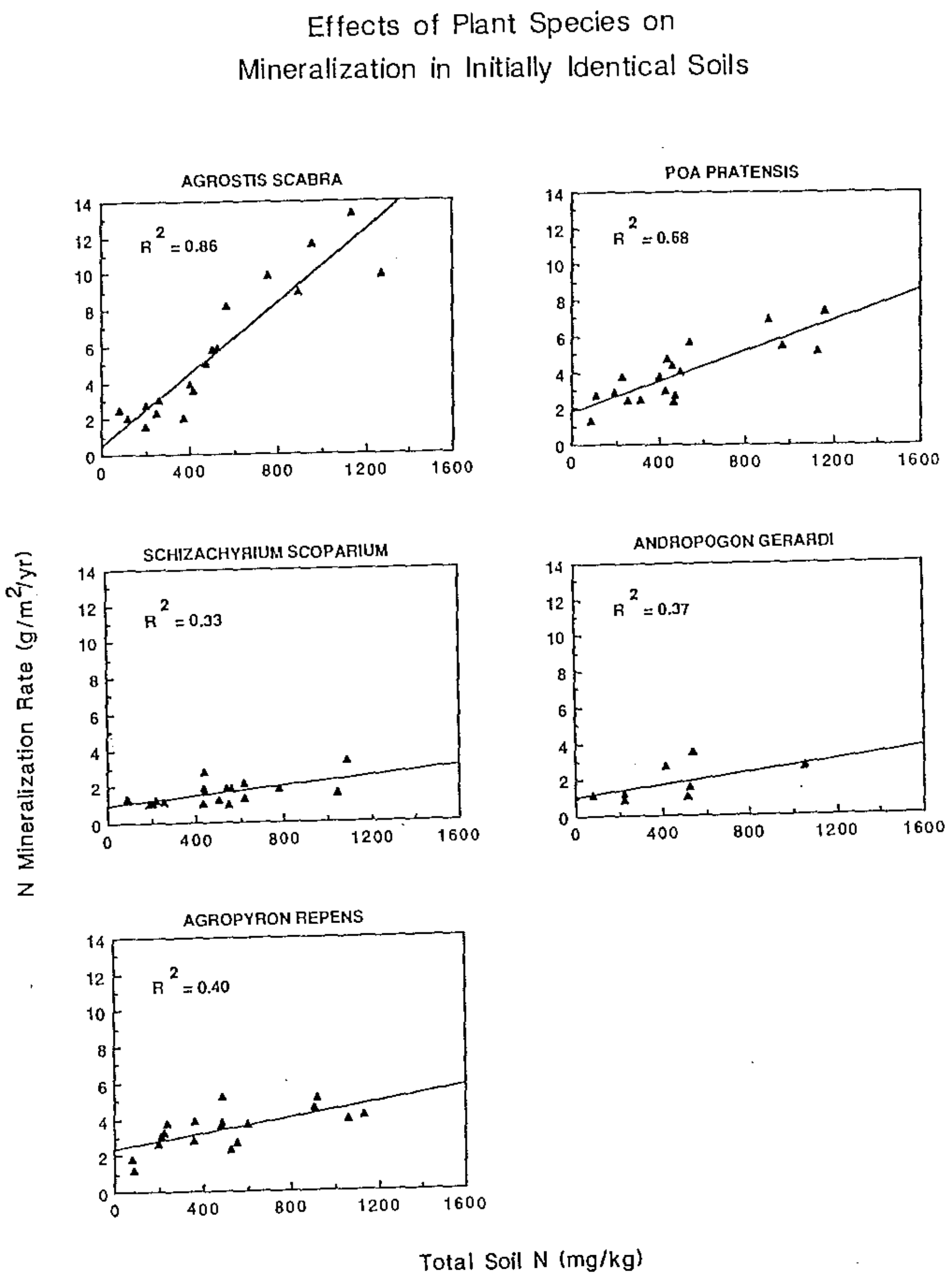


Figure 9. The in situ rate of N mineralization, for initially identical soils, diverged significantly, dependent on the species growing on a plot. Each point in each part of this figure shows the growing-season total rate of N mineralization, as measured using the buried bag technique (Eno 1960; Pastor et al. 1984). Monocultures of these 5 major CCNHA grass species were started on a range of soil mixtures that differed in their total N. Species were randomly assigned to the plots. The results shown above are for the second year of the experiment (1987). There were no significant differences in N mineralization rates the first year, but, by the second year, Agrostis scabra monocultures had a highly significantly ($F=33.7$, $df=8,71$, $P < .005$) steeper slope than the other 4 species. The steeper slope means that, for any given soil, the soil N mineralization rate is higher in Agrostis plots than in monocultures of other species. We are now analyzing plant tissue, litter, and root samples from all monocultures to determine C:N ratios, N:lignin ratios, etc., and will initiate litter bag studies to see what causes this divergence. Our current hypothesis is that species-specific differences in litter quality cause monocultures of different species to diverge because of a feedback effect of litter quality on N mineralization rates. We have also established competition plots to determine if this effects occurs in mixed-species plots and its effect on competition.

first accumulates, and the rate at which they become saturated. We will set up 12 large fiberglass lysimeters per region, each 1 m in diameter by 1 m deep. Ceramic cups at the bottom of each lysimeter will sample soil solution. There will be a control plus 3 rates of $^{15}NH_4{}^{15}NO_3$ addition (added once a month) with 3 replicates per treatment. We will measure soil solution chemistry and microbial biomass monthly, both for 1 year before N addition and indefinitely afterward. Once a year we will pull a soil core for root biomass and other analyses. Non-destructive methods (percent cover, light penetration) will be used for above-ground biomass. This manipulation of the N cycle will help determine the forces that cause N levels to equilibrate and that determine soil fertility.

2. Experimental Manipulations of Productivity

These determine the role of soil resources in controlling spatial heterogeneity, productivity, composition, diversity and successional dynamics of primary producers, and the feedback effects of plants on soil properties. The main experiments, are (1) addition of nutrients one at a time to determine which limit production; and 2) experimental productivity gradients of natural vegetation within deer and gopher exclosures.

From the 22 fields of the chronosequence we chose 3 fields and a prairie opening in native oak savanna for these experiments (Tilman 1987a). These 4 fields, described in detail in Tilman (1987a), were, in 1982, 14-years old (called Field A), 25-yr old (Field B), 48-yr old (Field C) and native oak savanna (Field D). By restricting most old field experiments to these localities, we obtain detailed information on several ecosystem processes and underlying mechanisms in one set of localities, so that they may be directly compared. This keeps other fields free of any inadvertent experimental effects.

Single-nutrient addition experiments: In 1982 in each of the 4 experimental fields, we established 36 plots, randomly assigned to receive one of 9 treatments. Treatments consist of single additions of potentially limiting soil resources, with a control. The nutrients, added twice a year, are N, P, K, Ca, Mg, S, a trace metal mixture, or water (2.5 cm/wk through the growing season). Harvests of above-ground plant biomass, analyzed by ANOVA with contrasts using Dunnett's **t** (Steel and Torrie 1980), show that N addition

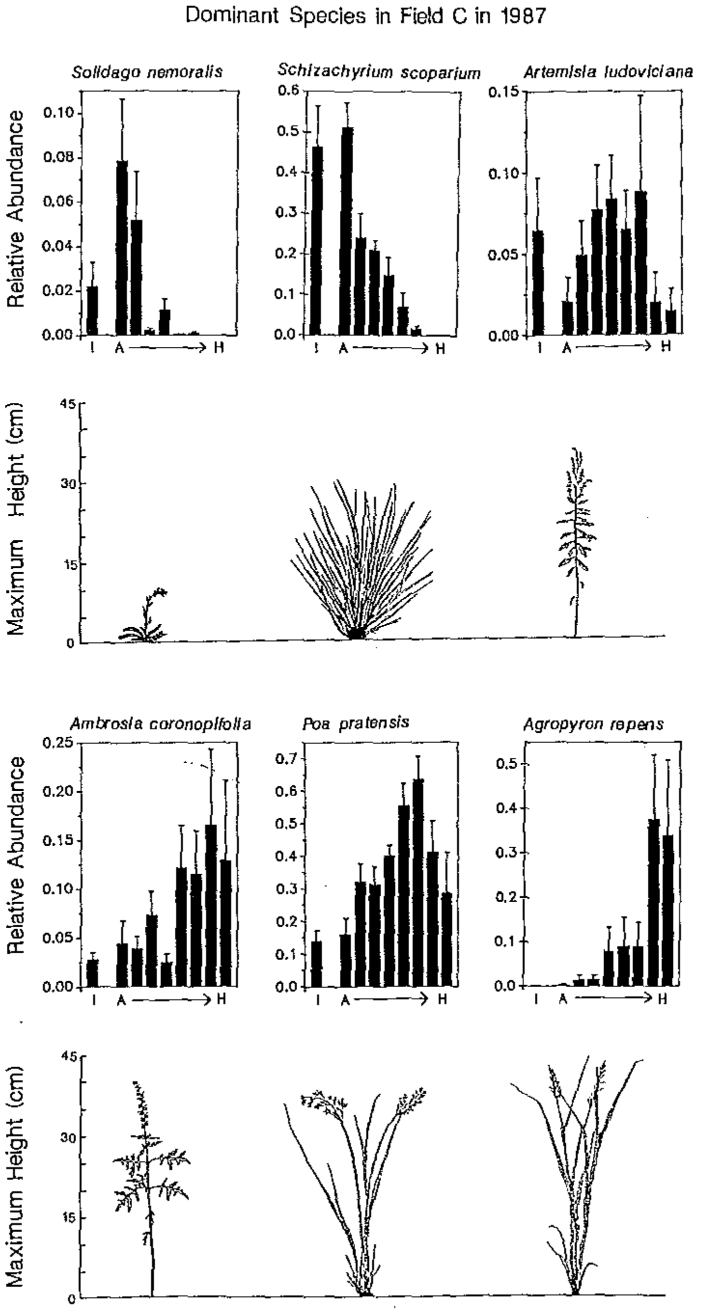


Figure 10. Species separation along an experimental nitrogen gradient. This figure shows the dependence of the relative abundance of the 6 most common species of Field C on the rate of nitrogen addition. Each of the 9 histogram bars shows a different rate of nitrogen addition, from no addition (Treatments I and A), to the highest rate (Treatment H). Note that no added N is at the left and the highest rate of N addition is at the right in each figure. The drawings below each species shown its physiognomy, with the height used being the maximal treatment-average height for the species in that field in 1987. The actual rates of N addition used, and other details of the experiment, are in Tilman (1987). Rates of N addition were chosen to give above-ground plant biomasses that span the range observed in CCNHA old fields. Except for the highest rate of N addition (Treatment H, which was chosen to be supra-normal), the other 8 treatments are representative of mineralization rates in soils in the region.

consistently led to significant increases in above-ground plant biomass. Other nutrients were never significant in more than 1 of 16 ANOVA's (Tilman 1987a; Inouye, Huntly, Tilman and Tester 1987; Tilman 1988a). The consistency of results from year-to-year and across fields of different ages, and their agreement with previous work (Tilman 1983, 1984), led us to focus on N as the soil factor most likely to influence primary productivity, plant community composition, and successional dynamics. However, they have raised a major question. Theory has predicted that a plant should adjust its morphology and physiology so as to be equally limited by all resources (Bloom, Chapin and Mooney 1985; Tilman 1982). Even when viewed on a species-by-species basis, CCNHA results suggest that plants are limited by two resources at most (N and light), and that P, K, Ca and trace metals are never limiting. Does this mean that plants are not as plastic (physiologically and morphologically) as theories have assumed? Could these ecosystems be invaded by species with higher requirements for P, K, Ca, and trace metals but lower requirements for N (i.e., legumes; Tilman 1982)? If so, why are legumes so rare at CCNHA? We have recently begun similar nutrient additions in a small, visibly zoned wetland, using 3 replicate plots per treatment in each of 4 zones. After 1 year, the 2 upslope zones showed significant N responses, but the 2 downslope zones did not respond to any nutrients.

Experimental Productivity Gradients Without Herbivores: Strong and consistent patterns of N limitation at CCNHA, correlations between successional dynamics and soil N (Figs. 4, 5), and separation of species along spatial or temporal N gradients (Fig. 6), raise questions that can only be tested using experimental N gradients:

1. Is the primary cause of secondary succession at Cedar Creek the slow increase in soil N, and the effects of this on plant competition for nitrogen and light (as hypothesized in the resource ratio hypothesis of Tilman 1982, 1985)?

2. How does the pattern of succession depend on the rate of N addition? Does N addition increase the rate of succession, but not the order in which species attain dominance, as predicted by the resource ratio hypothesis? Or, do different rates of N addition lead to distinctly different patterns of succession, as predicted by models of succession as transient dynamics (Tilman 1985, 1988a; Huston and Smith 1987)?

3. Can a high rate of N addition cause a temporary "retrogression," as predicted by models of succession as transient dynamics (Tilman 1988a), i.e., can a high rate of N

addition cause early successional species, that had already become rare in an old field, to reattain dominance? If so, are these species eventually displaced by other, late successional species, as predicted by this theory?

4. Do plant species become separated along experimental productivity (N) gradients in the same order as they are separated along natural productivity gradients? Can plant competition for N explain the point-to-point heterogeneity in plant abundances seen within old fields and oak savanna?

The **fenced nitrogen gradients** determine effects of various rates of N addition on productivity, species richness, spatial patterning, successional dynamics, and species composition of vegetation in the absence of the direct, indirect, and feedback effects of deer and gophers, the major herbivores. Each plot is 4m x 4m, separated from other plots by 1m-wide walkways and by metal flashing buried to 30cm. Each has 9 treatments, described in detail in Tilman (1987a), with 5 or 6 replicate per treatment in each of the 4 fields. Eight of the treatments receive the same mixture of P, K, Ca, Mg, S, Cu, Mn, Co, Cu, and Zn but differ in amounts of N added. The ninth treatment is a completely unmanipulated control. Nutrients are applied twice each year (starting in 1982), half in early May and half in late June. Application occurs in spring and early summer because that is when most N is naturally mineralized (Pastor et al. 1987b and unpublished). Each year since 1982, plots have been sampled for soil characteristics (total, available N; pH, etc.), plant biomass (sorted to species), vegetation height, litter, and light penetration. In 1986 and 1987, plots were sampled for below-ground biomass. This annual sampling will continue if the project is renewed.

These experimental productivity gradients have already provided numerous insights. As illustrated in Figure 2, and by other results in Tilman (1987a, 1988a), the dynamic effect of nitrogen addition is a successional sequence. Different rates of N addition cause different successional sequences. The "initial" effect (i.e., the effect within the first 6 years) of N addition has been to favor early successional species, including species that had already been previously displaced from the field. For instance, during old field succession, Agropyron repens reaches its peak abundance in 5 to 10 year old fields, and thus was quite rare in Field C (48 yr old) at the start of the experiment (Fig. 5).

Nitrogen addition caused it to increase more than 100 fold in abundance, especially in the highest N treatments, by 1987 (Fig. 10). Is this increase a transient effect resulting from Agropyron repens' high maximal growth rate, and thus its ability to more rapidly exploit the added nitrogen? If so, this would support the hypothesis that successional dynamics may be transient effects (Tilman 1988a), and not caused simply by the slow accumulation of nitrogen during secondary succession. This would refute the resource ratio hypothesis as the main explanation for succession at CCNHA. If the transient dynamics hypothesis is correct, Agropyron repens should be displaced from the high N plots by a series of other species that are taller than it, but that have slower maximal growth rates. There is already some indication that Rubus sp. (blackberry) and Rhus glabra (sumac) may be starting to displace Agropyron in some plots, but a longer time sequence is required to determine if that will occur.

N addition led to a marked decrease in the abundance of little bluestem, Schizachyrium scoparium (Fig. 10). Does this mean that little bluestem is a better competitor on poor soils than on rich soils? If so, why doesn't little bluestem normally reach its peak abundance early in secondary succession when soils are poor, rather than 40 to 50 years into secondary succession when soils are richer (Fig. 4A and 5)? Could the slow rate at which little bluestem comes to dominate successional fields be caused by slow colonization rates (10-12 years to invade most fields - Fig. 5), and slow competitive displacement of other species? Could it take 20 or 30 years for little bluestem to displace other species that are inferior competitors? If so, the first 50 years of succession at CCNHA could be transient dynamics. To test this, we have established a series of pairwise and multispecies competition plots (5 different grass species x 10 soil types; a total of 600 plots, with each plot being 0.75 x 0.75 m) to determine the rates of competitive displacement among various combinations of the 5 grass species most common during secondary succession. We will also perform invasion experiments (adding acorns, seed and seedlings of little bluestem, etc.) to plots to determine if succession is colonization limited. Succession is a slow, long-term process, that occurs over a period of decades. The experimental and observational data needed to test hypotheses that may explain succession must be collected over a comparably long period.

3. Herbivore Experiments

These experiments include (A) comparisons of the fenced N gradients discussed above with unfenced N gradients; (B) mammalian herbivore exclosures along successional and spatial productivity gradients; and (C) deer exclosures at the margins of forest and old fields to study the influence of deer on woody-plant invasion and soil nutrient dynamics.

Comparison of fenced and unfenced experimental N gradients: To determine effects of different rates of N supply in the presence of deer, gophers, and other mammalian herbivores, two sets of unfenced N gradients were established in the experimental old fields. Both allow mammalian herbivores free access. One set of 4m x 4 m plots is organized, treated and sampled as for the fenced gradient plots. The other set has 20 m x 50 m plots. Smaller plots have the advantage of greater replication but function as a foraging experiment for gophers, other small mammals, and deer. The larger plots, **unfenced macroplot N gradients**, have the disadvantage of fewer treatments and replicates (only 3 replicates of 3 treatments in each field), but are sufficiently large to show population responses of small mammals. Comparisons of fenced and unfenced plots allow determination of the direct effects and the indirect, feedback effects of herbivores.

Mammalian herbivore exclosures along spatial and temporal gradients: Initial CCNHA studies included small plots (a total of 168 plots, each being 2 x 4 m) from which various classes of herbivores were removed to determine how strongly they affected vegetation structure and its response to soil-resource supply. The largest effects were those of vertebrate herbivores, although we detected significant interactions among herbivore groups (e.g., removal of insects caused increased foraging by gophers). These studies suggest that many herbivore effects can be understood as effects on plant-resource dynamics (Tilman 1988a, Huntly, Inouye and Tilman, in prep). Unfortunately, our existing 2 x 4 m plots are too small to determine the long-term direct and feedback effects of herbivores. We require larger scale plots to test this hypothesis and determine the interactions of soils, herbivores, and plants. We propose establishing a series of 15 x 15 m plots. Because vertebrate herbivores are particularly important in plant-herbivore-soil systems at CCNHA and because insects cannot be eliminated without toxins that may directly affect soil processes, we will manipulate vertebrate herbivores only. This will parallel successional herbivore/plant/soil studies planned by the Taiga LTER.

Six sets of exclosures will be used to study the role of vertebrate herbivores in ecosystem dynamics and development along topographic and successional productivity gradients: 3 in old fields (newly abandoned, 20 yr old, 60 yr old fields) and 3 along Lindeman's Cedar Bog Lake transect (mixed oak forest, hardwood swamp, and cedar swamp). Each set will have 3 exclosures fenced to exclude deer and small mammals, including voles, pocket gophers, and hares, **and** 3 paired unfenced control plots. Thus, we will establish a total of 18 vertebrate herbivore exclosures and 18 control plots.

Consumer populations, plant populations, belowground biomass, and soil characteristics (organic matter, soil microflora, pH, total and mineral NH_3 and NO_3) will be measured yearly in each plot. Data will be used to develop and test models of herbivore feedback on soil development and plant productivity. These experiments will determine the role of vertebrate herbivores and changes in their effects along successional and spatial productivity gradients. Herbivore sampling will include invertebrates, documenting shifts that occur in response to manipulation of vertebrates.

Deer Exclosure Experiment: In addition to our exclosures of all mammals, we have deer exclosures. These test the hypothesis that winter-browsing by deer contributes to the slow invasion of old fields by trees and allow us to determine the feedback effects of a major herbivore on soils. CCNHA is a winter-yarding area for white-tailed deer (Odicoilus virginiana). Most saplings at field margins have been browsed repeatedly. The experiment, established in fall 1982, consists of 6 replicate 10 m x 30 m deer exclosures and controls in each of 2 old fields (Fields A & B). All saplings and adults are individually tagged and mapped; maximum height and DBH are used to measure tree size. Trees in control (unfenced) plots are measured in spring and fall; those in deer exclosures are measured in spring. The measurements provide data on height and species of CCNHA trees browsed each winter, the reduction in height due to browsing, and growth rates of individual trees.

Although excluding deer results in significantly greater sapling growth, the effect has been less than expected, averaging about 5 cm/year greater height growth in exclosures than in unfenced plots. Saplings < 15 cm are protected by snow and are infrequently browsed; terminal branches of trees >2 m tall are also rarely browsed.

Because tree height correlates positively with soil N, we hypothesized that trees are limited by N availability as well as by herbivores. We added N to treatment and control subplots starting in 1986. Although adding N has produced visible effects on herbs, as of fall 1987 added N had little effect on tree growth. (We have also added N and/or removed surrounding herbaceous vegetation in a separate experiment on sapling growth rates in old fields, and are following growth of tagged trees in the macroplot N gradients.)

A surprising result is the observation that about 1% of trees are killed each year by gophers. Because we can only identify dead trees, and not those that have had roots "browsed" by gophers, this is a conservative estimate of gopher effects on tree populations. We are mapping gopher mounds on the plots to monitor gopher responses to deer exclosures and to N addition, and to determine more accurately the impact of gophers on trees. By mapping trees and gopher mounds, our long-term record will allow us to examine effects of gophers on tree establishment as well as on mortality.

In summary, low levels of soil N, above-ground deer browsing, and below-ground gopher browsing may all contribute to the low rate at which trees invade old fields at CCNHA. Slow growth rates that result from low levels of soil N increase the time during which terminal branches of trees are susceptible to deer browsing. Gophers may also increase the time during which trees are susceptible to deer if they remove roots without killing trees. By continuing this experiment, and by starting experimental removals of all vertebrate herbivores, we will gather the long-term data needed to evaluate the effects of herbivores on the rate and pattern of old-field succession.

Feedback Effects of Deer on Soils: Previous studies at CCNHA have shown that fossorial herbivores alter spatial distribution of soil N through mound-building (Huntly and Inouye 1987, Inouye et al., 1987a). Herbivores can also alter soil N availability by feeding selectively on preferred species and thus altering litter returned to the soil (Pastor et al. 1987a). If selective feeding alters spatial patterns of plant communities (Schultz 1964, Bartholomew 1970, Batzli and Pitelka 1970, Huntly 1987), litter feedback could cause corresponding changes in the distribution of available soil N. Because N is limiting in CCNHA old fields (Tilman 1987), changes in N availability through selective foraging could amplify spatial heterogeneity, leading to multiple stable equilibria. Selective deer browsing on oak and pine can alter litter return by increasing the proportion of grass litter (which is less lignified than oak or pine litter; McClaugherty et al. 1985, Parton et al. 1987), by enhancing the proportion of root litter (because of greater root/shoot ratios in grasses), and by dispersing litter deeper into the soil (because of differences in root morphology of trees and grasses). However, the effects of deer exclusion will only be observable through long-term measurements of litter return, decomposition, and N availability in deer exclosures and controls. Roots, twigs, leaves and litter will be sampled for chemical analysis. Root biomass and production will be determined by monthly coring. Litter traps in each plot will be sampled monthly. Long-term litterbag experiments, that complement those already described, will be established to study decomposition over at least 10 years. Soil-N availability will be measured in situ by buried polyethylene bags (Pastor et al. 1984), and under optimal conditions by laboratory incubation (Stanford and Smith 1972). CO_2 evolution will be measured simultaneously in lab incubations. The proportions of N and C mineralized, and the ratio of N mineralized to CO_2 evolved, will be used to estimate organic-matter quality.

4. Disturbance Experiments

The most important disturbances at CCNHA before European settlement were fire, soil disturbances by mammals (especially gophers), and climatic change; the most important now is agricultural tillage. Our experiments are designed to determine impacts of each of these on CCNHA ecosystems, through (A) prescribed burns of various frequencies, now in continuous operation for 24 years in native oak savanna; (B) different fire frequencies in a 25-yr successional field; (C) effects of gopher disturbance; (D) studies of secondary succession after agricultural disking in plots that differ in rates of N supply; and (E) manipulations of water table for communities near the upland-wetland boundary.

Prescribed Burns in Oak Savanna: Fire was a major disturbance at CCNHA until the early 20th century, when road construction, tilling of fields, and active suppression greatly decreased its frequency. Paleoecological studies suggest that CCNHA was swept by fires approximately every other year until the start of the 20th century. What impact has fire suppression had on CCNHA ecosystems? What role did fire play in maintaining prairie and oak savanna at CCNHA? How does fire frequency influence soil characteristics, vegetation structure and composition, and herbivores? Questions such as these led Dr. Frank Irving (College of Forestry) to establish 15 burn compartments, ranging from 2.6 to 27.5 ha, in a block of oak savanna /oak woodland at CCNHA 24 years ago (White 1983). He assigned these randomly to different fire frequencies (3 control plots with no burns, the others having burn frequencies from one burn every 7 - 10 yr to annual burns). In 1984 we established 25 permanent quadrats per burn compartment and sampled vegetation and soils (Tester 1988). Following Irving's retirement, LTER has continued this experiment. Indeed, if it were not for LTER, these long-term experiments would have stopped when Irving retired. LTER will resample permanent quadrats in 1989 and every 5th yr thereafter, allowing analysis of results both for any sampling date, and in terms of changes since previous samplings. This experiment has shown dramatic effects of fire frequency on abundance of various plant life-forms (trees, shrubs, grasses, and forbs), but the effect on soil N and soil organic matter, though in the expected direction, is not statistically significant (Tester 1988). The compartments are still undergoing changes in response to fire. Many more years will be required to demonstrate steady-state fire effects, but by looking at changes (relative to archived samples) in soil organic matter and N in **permanent quadrats** over 5-yr intervals, we should be able to detect small changes.

Old Field Burns: In 1983 we began another burn experiment (in coordination with the Konza LTER) in a 26 yr field dominated by little bluestem. We use 4 fire frequencies (annual, every other yr, every 4th yr, and no burn). The 7 x 7 m plots are completely randomized, with 6 replicates per treatment. Sampling has shown almost no significant effects of fire on total or mineral N, plant-species composition or biomass, or plant life-form abundance during the first 4 years, in marked contrast to Konza where effects are rapid. We will meet with Konza scientists to try to determine why their burn experiments lead quickly to dramatic differences, but ours did not. One possibility is that in their more productive systems, litter accumulates more rapidly without fire, and this inhibits growth because of nutrients tied up within it.

Gopher-Disturbance Experiments: Work on pocket gophers (Geomys bursarius)in CCNHA old-fields suggests that these fossorial rodents are important to succession, small-scale spatial variability in productivity and vegetation, plant population structure, soil/vegetation equilibrium, and small-scale variation in resource availability and soil development. Effects of pocket gophers may be analogous to the "cascading trophic effects" proposed by Carpenter, Kitchell and Hodgson (1985). Although their model specifically considers "top-down" effects of predators on food-web structure and patterns of productivity, whereas gophers are primary consumers, gophers appear to have similar effects throughout the food web at CCNHA.

Gophers affect the small- and large-scale diversity of plant communities, and decouple otherwise tight correlation between soil characteristics (especially soil N) and plant dominance and diversity (Tilman 1983; Inouye, et al. 1987a, b; Huntly and Inouye 1988). Gophers also decouple soil resources and light; this appears to be a major mechanism by which they alter vegetation (Huntly & Inouye 1988). Gophers alter soils by depositing N-poor subsurface soils (Inouye et al. 1987a) and by creating caches of nutrient-rich plant and waste material (Zinnel 1988 and Tester).

We hypothesize that gopher effects can be modelled as effects of disturbance on resource supply and demand (Huntly and Inouye 1988, Tilman 1988a), a hypothesis that may apply to voles and other foliage-consuming herbivores. As part of our continuing study of ecosystem structure and dynamics along spatial and temporal productivity gradients, we shall further investigate several other questions concerning gopher/soil/vegetation interaction:

1) Do gophers decrease along successional productivity gradients despite apparent increase in food plants? Does the lower rate of above-ground disturbance by gophers reflect behavioral alterations caused by changes in established burrow structure, or in the distribution of vegetation (e.g., increased root biomass-Fig. 4I) or its nutritional value and secondary chemistry? The first step in this investigation will be direct determination of gopher densities and annual fluctuations in several unmanipulated old-fields. Trapping and marking will be done in areas adjacent to permanent sampling regions in these old fields.

2) How do pocket gophers affect coupling of soil characteristics, especially N-mineralization rates, and vegetation; and how do they alter vegetation/soil feedbacks? Preliminary data suggest that gophers decouple an otherwise tight correlation of soil organic matter, available N, vertical, light profiles, and vegetation structure (Tilman 1983, 1987; Huntly & Inouye 1988). We shall explore these relationships by observations on an unfenced experimental productivity gradient in Field E. Studies will include detailed sampling of the existing gradient of soil N availability with known histories of gopher activity and vegetation as well as the creation of artificial gopher mounds using sterile topsoil or N-poor subsoil and with or without shade. Artificial gopher mounds allow a direct test of mechanisms that underly the correlation between total soil N, standing crop of plant N, light, vegetation, and gopher activity.

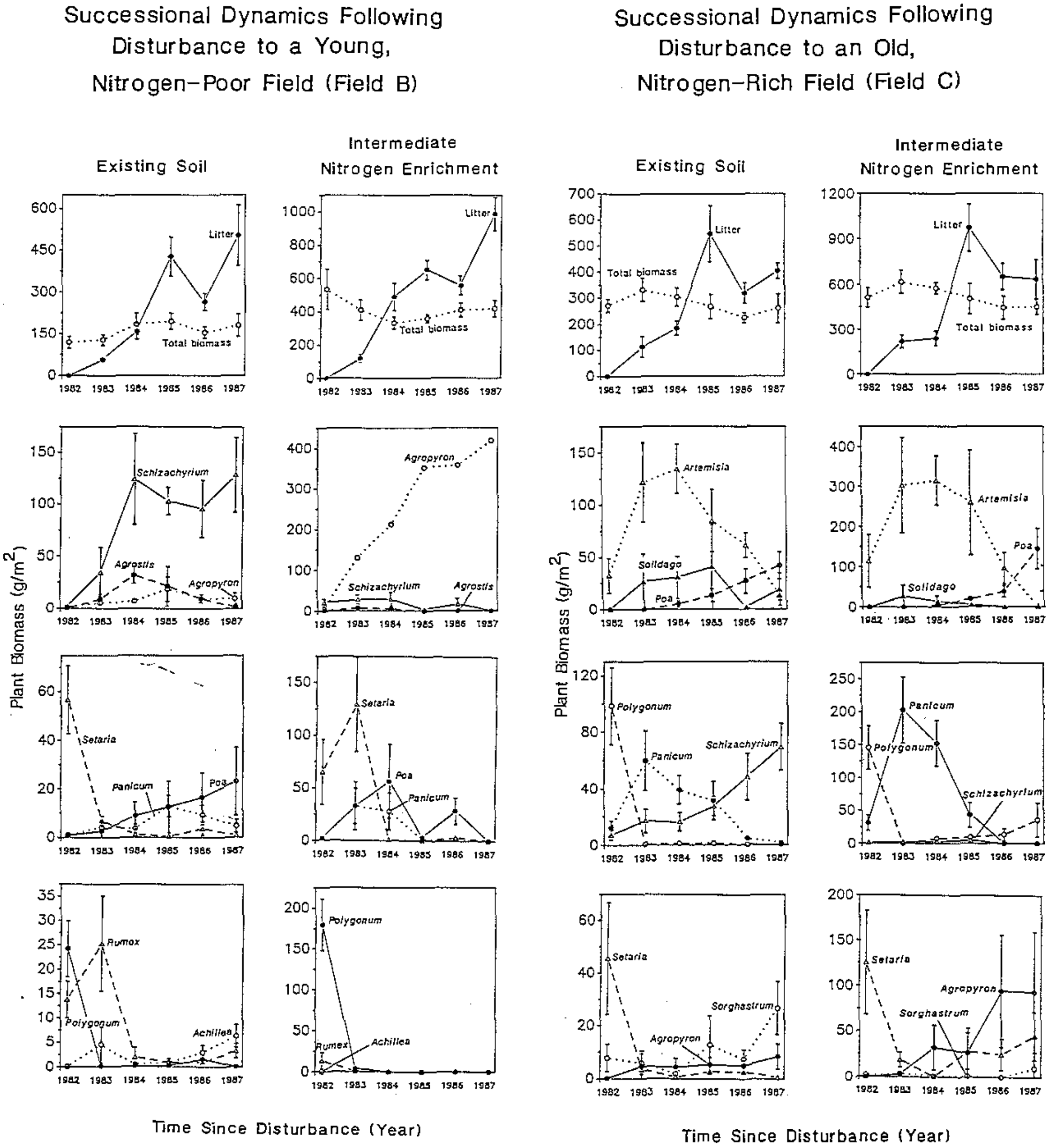
3) Gophers abundance in a field is the best predictor of abundance of grasshoppers, the dominant invertebrate consumers in recently abandoned fields. How do gophers affect grasshopper abundance? We shall use artificial gopher mounds to test whether they increase grasshopper abundance by increasing suitable oviposition sites. Mounds will be sampled for grasshopper eggpods, assayed in turn for parasitism. Artificial mounds will be placed in old fields designated for manipulative study (but not included in LTER samples), assaying effects on subsequent grasshopper population density and composition.

Disturbed versus Undisturbed Nitrogen Gradients: Clearcutting, plowing, and farming has created a landscape at CCNHA characterized by a mosaic of fields and remnant forests that differ in disturbance history and productivity. The old-field chronosequence suggested that both time since disturbance and soil N were major causes of succession (Inouye et al. 1987a). Is time important because succession is caused by transient dynamics resulting from differences in maximal growth rates or colonization rates (Tilman 1985, 1987, 1988)? Or, is time important because of slow accumulation of soil N? Can spatial heterogeneity in plant species abundances within individual fields, and among fields of the same successional age, be explained by differences in N-supply? How is succession influenced by starting conditions, such as initial species abundances?

To explore these questions we established disturbance experiments in the 3 experimental old fields in 1982 by thoroughly disking a region in each and dividing it into 54 plots, each 4 m x 4 m. These plots received different rates of N addition, with treatments identical to the fenced nitrogen gradient experiments (Tilman 1987). We have observed 6 years of succession on these disturbed plots (Fig. 11). N supply strongly affects successional dynamics, with a different trajectory for each rate of N addition. The pattern of succession also depends on the initial floristic composition of the plots and the colonization rates of different species. This raises several questions. What traits allow plants to be early successional species on poor soils? On rich soils? How do mid- and late- successional species of poor and rich soils differ in life history and morphology? Data on allocation to roots, stems, leaves and seeds by common species (being collected by Dr. Scott Gleeson) will help us address these questions.

To our surprise, the initial effect of N addition was **divergence** among replicates of a given treatment (Inouye and Tilman 1988). Might this occur because plot-to-plot differences in initial composition were magnified by rapid growth rates following N addition? Although trajectories of population density for major species suggest that replicates are starting to converge as species that were initially absent invade plots (Inouye and Tilman 1988), the slowness of colonization and competitive displacement mean that many more years of observation will be needed to test this hypothesis, and to document the pattern of succession following disturbance.

Responses to Climatic Change: Climatic warming over the next several decades will disturb ecosystems greatly. Annual monitoring of habitats and processes throughout the CCNHA landscape will allow us to document impacts of climatic change on these ecosystems.


Successional Dynamics Following Disturbance to a Young, Nitrogen-Poor Field (Field B)

Successional Dynamics Following Disturbance to an Old, Nitrogen-Rich Field (Field C)

Figure 11. The dynamics of succession on poor and rich soils. In 1982, plots in Fields A, B and C were disturbed via thorough disking (Tilman 1987), and then divided into replicated plots that received different rates of N addition. The rate of N addition had a major impact on the pattern of succession, as shown above for 2 of the 9 treatments, in 2 of the 3 fields. Thus, contrary to our initial hypotheses, N addition does not just speed up successional dynamics, it changes the successional trajectory. This, on the surface, is consistent with predictions of the theory of succession as transient dynamics in Tilman (1988a), but must be compared with allocation patterns to test this hypothesis.

Of all CCNHA habitats, wetlands and the wetland-upland ecotone are likely to show the most immediate and dramatic responses to of this disturbance. Wetlands are distinctly patterned in relation to water-table depth, fluctuation, and water flow (Jeglum 1971; Stewart and Kantrud 1972). Changes of a few cm in water level can alter species composition, productivity, carbon accumulation, and biogeochemical cycling in wetlands. Moreover, wetlands comprise almost 40% of CCNHA's surface area. We have, therefore, chosen them for one of our experimental studies of disturbance -- that of rapid climatic change.

Our experimental, observational and paleoecological work on wetlands is designed to answer such questions as: 1) How will wetlands respond to climatic warming? 2) Will they exhibit strong and early responses because of sensitivity to changes in water-table? 3) Will responses be especially rapid and substantial close to the forest/prairie border where annual precipitation and evaporation are about equal? 4) Will the main cause of species migration be physical change in environment or interspecific interactions? 5) Will the ordering of plant species distributions with respect to water-table remain the same, or will some species migrate rapidly and others -- owing to biological inertia (Gorham 1957) -- slowly? What are the time-lags between changes in water-table and changes in plant populations? 6) Will herbivores and parasites have greater or lesser effects on vegetation following climatic warming? 7) Will changing climate alter substantially the cycles of elements (C, N, and S) through effects on production, decomposition and storage of organic matter, and upon gas fluxes (C,N,S) and peat and pore-water chemistry -- especially redox potential? Finally, 8) What will be the effect upon chemical contributions of wetlands to groundwaters?

Because the direction of future climatic change in any given location is uncertain, and because effects of climate change upon runoff and soil moisture are likely to be complex (Mitchell and Warrilow 1987), we shall examine wetland responses to rising as well as falling water-tables. Wetlands depositing peat are of particular interest because their record of response to water-table changes -- especially that provided by fossil bryophytes (Janssens 1986) -- can be used to predict future changes in wetland ecology and biogeochemistry. We shall address the questions raised above by three approaches.

1) Observations will be made on the composition of visibly zoned plant communities, and their element cycling, in permanent plots along water-table gradients in small marshes and peatlands at CCNHA. A special focus will be measurement of annual tree growth as radial stem increment, which likely increased rapidly during the 1930's drought, and annual litterfall, a more direct surrogate for net primary productivity. Effects of changing herbivory (by insects and small mammals) will also be investigated.

2) We shall determine by paleoecological studies of dated short and long peat cores (50 cm to several meters) changes in vegetation, and in storage of carbon and other elements, in relation to past climatic warming, for instance the 1930's drought and the mid-postglacial warm period. Bryophyte-fossil assemblages, which can change dramatically on a time-scale of a decade or so, will be used to reconstruct changes in water table and pH (Janssens 1986).

3) We shall alter water tables experimentally at 2 scales: first, in a project begun at CCNHA in 1987, by raising and lowering small (50 x 50 cm) monoliths of peat and vegetation 10-15 cm in situ, or transplanting them to other lower and higher vegetation zones; and second, by drawing down larger (10 x 5 m) plots at CCNHA, isolated by impervious walls to 2 m depth, and pumping the water into similar plots nearby, altering water tables by 10-20 cm. In addition, Gorham is seeking other funds to perform similar experiments, including the drawing down of whole wetlands, in habitats such as the forested kettle-hole bogs of the North Central Forest Experiment Station's Marcell Forest, and the reed swamps of the Agassiz Wildlife Refuge.

In summary, the comparative observations, paleoecological analyses, and manipulative experiments proposed will aid greatly in predicting the magnitude and timing of wetland responses -- biological and geochemical -- to climatic disturbance caused by the accumulation of greenhouse gases. We are eager to establish this work at the present time, and believe that it is central to the mission of LTER because future climatic change may be one of the greatest disturbances to CCNHA, and, indeed, the globe.

C. Ecosystem Modelling and Ecosystem Theory

Modelling is an integral part of our program. CCNHA researchers are developing and testing models of soil C and N dynamics (NCSWAP; Clay, Clapp, Molina and Linden 1985), peatland hydrology (PHIM; Guertin, Barten and Brooks 1987), dynamics of soil base saturation and pH (TITRSOIL; Bloom and Grigal 1985), successional dynamics (the resource ratio hypothesis; Tilman 1982, 1985), transient dynamics that might follow ecosystem disturbance (ALLOCATE; Tilman 1988a), and plant life form (allocation to roots, stems, leaves and seeds) along productivity and trans-biome gradients (ALLOCATE; Tilman 1988a). These models are not developed for their own sake, but represent a constant feedback between theory, experimentation and observation -- all of which are essential aspects of ecological research. Modelling is essential because it explores the underlying logic of possible cause and effect and feedback relations in ecosystems, allowing the development of new hypotheses to explain patterns. Modelling never stands on its own, but can uncover the logical (i.e., mathematical) predictions that result from a given set of simplifying assumptions. If model predictions are inconsistent with observational or experimental data, one or more simplifying assumptions were incorrect. This is a crucial part of the scientific process, for it leads to rejection of old and creation of new hypotheses.

These points provide the rationale for our use of models in long-term experiments. Models are needed to interpret the dynamics of long-term experiments, to generate hypotheses, to make predictions that experiments can test, and to ensure that hypotheses and field experiments are logically consistent. Long-term observations and experiments are expensive. Models are essential tools for their efficient design and interpretation.

We do not have the space to elaborate on all the models we are using, but we shall highlight two new ecosystem models we plan for upcoming years. Each of these is spearheaded by a scientist who will join our team upon renewal: Dr. Anthony Starfield (Professor of Civil and Mineral Engineering and of Ecology and Behavioral Biology); and Dr. John Pastor (Adjunct Assistant Professor of Ecology and Behavioral Biology and Research Scientist at the University's Natural Resource Research Institute)

1. Soil-Plant-Herbivore Interactions and Feedback Effects

The structure of an ecosystem emerges from the interactions among its elements and their feedback effects on each other. We want to develop a model of the interactions and feedback effects among soils, plants and herbivores. We hypothesize that the structure of terrestrial ecosystems comes from the interplay of both the bottom-up effects of soils on plants and of plants on herbivores and the top-down effects of herbivores and plants on soils. Depending on whether such effects represent positive or negative feedback, and the time scales on which they operate, they can cause ecosystem convergence, divergence, or sustained, long-term oscillation (DeAngelis et al. 1986).

We will start by hybridizing existing models. There are several candidate models, including ALLOCATE (Tilman 1988a), NCSWAP (Molina et al. 1983), LINKAGES (Pastor and Post 1986), and CENTURY (Parton et al. 1987). Each has one or more advantages for our purposes, each overlaps to some degree with at least one other model, and each is deficient in one or more respects. Because only ALLOCATE and LINKAGES consider individual plants, and we will begin by coupling ALLOCATE and LINKAGES.

ALLOCATE predicts the growth and carbon and nutrient allocation of individual plants from seed germination through senescence. It is driven by data on N availability and disturbance, and will be modified to include temperature. It predicts how allocation patterns affect light extinction through the canopy. The disadvantages of ALLOCATE are that there is no feedback of litter on nutrient dynamics and herbivory is not included.

LINKAGES predicts the growth of individual trees from sapling size through maturity at annual time steps, and how changes in species abundance affect soil N availability through litter decay, thus complementing ALLOCATE. It is driven by data on climate and soil water holding capacity. It includes explicit feedbacks between light, water, and nitrogen availabilities and their resulting effects on species composition and productivity. However, as with other JABOWA/FORET models (Botkin et al. 1972, Aber et al. 1982, Shugart 1984), it assumes that plant allocation is fixed and that growth is determined by reducing a maximal diameter increment curve to the extent that resources are less than optimal. Germination and seedling-seedling competition are not included.

We will couple ALLOCATE and LINKAGES by using ALLOCATE to predict individual plant growth, allocation, and litter return and using LINKAGES to predict litter decay and nitrogen availability. We will begin by simulating the interactions between two species, a tree (nominally oak) and a grass. A model of mixed-life-form competition is essential to explain the grassland to forest transition that occurs at CCNHA. Additional species, including herbivores (selective and non-selective by tissue chemistry and leaf height) will be added to determine how life history strategies and trophic structure affect ecosystem properties, which are major topics of our long-term experiments. Pastor is currently simulating herbivory in boreal forests using LINKAGES under independent NSF funding (BSR-8614960), and many of the techniques developed in that project will be of use here. Parameters will be based on CCNHA data. Whether or not herbivory is required to validate the model is an interesting problem. Parton et al. (1987) could not validate the CENTURY model of grasslands without herbivory, but LINKAGES has been well validated for forests of the Great Lakes region without inclusion of herbivory (Pastor and Post 1986). We suspect that herbivory will be needed to validate our model because of the differences in herbivory caused by size differences between herbaceous and woody species.

We will use this model to explore other questions. Disturbances can be simulated as stochastic events, but we hypothesize that the frequency of some disturbances may arise from feedbacks and constraints. Fire, a key disturbance at the forest-prairie border, is a function of fuel supply and moisture, and is therefore an integral part of the plant, litter, soil feedback loop. We wish to understand how fire interacts with ecosystem processes at CCNHA. Data available at CCNHA on the effects of fire can provide a basis for construction of a modified version of the ALLOCATE-LINKAGE hybrid model. Under independent NSF funding (BSR-86159), Pastor is incorporating a fire simulation model (Van Wagner and Pickett 1985) into LINKAGES.

Finally, we will embed our hybrid model in a spatial context so as to simulate dispersal of organisms and disturbances. Each simulated plot would be affected by events in neighboring plots. For example, plant germination rates would be functions of seed production in a plot and in adjacent plots. Similarly, the probability of fire in a plot would depend on conditions within a plot and within its neighborhood. We will embed the model in a landscape context by coupling it with a geographic information system (GIS). The GIS will provide data on spatial distribution of driving variables for the model, and ouput of model predictions will be reentered into the GIS to examine spatial patterning of ecosystem processes. NRRI, Pastor's home institution, currently has an ERDAS GIS, and a proposal has been submitted to the NSF Biological Facilities Centers Program for additional GIS capability. Further, we will coordinate our modelling with W. Parton and H. Shugart, who are exploring methods to extend FORET-type models to grasslands as part of programs at the CPER LTER and the Virginia Barrier Island LTER.

2. Expert System Modelling

There are two ways to conceptualize an ecosystem: as a system structured by the intricacies of the interactions among all its constituent parts, or as a more holistic structure that can be understood in its broad outline by the interactions among a few major variables. These two views correspond roughly to simulation models versus simple, qualitative overview models of ecosystem structure and function. We believe that it is important to develop both. Thus, in addition to the simulation models discussed above, we will build qualitative models. A picture representing a nutrient cycle or food-chain is a rough representation that helps show how different components of the system interact. Unfortunately, such a picture is static: it imparts no information about rates of transfer, system dynamics, or effects of disturbances. Starfield and Bleloch (1986) suggested that it should be possible to build qualitative models using the technology of **rule-based expert systems.** Starfield, Farm and Taylor (1987) developed a qualitative, rule-based model of a shallow estuarine lake. It has shown the importance of including dynamics and feedback effects, even in a course and qualitative way: the model predicted that rates of change of salinity had a greater impact than salinity levels per se.

The LTER at Cedar Creek offers an opportunity to develop and test qualitative, rule-based models as an integral part of our studies. We will start by developing expert system models for nitrogen cycles, for secondary succession, and for soil-plant-herbivore interactions. These models would parallel the more complex simulation models we are developing (NCSWAP, ALLOCATE, the hybrid of ALLOCATE and LINKAGES). By comparing and contrasting the predictions of these two approaches to modelling, we should be able to determine the essential features of the models. This project will be cooperative and interactive, with Starfield working with interested faculty and graduate students in model development, testing and modification.

D. CROSS-SITE SYNTHESES

We are interested in developing and testing general ecological principles at several spatial and temporal scales. A major new thrust of the CCNHA LTER project will be cross-site integration and synthesis. With our strong local data base, and the similar data sets that have now developed at other LTER sites, we are excited by the potential for cross-site syntheses, 6 of which we list below.

1. **Regional and global cross-site comparisons of controls on N availability**

Soil-N mineralization often limits the rate of net primary production and is part of a reciprocal feedback loop between the C and N cycles (Pastor and Post 1986). Because different species have different requirements for N and have litter of different C qualities, patterns of N mineralization both influence and are influenced by plant competition. At global scales, N mineralization and species composition are controlled by climate, but there has been no systematic examination of the relations between N mineralization, organic-matter quality, and climate. Pastor and Tilman propose to undertake such a synthesis, in conjunction with researchers at other sites.

N mineralization data, obtained using comparable methods, are available for a soil chronosequence at CCNHA (Pastor et al. 1987b), old-growth pine, oak, maple and hemlock forests and second-growth pine plantations and successional stands in S. Wisconsin (Nadelhoffer et al. 1983, Pastor et al. 1984), boreal forests on Isle Royale (Pastor and Naiman, ongoing), second-growth maple and oak forests in S. Michigan (Zak et al. 1987) and old-growth maple and hemlock forests in N. Michigan (Mladenoff 1987). There is a strong climatic gradient across these sites, with mean annual temperature and actual evapotranspiration increasing southwestward and precipitation decreasing westward. Similar data are available for LTER sites: Hubbard Brook (Melillo 1977), Konza and Central Plains (D. Schimel, pers. comm.), Bonanza Creek (Gordon et al. 1987), Arctic Tundra (Nadelhoffer pers. comm.) and Jornada (W. Whitford, pers. comm.). This provides a wide range of N-mineralization data spanning northern hardwoods, boreal conifers, grasslands, desert, and tundra, with the greatest concentration in the region of steepest climatic gradients. Data are also available on other soil properties for these sites. Organic-matter quality has not generally been measured except for C/N or C/P ratios. We will obtain samples of these soils for organic-matter fractionation (Johnson 1979, Spycher et al. 1983, McClaugherty et al. 1985). We will collate, verify, analyze, synthesize and publish these data in collaboration with interested scientists at these other sites.

2. The Trans-Biome Life Form Gradient of North America

A striking feature of North America is the complex productivity and physiognomic gradient from desert grasslands, to shortgrass prairie, to tallgrass prairie, to oak savanna, to deciduous forests. It is all the more striking because of its similarity to productivity gradients on other continents, reviewed in Whittaker (1975) Beard (1983) and Tilman (1988a). Whittaker (1975) synthesized IBP data to describe and explain the North American gradient. Since then there has been an immense increase in our knowledge of processes that might cause these patterns, but data are site-specific and have not undergone cross-site comparison and synthesis.

Tilman is interested in causes of trans-biome gradients; his recent book reviews them and proposes theoretical explanations (Tilman 1988a). He will lead in synthesizing data from LTER sites along the North American gradient, and has requested partial support for this in a renewal request for the LTER National Coordinating Grant.

Such a synthesis is appropriate at this time for several reasons. First, 7 LTER sites span the major biomes along this gradient (Fig. 3): the most productive end is represented by cove forests (Coweeta), then come northern hardwood forest (Hubbard Brook), oak-beech-maple forest (Kellogg), oak savanna and prairie (CCNHA), tallgrass prairie (Konza), shortgrass prairie (CPER), and finally desert shrublands and grasslands (Jornada). Each LTER site has gathered detailed information on underlying processes that influence primary productivity and vegetation structure, including data on nutrient limitation and nutrient dynamics. Tilman has contacted scientists at each site to start developing a network for this cross-site research. Second, there is growing interest in explaining these broad-scale patterns using a variety of conceptual or theoretical approaches (Oksanen et al. 1981; Menge and Sutherland 1987; Tilman 1988a; Shugart and Parton, pers. comm.). To test among these hypotheses, we need a detailed record of the ways that various attributes of populations, communities and ecosystems change along the gradient.

In cooperation with scientists at the other sites, Tilman will coordinate collation of data. If the LTER National Coordinating Grant can provide funds, he would also coordinate collection of any data currently missing at a particular site. We hope to use data from 3 replicate stands (relatively free from anthropogenic disturbance) within each site. At each we will either collate or collect information on:

(1) Net primary productivity, plant heights, growth forms, and biomass distribution among leaf, root and stem;
(2) Root distribution at various depths in the soil;
(3) Storage of C and N in different soil horizons;
(4) Proportion of net annual productivity consumed, as well as identities and densities of major herbivores;
(5) Levels of extractable NH_4 and NO_3, preferably once a month through the growing season;
(6) <u>In situ</u> N-mineralization rates and rates of supply of other limiting soil resources;
(7) Concentrations of other soil resources that limit productivity at the site,
(8) Vertical light profiles once a month during the growing season;
(9) Soil incubations from each site under a range of standardized temperature and moisture to determine N-mineralization rates and the level to which nitrifying bacteria can reduce NH_4 in the absence of vascular plant uptake;
(10) Climatic data (mean and variance for precipitation, actual and potential evapotranspiration, and temperature for each month of the growing season; and
(11) Seasonal changes in water-table depth;
(12) Soil-profile descriptions;
(13) Frequencies, intensities, and spatial and temporal extents of disturbance.

Although this data set is massive, it can be assembled within a few years. Much has been collected, and can be compiled by interactions among data-managers at the sites. For instance, this full data set has already been collected at CCNHA. The CCNHA data-manager will take a lead role. Soil incubations would be performed by Dr. D. Zak, a post-doc at CCNHA. Chemical analyses would be performed at CCNHA to assure intersite comparability. Standardized samples for chemical analysis would be provided to all sites contributing data. Once the multisite data set is assembled, Tilman will perform preliminary analyses and send tables, figures, and the compiled data set to interested scientists at other sites. This group would then discuss the data and prepare papers for publication.

This project will determine if there are broad, inter-biome patterns in vegetation structure, nutrient dynamics, and herbivory that are linked to differences in productivity along this North American gradient, and the extent to which such patterns result from similar underlying constraints and mechanisms. Comparison of population, community and ecosystem processes along this complex productivity gradient may help explain it and yield insight into processes controlling similar gradients around the globe.

3. A Hierarchical Approach to Disturbance and Persistence

Dr. Timothy Allen of the Northern Lakes LTER has been funded by the LTER National Coordination grant to perform cross-site comparisons of the role of hierarchical processes throughout the LTER network. We are collaborating with him in this endeavor by providing data needed for these cross-site comparisons. As an outgrowth of our interactions with him, we have broadened our efforts to understand the role of spatial hierarchies at Cedar Creek. We have chosen as our starting point the question of the forces that allow the persistence of a species within a landscape. Such persistence depends on the interactions between an individual and its microsite, the probability that propagules will migrate to a suitable microsite, the rate and spatial patterning of the creation of suitable microsites, and the rate of extinction at microsites. As such, it encompasses several different spatial and temporal scales. The basic question -- whether or not a species will persist -- can only be answered by considering all these scales and the interactions among them. Dr. Mark Davis is working in conjunction with Tim Allen on a project that looks at the role of fire, pocket gophers, and microsite successional processes in determining the persistence of a prairie forb (Penstemon grandiflorus) on the oak savanna of CCNHA. The work combines microsite studies of local persistence, larger scale studies of colonization of gopher mounds, and landscape level studies (using GIS) of patterns of fire and long-term habitat creation, and uses these to test hierarchy theory (Allen and Starr 1982;

Allen et al. 1984; O'Neill, et al. 1986). Hierarchy theory is a new, largely theoretical, speculative and controversial area (Ricklefs 1987) that needs studies such as this to test, refine, and/or reject it. This work was initiated with funding from the CCNHA LTER grant and now has additional direct NSF support ("Disturbance and the Dynamics of Pattern in a Sand Plain Oak Savannah: A Hierarchical Approach to the Problem of Species Persistence," NSF/BSR 8717847 for $125,444 for 6/1/88 to 5/31/91).

4. Intersite Comparisons of Succession

Succession is often defined as the dynamic response of an ecosystem to disturbance. Because disturbance is one of five core LTER areas, all LTER sites, in effect, study succession. Although interest has been growing in processes and mechanisms that underly successional patterns (West, Shugart and Botkin 1981), most research has involved detailed studies at a single site or compared ecosystems dominated by a single life form or starting condition, as in old field succession. Past studies of succession may have suffered because of emphasis on similarities rather than differences. Cross-site studies involving explicit comparison of successions in widely different habitat types and with widely different starting conditions have been rare, but may provide new insights into successional processes.

Many LTER sites, and several other sites in which succession has been studied, afford an opportunity to compare and contrast successional dynamics in diverse ecosystems, determining dependence of the rate and pattern of succession on primary productivity, climate, substrate, disturbance history, herbivory, and initial composition. These sites form a gradient from old field successions on N-poor, unproductive soils (CCNHA and Savannah River laboratories) to those on moderately productive soils (Buell's old fields at Rutgers, the North Carolina Piedmont, and old fields at Kellogg LTER), to old-field successions on highly productive soils (Coweeta LTER). LTER sites at Hubbard Brook, the Alaskan Taiga and Andrews Experimental Forest provide similarly great contrasts in climate and productivity for successions in clearcut or burned forests, as well as contrasts with old-field successions.

These sites span a large portion of the geography, soils and climate of North America, as well as types of disturbances that can initiate succession. Although all (presumably) will eventually be dominated by forest, they have markedly different dynamics. Old fields at Coweeta have a closed canopy of trees 10 m tall after 15 years, whereas 60-year fields at CCNHA have at most 15% cover by woody plants, most of them vines, shrubs, or stunted trees under 1 m in height. There may be equally great differences among these successions in other parameters, such as extractable NH_4 and NO_3, root:shoot ratios, N-mineralization rates, and plant life-histories.

We are establishing contacts at these sites and the CCNHA data manager will coordinate data collation among them. Maximum effectiveness depends on additional funds, which Tilman has requested as part of the renewal request for the LTER National Coordinating Grant. We will coordinate our work with a project initiated at the Savannah River Laboratories, where a group will meet on March 14 and 15, 1988 to compare and contrast studies of old field succession. Once data are collated and preliminary analyses have been performed, interested scientists from all sites will meet to discuss the data and to begin preparing papers(s) based on it for submission to peer-reviewed journals.

5. Dynamics of Carbon and Nitrogen

Dr. Jean Molina has been working to verify NCSWAP, a dynamic model of interactions among soil microorganisms, C sources, and N at CCNHA, and will use it to predict both long and short-term dynamics of organic matter and N in CCNHA soils. It is similar in approach to PHOENIX (McGill et al. 1981), which was developed at the CPER LTER. It provides an interesting contrast with Parton's CENTURY model, which predicts long-term dynamics of soil organic-matter and N. In cooperation with CPER scientists, we will compare and contrast these models by applying each to data gathered in the other system.

6. Other Cross-Site Comparisons

CCNHA scientists are involved in several other cross-site syntheses and comparisons.

A. Grigal is collaborating with K. Pregitzer (Kellogg) in developing a GIS for regional comparisons of forested ecosystems. We have also discussed with participants at Kellogg the application of GIS to ecosystem hydrology, especially in poorly-defined drainage systems in recently-glaciated areas of low relief. This is relevant to assessing movement of materials derived from natural or anthropogenic activities to ground water. We and those investigators are preparing a proposal to explore such topics.

B. We are collaborating with J. Magnuson to compare patterns of spatial and temporal variance within and among a series of LTER sites. We have contributed all relevant data from the first 6 years of the CCNHA project, and will participate in an upcoming session to synthesize results for all participating sites in the LTER network.

C. Successional dynamics are a major theme of the research being performed at both CCNHA and at the Taiga site. Van Cleve et al. (1987) have recently reported that depth to the water table is an important soil-associated property that varied in a predictable way with successional stage. Changes in that property affected many other physical and chemical processes in their systems. We will coordinate and compare our studies on effects of water table with theirs.

D. During the second year of the CCNHA LTER, a group of scientists visited Konza and planned coordinated fire experiments. This past summer we completed the first 4-year burning cycle and are analyzing data to compare our results with those at Konza.

E. We are interested in the importance of ecological inertia, i.e., the possibility that ecosystems may have a structure more in tune with past than with present environmental conditions. If correct, disturbance may allow an ecosystem to come more rapidly to equilibrium with its present environmental conditions. This is a major theme at Niwot Ridge LTER and we plan to compare our results with theirs.

F. We have encouraged cross-site comparisons by organizing and participating in the first LTER All-Scientists Meeting at the University of Minnesota' Itasca field station. We have also participated in and organized many other cross-site workshops.

G. There are many other areas with significant overlaps between our studies and those at other LTER sites. We believe that ecological knowledge can advance most rapidly if we combine detailed studies of site-specific processes performed at CCNHA with comparisons among various sites. To that end we shall continue to initiate other cross-site comparisons, will continue to be willing contributors of data and ideas to projects suggested by others, and will continue to gather additional data requested by others to the fullest extent possible within our resources. For instance, we helped Dr. Tim Schowalter of Andrews LTER establish an experimental study of log decomposition processes and rates at CCNHA for comparison with rates in other localities. We will also continue our active participation in the LTER National Coordinating Committee.

E. THE FIVE CORE AREAS FOR LTER

The National Science Foundation has identified five core topics that all LTER sites are expected to address. These core topics have formed an important focus for CCNHA research and provide the breadth needed to address causes of ecosystem patterns and the comparability of data required for syntheses among the LTER sites. Our observational and experimental research, described in the preceeding sections, in combination with additional studies mentioned below, is designed to equitably cover the five core topics. To avoid redundancy, we will only briefly mention the most relevant aspects of our previously described work, and, and because of space limitations, can only briefly outline our other work in each of these 5 areas.

1. Pattern and Control of Primary Production

We are studying the pattern of primary production on a variety of spatial and temporal scales. In old fields, our finest temporal scale of resolution comes from bi-weekly sampling of above-ground plant biomass (identified to species), litter, and below-ground biomass. This allows us to accurately calculate total annual primary production. It also allows us to estimate total annual production for the 42 permanent, unmanipulated plots that we sample once each year for above- and below-ground production. These 42 plots, which are distributed among old fields and native oak savanna, are providing detailed information on year-to-year variation in primary productivity in relation to climate, herbivory, and soil nitrogen status. Our measurements of primary production throughout the 22 field successional chronosequence, including the new annual sampling we will begin in 1988, provides data on a much longer temporal scale. The research that we will initiate along the upland to lowland spatial gradient will document patterns in primary productivity on a broad spatial scale in post-successional ecosystems. Our long-term monitoring in all these habitats will allow us to determine the correlations between primary productivity, soil nutrient dynamics, disturbance, climatic variation, and herbivory, as well as the temporal dynamics of primary production during succession and its spatial patterning within and among sites. Our bi-weekly sampling revealed strong seasonal differences in primary productivity among plant species. Some data suggest shifts in species abundance caused by year-to-year climatic variation, but we need a longer-term record to determine if the trend is significant.

Our experimental additions of various nutrients (N, P, K, Ca, Mg, S, trace metals, or water; each applied singly) has shown that N is the main limiting resource throughout succession and in oak savanna at CCNHA, and that water is infrequently limiting. By continuing these experiments, we can determine if water becomes limiting during periodic droughts and if other species, presently rare or absent in the plots, eventually increase after addition of P, K, Ca, Mg, etc. Our various experimental nitrogen gradients (with and without herbivores; with and without disturbance) are demonstrating the effects of nutrient supply, herbivory, and disturbance on primary productivity and on the species composition, diversity, and successional dynamics of old fields and oak savanna. The presence of transient dynamics means that these experiments must proceed for many years before they can provide rigorous tests of hypotheses emanating from our observational and theoretical studies. Our herbivore removal experiments suggest that all herbivores, combined, reduce annual above-ground production at CCNHA by about 10%. We are presently analyzing the effects of removal (using barriers, insecticides and other toxins) of various below-ground herbivores to determine how large a component this is at CCNHA. In total, our work suggests that the processes that control N mineralization exert the greatest influence on primary production. Thus, much of our work on controls of nitrogen budgets, cycling, and dynamics is directly relevant to controls of primary productivity.

2. Spatial and Temporal Distributions of Populations on Different Trophic Levels

Because our research is an attempt to synthesize population and community ecology into the ecosystem perspective, we identify organisms to species whenever possible. In sampling for primary productivity, we identify **plants** to species, and thus are obtaining a detailed record of the dynamics of the major producer species through time in unmanipulated plots (e.g., Figs. 2, 5 and 8) and in response to various treatments (Figs. 2, 10 and 11; Tilman 1987). We also estimate densities of major **herbivore** species both in completely unmanipulated old fields and, beginning with renewal, along our upland to lowland gradient. At present, in each of 18 old fields, we census all **small mammals** annually (5 common species, with one being an insectivore; Fig. 7) and all **grasshopper species** (Fig. 7) each month of the growing season each year (with 6 common grasshopper species being the major insect herbivores in old fields). Although we do not census deer directly we do obtain annual data on over-winter browsing rates, and we have access to DNR data on **deer** densities in our portions of Anoka and Isanti counties (Fig. 7). The high mobility of deer would make local estimates hard to obtain and difficult to interpret. We asserted when LTER began, and still believe, that it would not be cost effective for us to study the dynamics of vertebrate predators, because of their rarity and high mobility. We do study the dynamics of various **soil organisms**. Dr. Edwin Schmidt is currently analyzing the effects of soil pH and nitrogen supply on the dynamics of various **itrifying bacteria** at Cedar Creek, a project jointly supported by LTER and a separate NSF grant to Schmidt. Martha Christensen, supported by her own NSF grant, is working in conjunction with the CCNHA LTER in a study of the dynamics of soil microorganisms during succession. Her studies of the dynamics of **soil microfungi** is parallelled by Nancy Johnson's study of **mycorrhizal fungi** and **soil microarthropods**, and Don Zak's work on **microbial biomass**. We will add more studies of plant, herbivore, and soil organism dynamics upon renewal when we expand our work into the post-successional upland to lowland gradient.

We must stress that our work includes observations both in unmanipulated areas and in a variety of experiments. To the greatest extent possible, we determine the responses of ecosystem processes and major species on several trophic levels to each of our experimental manipulations. This means that most members of our research team have an interest in and participate in most of the experimental studies.

3. Pattern and Control of Organic Matter Accumulation

Our sampling of soil organic matter in the 2300 permanent plots in the old field chronosequence allowed us to **infer** the long-term dynamics of carbon accumulation during succession. When we re-sample each of these quadrats, and calculate changes in organic carbon and nitrogen, we will be able to **test** the validity of the **inferences** drawn from the chronosequence and more effectively infer the long-term dynamics of organic matter accumulation during succession. Our old field burn experiments and our oak savanna burn experiments will demonstrate the effects of fire frequency on carbon and nitrogen accumulation. Our work to date suggests a tight coupling between organic matter dynamics and nitrogen dynamics in old fields, oak savanna, and oak forest, a hypothesis that the nitrogen addition experiments will test. The rate of accumulation of organic matter is determined by the difference between the rates of organic matter production and loss. Organic matter is added to the soil surface as litter and to the rhizosphere as dead roots, organic exudates of roots, and leachate from the litter layer. Our studies of the decay rates of litter (Pastor et al. 1987c) and of cellulose strips (with different C:N ratios) and of the rates of above- and below-ground production will allow us to better understand the causes of the organic matter dynamics that we observe. This will be aided by our modeling of N and C dynamics using NCSWAP and of soil-plant-herbivore interactions using the hybrid of ALLOCATE and LINKAGES. We will study similar processes along the upland to lowland gradient, as well as downslope transport of C and N, and accumulation in wetland sediments. The long-term rates of accumulation of C and N in wetland sediments will be determined through paleoecological studies of peat and sediments.

4. Patterns of Inorganic Inputs and Movements

The wetfall and atmospheric collectors at CCNHA document the input rates for N, S, P, K, Ca, Mg, and many other mineral elements. Data collected at two nearby NADP sites suggest that, on a seasonal or annual basis, our region receives fairly uniform atmospheric loading rates. The long-term effects of these atmospheric loading rates are not yet at all obvious. Some nutrients are limiting to plants and soil organisms, and may thus increase the rate of nutrient accumulation and productivity during succession, at least in the short-term. However, these and other nutrients may also increase the rate at which bases are leached from the soil, and thus cause a long-term decrease in site fertility. The lysimeters already in place, when supplemented by the ceramic cup collectors that we will install in the old fields and along the upland to lowland gradient, should, as previously discussed, allow us to better determine the dynamics of soil nutrients. This will be aided by the groundwater chemistry monitoring wells that we will install and those that USGS has installed at CCNHA, by the hydrologic model (PHIM) that we will calibrate for CCNHA, by our model of cation and anion dynamics (Bloom and Grigal 1985) and by our periodic sampling of old field soils. The dynamics of inorganic nutrients within the soil are greatly influenced by, and, in turn influence, soil microorganisms, vascular plants, and soil organic matter. Thus, the work summarized here, for this core topic, is intimately related to our work in the preceding two core areas, as well as our work on disturbance (which influences nutrient loss rates). In addition to observing nutrient inputs, recycling rates, and losses, our nutrient loading experiments will determine the effects of N addition on loss rates of anions and bases.

5. Patterns and Frequencies of Disturbance

We view CCNHA as a mosaic of patches that differ in their productivity and their disturbance frequency and history. Therefore studies of disturbance patterns, frequencies and effects are a major component of our research. At present, gopher mounds are the main disturbance in old fields and oak savanna, and windthrowing of trees, and pathogens such as oak wilt are the major disturbances of forested areas. Before settlement, fire was an important disturbance. Clearcutting and the constant disturbance of agriculture tilling were major post-settlement disturbances. Our annual survey of gopher mounds and other soil disturbances in old fields and oak savanna, of tree fall gaps and tree death from pathogens in forested sites, and of responses to these natural disturbances will document the pattern, frequency and effects of these disturbances. In addition, we have observational and experimental studies designed to determine the effects of soil disking and of various frequencies of prescribed burning in both old fields and oak savanna. Our old field successional chronosequence is an intensive study of the long-term dynamics of ecosystem recovery from agricultural disturbance. We are also studying the impact of global climatic change, a potentially major disturbance, on ecosystems at the wetland-upland ecotone. Measurements of soil solution chemistry in plots subjected to different rates and frequencies of disturbance are determining the effects of disturbance on rates of nutrient loss and on nutrient availability, as well as effects of disturbance on community composition. Furthermore, Dr. Scott Wilson, a National Science and Engineering Research Council of Canada Post-Doctoral researcher at CCNHA, is starting a large-scale experimental study of the joint and interactive effects of disturbance and productivity on plant community diversity and structure in old fields.

Recent Changes in the Cedar Creek LTER Project

When the CCNHA LTER applied for renewal after 5 years of support, we were given a 2 year renewal, and asked to modify our project so as to broaden our group of senior investigators, to increase the range of the Cedar Creek landscape that we investigated, and to strengthen our work on whole-ecosystem modelling. D. Grigal, who had been involved in CCNHA research from the start of LTER, greatly increased his involvement at that time and became a Co-PI. Since then, E. Gorham has become actively engaged in LTER, and will serve as one of the 3 Co-PI's (with D. Grigal and D. Tilman). Mark Davis and Patrice Morrow received support through the LTER project, and both have now received NSF grants for research at CCNHA. J. Molina also joined the group at that time. J. Pastor decided to greatly increase his participation in LTER. The University of Minnesota has committed $55,0000 per year as matching support to the CCNHA LTER. Some of these funds will be used to pay 25% of Pastor's salary and to hire a graduate research assistant to work with Pastor. The renewal time two years ago was also a time of uncertainty for two other CCNHA researchers, R. Inouye and N. Huntly. Huntly and Inouye had joined the CCNHA group as post docs in 1982, but left Minnesota for Idaho State University in 1986. They have decided that CCNHA is their major research site. They came back to CCNHA this past field season, and will receive LTER support for their work at CCNHA as a subcontract on this renewal. CCNHA will provide them with on-site housing, as in the past.

The CCNHA LTER has a large, multi-disciplinary team of scientists who share interests and a desire to cooperatively pursue long-term research. There is a core of 8 faculty-level researchers who are actively engaged in the project, and who have a long-term commitment to its success: E. Gorham, D. Grigal, N. Huntly, R. Inouye, J. Molina, J. Pastor, A. Starfield and D. Tilman. In addition, J. Tester (U. Minnesota), M. Davis (Macalester College), K. Brooks (U. Minnesota), P. Morrow (U. Minnesota), M. Christensen (U. Wyoming), J. Gurevitch (Suny Stony Brook), and E. Schmidt (U. Minnesota) are performing research at CCNHA that complements and is coordinated with the LTER program. These 7 additional faculty-level scientists will contribute to LTER during the next 5 years, with the depth and extent of their involvement determined by their interests and desires, and the needs of the project. The project's breadth and depth is also increased by the 3 post-doctoral researchers and the 9 Ph.D. students who work at CCNHA. During the past 2 years, we have considerably broadened our work, both conceptually and in terms of the landscape elements we consider. We are excited by the opportunities we see for collaboration within our group. All 3 Co-PI's are fully committed to the long-term success of the project. We will share administrative duties among the three of us, making major decisions by consensus. The responsibility of serving as project coordinator will rotate among the three of us on an annual basis. Although we do not anticipate turnover in this group, by sharing duties among 3 scientists, by having our group include several additional faculty-level researchers, and by continuing to encourage new researchers to join the group, we will be able to maintain long-term continuity of project leadership.

Data Management and Experimental Design: Guiding Principles

The LTER program has provided CCNHA with a unique opportunity to make major contributions to ecology. We spent much time discussing long-term research before we began, and have continued these discussion formally and informally. The discussions have led to some guiding principles for our research:

1. Investigator Disturbance: We are sensitive to the possibility that sampling an experiment could influence its course. We never allow anyone to enter our smaller-scale plots (4 m x 4 m). All sampling is from the margins or, if needed, from a boardwalk suspended over plots. Even when we collect destructive samples (total plant biomass, species composition, soil samples) we limit the area sampled each year to <2%, so that plots could be sampled annually for 50 years before resampling was necessary. In the old fields, we collect destructive samples in a quadrat sufficiently narrow (10 cm) that we have not observed any plants responding to it as a disturbance; instead we see rapid regrowth of clipped vegetation as well as vegetative spread into the plot from its margins. For larger-scale plots (20 m x 50 m) we have laid a trail of cement patio blocks from which to sample, confining investigator disturbance to the smallest possible area. Less than 0.1% is destructively sampled each year in the large plots.

2. Research Documentation: We are sticklers for documentation, striving to document the materials, methods and design of each study sufficiently well that an ecologist with no previous knowledge should be able to continue the work and understand the intricacies of data already collected. Documentation of all experiments includes maps of location in the field and the field layout of individual plots. Experimental and observational plots are permanently marked in the field using epoxy-painted steel rods and weather-proof aluminum tags. Such documentation is required before any project begins. Our data manager is in

charge of collating, storing and updating this documentation in cooperation with involved researchers. To facilitate this, we require that all new projects be planned in consultation with our data manager.

3. Archiving soil samples: When we start a major experimental or observational study, we archive dried soil samples for each plot. We realize from past long-term research, (e.g., at Rothamsted) that samples archived in the 1840's have proven extremely useful for purposes not even suspected when they were collected.

4. Data Archiving: Duplicate copies of all data sets, records, and documentation are maintained at CCNHA and in our Data Manager's office on the main campus of the University. Data are maintained as hard copy and in computer files. Copies of all data disks are also kept at D. Tilman's home, the home of the data manager, and at Idaho State University.

5. Data Quality: Most data are gathered directly onto computers via interfaces with balances, pH meters, autoanalyzers, etc. We have written software specific for particular experiments and measurements, so that potentially incorrect data can be identified immediately. For many situations the software prompts users to verify each datum as it is collected. We have written software to convert these data sets rapidly to forms usable for statistical analysis; an investigator can know immediately what the data show. This is an important part of quality assurance, because unusual or unexpected patterns can be validated or corrected immediately, when it is still possible to resample in the field.

6. Data Comparability: We do all possible to assure that data are comparable from year to year. We have prepared explicit written directions for the methods used in all routine data collection. We have large batches of standardized soils and plant tissues to allow calibration of future measurements. For plant and insect identification, we maintain a **working herbarium with voucher sheets**, and a large **insect collection**, at CCNHA.

7. Data Availability: All data are available to other researchers within and outside the project who are interested in collaborating in new analyses. Although specific hypotheses guide our work, other scientists will find our data useful for other reasons. We have had many interactions internally (e.g., among Pastor, Tilman, Gorham, Huntly, Grigal, Molina,

and Inouye) and externally (e.g., 6 yr data set provided to J. Magnuson for cross-site comparison of spatial and temporal variability in different ecosystem elements). Availability also implies access. We have microcomputers and software that allow our investigators to analyze data easily and to see on screen relationships among variables of interest. Our budget includes a request for additional microcomputers to allow new investigators such data access.

8. Data Manager: We consider all the data we gather to be not only of immediate value for addressing current questions, but to have much future potential value to others. Thus, we treat all data as if they are being held "in trust" for others. This requires that we spend much more time documenting data and establishing suitable data bases to allow easy retrieval and analysis in the future. Moreover, we consider all our data to be part of one data set. We want any researcher to be able to compare any variable with any other variable. We expect our data manager to interact with data managers at other sites and to assist with intersite data transfer and comparisons. We have found that the only way to meet these data management goals, as well as the others listed in the preceeding sections, is to have a full-time, professional data manager. Our Data Manager, A. El Haddi, has a M. S. in Statistics and Agronomy plus an additional 30 credits in Computer Science and had data management experience before we hired him.

Appendix. I. Literature Cited

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Appendix II. **SITE DESCRIPTION, FACILITIES, SITE USE PROMOTION**

1. Site

Cedar Creek Natural History Area is a 2,185 ha (9 square mile) experimental ecological reserve located 60 km north of the University of Minnesota in Minneapolis. It lies in a floristic transition zone with many species near their southwestern limits while others are at their northern limits. CCNHA's southern relict outpost of boreal forest species, its extensive oak savanna, prairie openings, old fields, marshes, many soil types, and closeness to the University make it a unique research site. CCNHA is owned and managed by the University of Minnesota. The Site Director, Dr. John Tester, and the Cedar Creek Advisory Panel regulate all research and resolve any potential conflicts in site usage. This procedure has worked very well for CCNHA and the LTER project. Although CCNHA lies near a large metropolitan area, it is large enough to withstand urban pressures; its important natural areas are buffered by extensive oak forests and abandoned fields.

CCNHA is used the year around by research scientists, post-doctoral researchers, and graduate student researchers. Because CCNHA is only a 40 minute drive from the University of Minnesota, researchers have the dual advantage of a natural area and nearby urban facilities, including the University's library, herbarium, entomological collections, computer facilities, and analytical laboratories. Most University faculty working at CCNHA commute there on a daily basis during the field season. On-site housing is available for visiting researchers, post-docs, graduate students, and undergraduate research assistants.

CCNHA contains a variety of natural and culturally disturbed habitats, including a thorough sequence of successional areas with known past history (Inouye et al. 1987). The major vegetation types at CCNHA and their approximate sizes are: old fields (850 ha); wetland, marsh and carr (710 ha); oak savanna (250 ha); oak-hickory-aspen forest (130 ha); conifer bog (70 ha); and Great Lakes pine forest (40 ha). Woodlots have been free of grazing and cutting for 45 or more years and are semi-natural. Forest composition is strongly dependent on relation of natural firebreaks.

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

2. Facilities

CCNHA has nine permanent buildings, including a new, modern, year-round research laboratory, a newly-remodeled dormitory-kitchen, a shop building, a large storage building and work area, a winterized animal holding facility, and four year-around family homes. The facilities, which have been considerably expanded during the past five years because of the needs of the LTER project and of other new research projects provide all the space and services we need to perform our research.

We have an automated weather station, and a complete, well-equipped analytical chemistry laboratory that is used for soil, water and plant tissue analyses. Major items of equipment in the laboratory are: two Technicon Auto Analyzers; two Apple II-e microcomputers that control the Auto Analyzers and act as data loggers; analytical balances; shaker tables; centrifuges; fune hood; three spectrophotometers, muffle furnace; high-volume still; drying ovens; pH meter; culture boxes; autoclave; block digester. Other major items of equipment include: a Licor IRGA photosynthesis system; a Licor leaf area meter with automatic feed; a walk-in drying oven; three IBM-PC controlled analytical balances for automated weighing and data entry; two IBM-PS 80 microcomputers with 72 M Byte hard disks (one of them a gift from IBM!); three IBM-XT microcomputers; a Hewlett-Packard Vectra microcomputer; two graphics plotters; a HP laser printer; one letter quality and four dot-matrix printers; drafting equipment and automated lettering machine; microcomputer-controlled automatic radio tracking grid for small mammals; Lambda PAR collector and meter; wet- and dry-fall atmospheric collectors; a truck; a station wagon; a tractor.

3. Site Use Promotion

CCNHA is open and available for research to any interested scientist from any institution. We have both formal and informal mechanisms to encourage the use of Cedar Creek Natural History Area. Once each year CCNHA announces a competition, open to any faculty at any college or university, for small grants designed to encourage the initiation of new research at Cedar Creek. Last year, grants totaling $20,000 were made to 5 scientists using funds provided by the University of Minnesota. The LTER grant provided additional support, totaling more than $20,000, to the projects that were most relevant to LTER. The funds distributed last year were instrumental in getting Drs. Eville Gorham, Mark Davis, and Jean Molina working at CCNHA. They also supported Dr. Patrice Morrow. Both Davis and Morrow have since obtained separate NSF funding to support their CCNHA research, and Gorham, Molina and Davis are now active members of the LTER group. A previous CCNHA grant to J. Reichman of Kansas State University also led to an NSF grant for research at CCNHA.

We use several methods to "advertise" CCNHA. The booklet "Long-Term Ecological Research in the United States: A Network of Research Sites" is widely distributed and has led several scientists to contract us regarding work at CCNHA. Our visibility is increased by the frequency with which we publish papers in major journals, present papers at national and international meetings, and give invited seminars in outside departments. Because of our interest in encouraging others to work at CCNHA, whenever possible, we point out the virtues of working in the data rich environment that we provide. These activities have led to an increasing number of inquiries by outside scientists, of grant proposals submitted to various agencies for CCNHA research, and of funded projects. Some examples are:

> Dr. Martha Christensen of the University of Wyoming now has NSF support for a study of the successional dynamics of soil microfungi at CCNHA.
>
> Dr. Mark Davis has NSF support for studies of spatial and temporal hierarchies, and will spend his sabbatical year, 1988-1989, at the University of Minnesota with the LTER group.
>
> Dr. S. Wilson had a proposal to do post-doctoral research at CCNHA funded by the National Science and Engineering Research Council of Canada, and now has a proposal pending to NSF for support of experimental studies of the interactive effects of productivity and disturbance.
>
> M. Palmer, a Ph. D. student at Duke University, is collecting data in permanent plots in an area subject to severe windthrow in 1983.

Dr. T. Schowalter of the Andrews LTER established, with our cooperation, a log decomposition study at CCNHA.

Dr. E. Schmidt, in a project that has been supported by NSF, is studying nitrifying bacteria population dynamics at CCNHA.

Dr. J. Reichman has now completed an NSF-supported study of gopher foraging dynamics at CCNHA.

Dr. L. Tieszen of Augustana College, Sioux Falls, South Dakota, has an NSF proposal currently in review to use stable isotopes to assess paleoecological changes in C_3 and C_4 grasses at CCNHA.

Dr. S. Collins of the University of Oklahoma has a proposal in review at NSF for studies of mechanisms of colonization of disturbed sites at CCNHA.

Dr. Michael Farris of St. Olaf College, Northfield, MN, has initiated research on the evolutionary importance of physiological variation in plants, and plans to submit a proposal to NSF on this.

Dr. S. Eisenrich of the Department of Civil and Mineral Engineering initiated a program of monitoring the atmospheric loading rates of EPA class I toxins at CCNHA.

Dr. J. Gurevitch of SUNY Stony Brook has established a series of experimental studies of plant competition at CCNHA, and plans to submit a proposal to NSF for an expanded version of the project.

Dr. Kathy Shea of St. Olaf College, Northfield, MN, has initiated research on the evolution of sex in plants at CCNHA.

Dr. M. Seeley of the University's Institute of Agriculture, Forestry and Home Economics, has started meteorological research at CCNHA

The Minnesota Pollution Control Agency has chosen CCNHA as a site for their Acid Deposition Sampling Network.

Dr. Henry Anderson of United States Geological Survey has established ground water monitoring wells at CCNHA.

All of these activities have begun since LTER was initiated in 1982. All of them add to the breadth and depth of research activities at CCNHA. They increase the size of the research group at CCNHA and the "data richness" of the environment. Each of them provides data of interest to others, and each of them benefits from data collected by others.

Appendix III. **PERSONNEL**

THE LTER WORKING GROUP

The LTER project has a core composed of 8 faculty-level researchers. Five of these, including the CO-PI's, are tenured Full Professors at the University of Minnesota. Their commitment to the project, and the stability of their positions, will provide the continuity and stability that long-term research requires.

CCNHA Core Researchers

Dr. Eville Gorham, Co-PI, Professor, Department of Ecology and Behavioral Biology
Dr. David Grigal, Co-PI, Professor, Department of Soil Science
Dr. Nancy Huntly, Assistant Professor, Department of Biological Sciences, Idaho State University
Dr. Richard Inouye, Affiliate Assistant Professor, Department of Biological Sciences, Idaho State University
Dr. Jean Molina, Professor, Department of Soil Science
Dr. John Pastor, Research Associate, Natural Resources Research Institute and Adjunct Assistant Professor, Department of Ecology and Behavioral Biology
Dr. Anthony Starfield, Professor, Departments of Ecology and Behavioral Biology and Civil and Mineral Engineering
Dr. David Tilman, Co-PI, Professor, Department of Ecology and Behavioral Biology

There are several other faculty who are performing independently-funded research in coordination with the LTER project and who thus add to the breadth of our research team. All of these have received benefits and support from the LTER grant, but it is not a main source of support:

Dr. Kenneth Brooks, Professor, Forestry and Certified Hydrologist
Dr. Martha Christensen, Professor, Department of Botany, University of Wyoming
Dr. Mark Davis, Associate Professor, Macalester College, St. Paul, MN
Dr. Jessica Gurevitch, Assistant Professor, Department of Ecology and Evolution, SUNY Stony Brook
Dr. Patrice Morrow, Professor, Department of Ecology and Behavioral Biology
Dr. Edwin Schmidt, Professor, Departments of Microbiology and Soil Science
Dr. John Tester, Professor, Department of Ecology and Behavioral Biology

In addition, there are four post-doctoral researchers who are integral members of the research group. As we did with Inouye and Huntly, we will encourage these post-doctoral researchers, and others whom we hire in the future, to continue using CCNHA as their main research site after they leave Minnesota:

Dr. Scott Gleeson, Post-Doctoral Researcher
Dr. Jan Janssens, Post-Doctoral Researcher
Dr. Scott **Wilson**, National Science and Engineering Research Council of Canada Post-Doctoral Fellow
Dr. Donald Zak, Post-Doctoral Researcher

The final group of of CCNHA researchers are graduate students working toward a Ph. D. Because most of these have salary support directly from the University, we have been able to attract a large number of Ph. D. students to CCNHA by offering supply and equipment funds:

Taber Allison, Ph. D. Student in Ecology and Behavioral Biology
Jeff Brokaw, Ph. D. Student in Ecology and Behavioral Biology

Nancy Johnson, Ph. D. Student in Ecology and Behavioral Biology
Robert McKane, Ph. d. Student in Soil Science
Mike Norland, Ph. D. Student in Soil Science
Martha Phillips, Ph. D. Student in Ecology and Behavioral Biology
Sharon Strauss, Ph. D. Student at Florida State University
David Wedin, Ph. D. Student in Ecology and Behavioral Biology
Kathleen Zinnell, Ph. D. Student in Ecology and Behavioral Biology

In addition to these researchers, CCNHA has a full-time, year-around staff that includes a resident manager (Dave Bosanko), a secretary (Bev Medvecky), a chief electronics engineer (Larry Kuechle), as well as part-time maintenance workers.

EXTERNAL ADVISORY COMMITTEE

From its inception, the CCNHA LTER has been guided by an External Advisory Committee. This committee, which meets once a year, has provided valuable input concerning the breadth, depth and scope of our project, as well as administrative details. Four scientists serve on the committee. We try to arrange our annual meeting so that at least 2 (and preferably 3) committee members may attend. The members are:

1) **Dr. Gene Likens**, Institute of Ecosystem Studies, New York Botanical Gardens, Cary Arboretum, Millbrook, NY.

2) **Dr. Jim MacMahon**, Department of Biology, Utah State University, Logon, Utah.

3) **Dr. Henry Horn**, Biology Department, Princeton University, Princeton, NJ.

4) **Dr. William Parton**, Natural Resource Research Institute, Colorado State University, Fort Collins, CO.

The next scheduled meeting is May 12-13, 1988.