PROPOSAL TO THE NATIONAL SCIENCE FOUNDATION
Cover Page

FOR CONSIDERATION BY NSF ORGANIZATIONAL UNIT (Indicate the most specific unit known, i.e. program, division, etc.)	IS THIS PROPOSAL BEING SUBMITTED TO ANOTHER FEDERAL AGENCY? Yes ___ No X IF YES, LIST ACRONYM(S):
Long-Term Ecological Research (LTER) Division of Environmental Biology	

PROGRAM ANNOUNCEMENT/SOLICITATION NO.:	CLOSING DATE (IF ANY): April 1, 1981

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

Regents, University of Minnesota

ADDRESS OF ORGANIZATION (INCLUDE ZIP CODE)

Office of Research Administration, 1919 University Avenue, St. Paul, MN 55114

TITLE OF PROPOSED PROJECT

LTER: Micro and Macro Views of Succession, Productivity, and Dynamics in Temperate Ecosystems

REQUESTED AMOUNT	PROPOSED DURATION	DESIRED STARTING DATE
$1,499,178	1/1/82-12/31/86	1/1/82

PI/PD DEPARTMENT	PI/PD ORGANIZATION	PI/PD PHONE NO.
Department of Ecology and Behavioral Biology	University of Minnesota	612-376-9455

PI/PD NAME	SOCIAL SECURITY NO.*	DATE OF HIGHEST DEGREE ACHIEVED*	MALE*	FEMALE*
G. David Tilman	[redacted]	1976	X	
ADDITIONAL PI/PD John R. Tester	[redacted]	1960	X	
ADDITIONAL PI/PD				
ADDITIONAL PI/PD				
ADDITIONAL PI/PD				

FOR RENEWAL OR CONTINUING AWARD REQUEST, LIST PREVIOUS AWARD NO.:	IF SUBMITTING ORGANIZATION IS A SMALL BUSINESS CONCERN, CHECK HERE ☐ (See CFR Title 13, Part 121 for Definitions)

*Submission of SSN and other personal data 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 proposals. SSN solicited under NSF Act of 1950, as amended.

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

☐ Animal Welfare ☐ Human Subjects ☐ National Environmental Policy Act

☐ Endangered Species ☐ Marine Mammal Protection ☐ Research Involving Recombinant DNA Molecules

☐ Historical Sites ☐ Pollution Control ☐ Proprietary and Privileged Information

PRINCIPAL INVESTIGATOR/ PROJECT DIRECTOR	AUTHORIZED ORGANIZATIONAL REP.	OTHER ENDORSEMENT (optional)
NAME G. David Tilman	NAME A. R. Potami	NAME David F. Parmelee
SIGNATURE	SIGNATURE	SIGNATURE
TITLE Associate Professor Dept. of Ecology and Behavioral Biology	TITLE Director, Office of Research Administration	TITLE Professor and Chairman Field Biology Program
DATE 3/18/81	DATE	DATE 3/18/81

(11/78)

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NOTICE OF RESEARCH PROJECT
SCIENCE INFORMATION EXCHANGE

SMITHSONIAN INSTITUTION
NATIONAL SCIENCE FOUNDATION
PROJECT SUMMARY

PROJECT NO. (Do not use this space)
NSF AWARD NO.

1. NAME OF INSTITUTION (INCLUDE BRANCH/CAMPUS & SCHOOL OR DIVISION)

Field Biology Program
University of Minnesota

2. MAILING ADDRESS

108 Zoology
318 Church Street, SE
Minneapolis, MN 55455

3. PRINCIPAL INVESTIGATOR AND FIELD OF SCIENCE/SPECIALTY

G. David Tilman and John R. Tester

4. TITLE OF PROJECT

LTER: Micro and Macro Views of Succession, Productivity and Dynamics in Temperate Ecosystems

5. SUMMARY OF PROPOSED WORK (LIMIT TO 22 PICA OR 18 ELITE TYPEWRITTEN LINES)

Most current ecological research consists of short-term, intensive studies of a few species or a few ecosystem-level processes, with other system components assumed constant. We believe that major advances in ecological understanding will only come when micro studies of population processes are combined with macro views of whole system processes. Such an approach would allow the synthesis of the direct, indirect, and feedback effects which must form the basis of a mechanistic, predictive approach to ecosystem structure and function.

Succession provides the ideal framework for such a study, for succession is a long-term process which is the result of numerous short-term direct, indirect, and feedback processes. We propose a long-term study of succession at the Cedar Creek Natural History Area, Minnesota. The study would include long-term monitoring of primary productivity, litter accumulation, disturbance, soil processes and nutrient cycles, plant population dynamics, herbivore dynamics, and climatic variability in a series of manipulated and unmanipulated permanent plots. Treatments will be replicated in three different stages in the natural secondary successional sequence. Manipulations include fertilizations with different ratios of limiting nutrients, watering, herbivore removals, several patterns of imposed microsite disturbance, and the exclusion of fire in an otherwise annually burned area. This combination of small-scale micro studies with long-term observation of unmanipulated and manipulated areas will provide the experimental and observational data needed to test numerous hypotheses concerning succession and ecosystem structure. Moreover, by performing these studies in the framework of a network of LTER sites, we will be able to address a series of broad, synthetic questions on a geographic scale which was previously impossible.

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DIVISION (OFFICE) AND DIRECTORATE	PROGRAM	
SECTION	PROPOSAL NO.	F.Y.

FOR DGC USE ONLY

START AND END DATES	AMOUNT GRANTED

NSF FORM 4 (7-78) 1. Proposal Folder 2. Program Suspense 3. Division of Grants & Contracts 4. Science Information Exchange 5. Principal Investigator 6. Off. of Govt. & Pub. Progs. 7. Assistant Director

(11/78)

I. PHYSICAL DESCRIPTION OF SITE

A. Location and Uniqueness of Site:

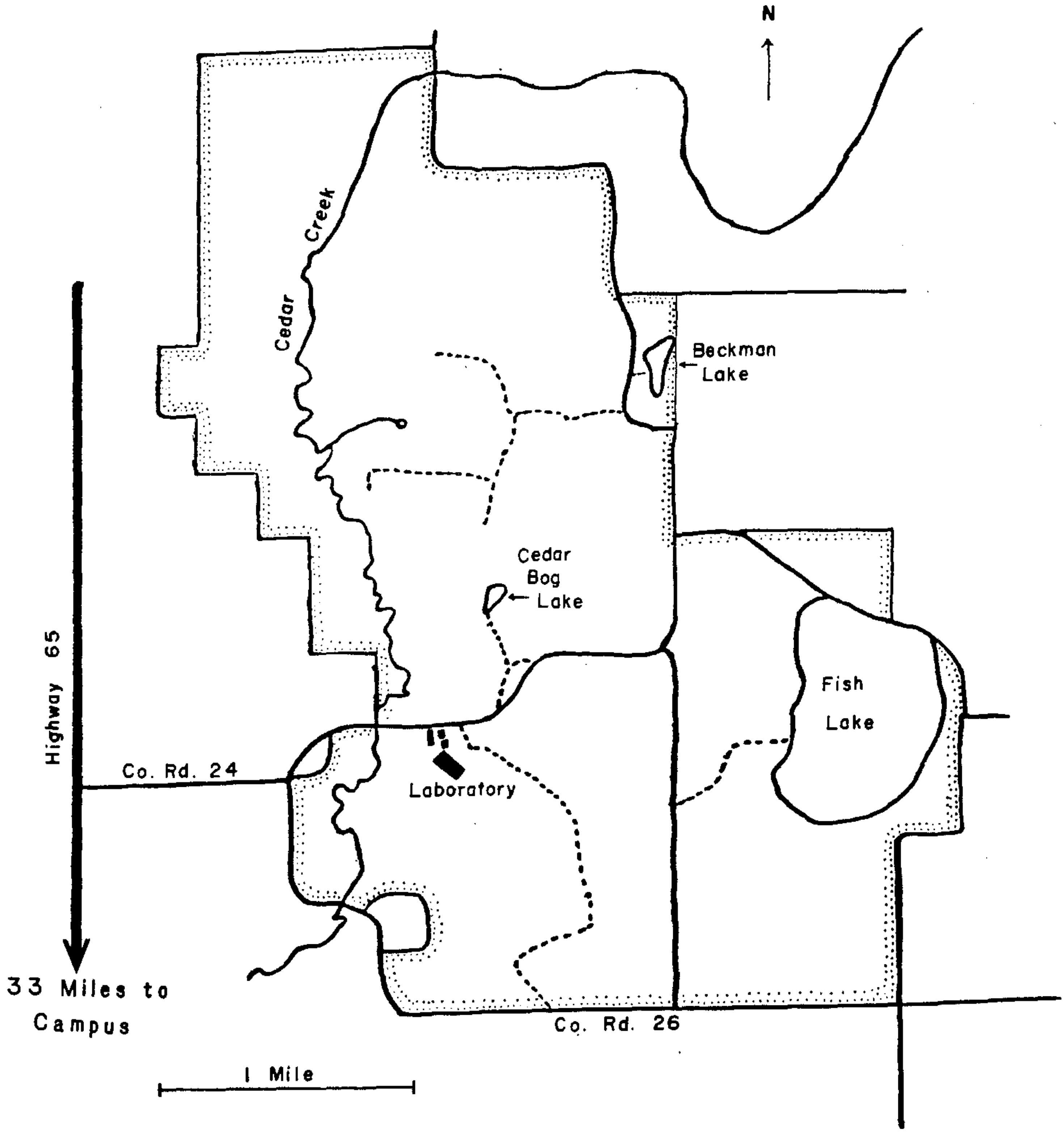
Cedar Creek Natural History Area (see map on next page) is a large tract approximately 2,185 ha in size, at 45°24'N and 93°12'W, between 174.9 and 288.3 m elevation, in Anoka and Isanti Counties, Minnesota. It is readily accessible by auto, bus (3.0 km), train (60.0 km) or international airport (83.0 km), and is a 40 minute drive from the main campus of the University of Minnesota in Minneapolis-St. Paul. The area lies in a floristic tension zone with many species near their southwestern limits while others are at their northern limits. Cedar Creek's southern relict outpost of boreal forest species, its extensive oak savannah, western prairie-type lakes and marshes, many soil types, and closeness to the University make it a unique research site.

B. Site Integrity, Ownership and Management

Cedar Creek is owned by the State of Minnesota and managed by the University of Minnesota. In 1975 it was designated one of the Nation's NATURAL LANDMARKS by the National Park Service; in 1977, as one of the EXPERIMENTAL ECOLOGICAL RESERVES in a national network proposed by The Institute of Ecology and National Science Foundation. Parts of Cedar Creek are currently being considered for designation in the Minnesota Department of Natural Resources' Natural and Scientific Area program. Although Cedar Creek lies at the edge of a large metropolitan center, the area is large enough to withstand urban pressures; its important natural areas are buffered by extensive oak forests and abandoned fields.

All research and other station activities are monitored by the Field Biology Program under the direction of Dr. D. F. Parmelee, with assistance from the Cedar Creek Advisory Committee. This committee is composed of faculty from the Colleges of Biological Sciences, Agriculture and Forestry and representatives from the Minnesota Academy of Science. Drs. Tilman and Grigal are currently members of the committee.

CEDAR CREEK NATURAL HISTORY AREA



On February 1, 1981, Dr. Tilman was appointed Associate Director of the Field Biology Program with his responsibilities including:

1) Coordination of all research at Cedar Creek.
2) Promotion of on-site research by faculty and independent researchers from the University of Minnesota and from other institutions, using funds available in the Field Biology Budget.
3) Development of a continuing post-doctoral program at Cedar Creek, with funding provided by the Field Biology Program.
4) Selection and chairing of an outside advisory panel for Cedar Creek.
5) Extension of the computer-based system for managing data from Cedar Cedar Creek research.

C. Habitat Types at Cedar Creek:

Cedar Creek contains a variety of natural and culturally disturbed habitats (see photographs on next page), including a thorough sequence of successional areas.

Following the guidelines of the T.I.E. report on Experimental Ecological Reserves, we list the following vegetation classification, with areas in hectares, and give the common names for the major biotic components of each vegetation type:

1) Oak Savannah K-81 (250 hectares):
Bur oak, big bluestem, Indian grass, little bluestem, porcupine grass, bluegrass, tussock sedge, sand reedgrass, three-awn grass.
2) Oak-Hickory Forest (including Aspen Forest) K-100 (130 hectares):
northern pin oak, bur oak, aspen, smooth sumac, big bluestem.
3) Conifer Bog K-94 (70 hectares):
White cedar, tamarack, black spruce, sphagnum, leatherleaf, labrador tea, alder, willow.
4) Great Lakes Pine Forest K-95 (40 hectares):
White pine, red oak, red maple, paper birch, red pine, jack pine, northern pin oak, aspen, sugar maple, basswood, red oak.
5) Old Fields (850 hectares):
Foxtail, ragweed, milkweed, hawksbeard, evening primrose, mullein, goatsbeard, goldenrod, bluegrass, quack grass, three-awn grass, big and little bluestem, Indian grass, northern pin oak, bur oak, sumac, black cherry, choke cherry.
6) Wetland marsh and carr (710 hectares):
Speckled alder, willows, red-osier dogwood, sedges, cattail, bluejoint, reed-canary grass.

The vegetation of approximately 25% of Cedar Creek has been mapped, and the information contained in a computer-accessible data bank. Software developed by our Systems Software Programmer allows researchers to obtain detailed habitat maps for any portion of the mapped area. In addition, the coordinate system used in mapping is also used in all data entry into the data bank. A condensed version of this map is given on the next page.

Cultivated fields are kept in crop rotation typical for the region. There is a schedule whereby farmland is abandoned at a constant rate to provide a variety of ages for old fields at Cedar Creek. Woodlots have been free of grazing and cutting for 40 or more years and are semi-natural. Forest composition is strongly dependent on relation to natural firebreaks. About 145 ha are being managed by fire to preserve natural savannah and prairie openings. (See Irving, 1970, in Appendix A).

D. Physical Components:

Soil taxonomy is a comprehensive soil classification system developed by the National Cooperative Soil Survey. In Soil Taxonomy, all the earth's soils are classified as being in one of ten soil orders. Six of the ten soil orders occur in Minnesota, and because of the unique combination of soil forming factors, five of these six orders are found at Cedar Creek (see Grigal, et al., 1974, in Appendix A).

Cedar Creek lies within the Anoka Sand Plain, a large outwash plain covering about 2200 km^2. In some of the area, outwash sands have been reworked by wind, resulting in a dune-shaped topography dominated by the Sartell soil series, which is an Entisol showing very little development. 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, which are Alfisols showing considerably more development than do Entisols. These two soils are characteristic of forest vegetation. On the broad flats located some distance above the water table, soils of the Nymore series, under the influence of savannah vegetation, have formed a Mollisol or prairie soil. The Zimmerman series is represented on much of the remaining mineral upland; the Zimmerman soil is a member of a hydrosequence which also includes the Lino and Isanti soils. Glacial till appears either at or very near the surface on some spots in the area, and both Inceptisols and other Alfisols can be found there. Cedar Creek also has extensive areas of organic soils, or Histosols. These are associated with a variety of lowland vegetation ranging from open sedge to lowland shrub to forest, and are represented by four series of organic soils.

II. RESEARCH FACILITIES

A. Physical Plant and Equipment

Cedar Creek Natural History Area has eight permanent buildings, including two year-around research laboratories, a shop building, a newly completed storage building and work area, a winterized animal holding facility, and three year-around family homes. The two research laboratories, shop, and storage building shown in the photos on the next page provide all the space and services that we need to perform this research. A more complete description of these facilities and the major items of research equipment are given in the following lists.

a. Buildings:

1) Research Laboratory (386.2 m^2; top photograph), year around, equipped with bio-electronics shop, three bioelectronics offices, three offices for researchers, one office for resident manager; also an assembly hall, records room, drafting room, kitchen and bathroom facilities.
2) Research Laboratory (155.9 m^2; second from the top photograph), year around, equipped with bioelectronics laboratories, including computer, animal preparation room, machine shop; also weather station, dormitory (12 people), bathroom facilities.
3) Storage Building (223 m^2; bottom, left photograph).
4) Garage-Shop Building (68 m^2; bottom, right photograph)
5) Winterized Animal Holding Facility (172 m^2).
6) Three year-round family homes.
7) Three large waterfowl enclosures and flight pens.

b. Major Research Equipment:

1) Data General Nova minicomputer with tape deck to provide data for telemetry and meteorological parameters.
2) Hewlitt Packard programable calculator and plotter
3) Texas Instruments 40K Bubble Memory Portable Data Terminal
4) Hewlitt Packard oscilloscope
5) Tectronix oscilloscope
6) Spectrum analyzer
7) Signal generator
8) Wire bonder
9) Microprocessor support system
10) Electronic counters
11) Test chambers
12) Thelco oven
13) Beckman zeromatic Ph meter
14) Beckman infrared analyzer
15) Sartorius balance

16) Meteorological equipment (Honeywell)
17) Drying ovens
18) Two Jeeps (for use at Cedar Creek only)

B. Working Environment:

Cedar Creek is used the year around primarily by research scientists and graduate students involved in research. Because it is only a 40 minute drive from the University of Minnesota, researchers have the dual advantages of a natural area and nearby urban facilities. The Field Biology Program owns several 12-passenger vans which are used for transportation between Cedar Creek and the University during most of the year. However, these vans were purchased for use at the Lake Itasca Biological Station, and are thus unavailable from June 15 to August 15 of each year. Currently, researchers commuting to Cedar Creek car pool during this period. We propose the purchase of a fuel-efficient, six passenger station wagon to be used to provide regular transportation to and from Cedar Creek. This would provide critical service during the busy summer months and be much more fuel efficient then the large vans.

Most scientists working at Cedar Creek have been from the University of Minnesota, but the Field Biology Program encourages use of the Cedar Creek facility by researchers from outside the University of Minnesota. Free dormitory accomodations are available to researchers working at Cedar Creek; three year-round residences are also available, and are currently occupied by a resident manager, an electronics engineer, and a postdoctoral researcher. Additionally, eight Cedar Creek Research Stipends ($1000 each) are available annually to independent investigators and students from within and outside the University. These stipends, which include free housing at Cedar Creek, have been advertised widely in Minnesota since 1979; a broader coverage is planned to encourage investigators from other universities.

C. Resident Staff:

Only those individuals that have offices and/or work daily on the premises of Cedar Creek are listed below.

1) Building and Grounds:
   Alvar Peterson, Resident Manager
   John Koecher, Laborer
   Beverly Medvecky, Secretary (1/2 time)
2) Lecture and Tours:
   Neil Bernstein, Field Biology Program Teaching Assistant
3) Bioelectronics Laboratory
   Larry Kuechle, Research Associate (Chief Electronics Engineer)
   Richard Reichle, Associate Scientist
   Ralph Schuster, Electro Mechanical System Specialist
   Leonard Cramer, Electronics Technician
   Kathlean Zinnel, Systems Software Programmer
   Jon Ross, Assistant Scientist
4) Current Research Programs:
   Old Field Succession
   David Tilman, Associate Professor
   Waterfowl Behavior Project
   Jeff Burns, Utility Assistant (partial year)
   Kimberly Cheng, Research Fellow (partial year)
   Squirrel Project
   Richard Huempfner, Assistant Scientist (1/2 time)
   Antarctic Project
   Stephen J. Maxson, Postdoctoral Research Fellow

III. RESEARCH HISTORY

Cedar Creek Natural History Area is primarily a research facility for faculty, students and visiting researchers. Lectures and formal classes are not held at Cedar Creek; the University's field-training program is mainly carried on at its Lake Itasca Forestry and Biological Station in northern Minnesota. Classes from the Twin Cities campus have useo the Cedar Creek facility for one-day field trips only, although more extensive use of the area for field courses is planned for the future. All who enter Cedar Creek's habitats do so under strict regulations and permits.

Through the joint efforts of the Minnesota Academy of Science and the University of Minnesota, backed by individuals from the private sector, Cedar Creek's first forty-acre tract was purchased in the early 1940's at a time when pioneer studies on ecological succession by R. L. Lindeman were taking place. By the late 1940's the area encompassed some 620 acres and has since increased to 5400 acres (2,185 hectares).

Lindeman's 1941-1942 classic studies at Cedar Bog Lake have been followed by various ecological and botanical projects. For example, rates and patterns of primary productivity, nutrient cycles, secondary succession and other community and ecosystem studies have been performed at Cedar Creek by Bray, Buell, Lawrence, Ovington, Reiners, Pearson and others (see publications list in Appendix A). In an ongoing project started 8 years ago by D. Lawrence, an agricultural field is being abandoned in 0.25 hectare strips each year. Permanent sampling plots are established in each strip as it is abandoned. A wealth of information on successional patterns in these permanent sampling plots has already been collected. D. Lawrence, an emeritus faculty member, continues his strong interest in these experiments. D. Tilman has begun additional sampling in these plots in conjunction with his other work at Cedar Creek on the role of nutrients, light and disturbance in controlling the diversity and species composition of grassland communities.

A long-standing interest in bird and mammal ecology lead to pioneering work in radio telemetry at Cedar Creek; techniques developed and equipment produced by the electronics staff are currently being used in many research projects both at Cedar Creek and around the world. Studies of waterfowl behavior have also been a major research effort at Cedar Creek. An elaborate system of artifical ponds, deep-water wells, flight pens, and observation lookouts are used in ethological research on both native and exotic species.

As a result of such projects, researchers at Cedar Creek have available a wealth of observational and experimental information on the past ecology of various sites and organisms, including complete species lists, animal and plant collections, vegetation maps, land use history maps, topographic maps, soil maps, several series of aerial photographs, and climatological data. Moreover, the management plan of Cedar Creek since its conception has been to maximize research potential. This is reflected in the planned abandonment of agricultural land at Cedar Creek, and a regular pattern of controlled burns which was initiated at Cedar Creek 17 years ago, with some areas burned every year and other areas burned on a 2, 5 or 7 year cycle. The areas provided by this past management are an important part of the proposed research.

Faculty from various colleges and departments within the University system utilize Cedar Creek. Currently, the most active are the Departments of Ecology and Behavioral Biology and Botany in the College of Biological Sciences; and the Departments of Soil Science, Entomology, Fisheries and Wildlife, and Plant Pathology in the College of Agriculture. A list of funded research at Cedar Creek for the past decade is given in Appendix B for on-site work and in Appendix C for off-site research.

IV. PROJECT PERSONNEL

The nine scientists who will be cooperatively working on this project come from four different departments within the University of Minnesota (Ecology and Behavioral Biology, Bell Museum of Natural History; Entomology, Fisheries and Wildlife; Soil Science) and from the Kellogg Biological Station of Michigan State University. Except for Dr. P. Werner from Kellogg Biological Station, all of the scientists have performed research at Cedar Creek. The research skills and interests of the group complement one another and span the full breadth of questions that we will pursue. Although the details of the past research of various scientists are given in Vitae at the end of this proposal, we might note that Drs. P. Werner, D. Lawrence and D. Tilman are experienced in work with plants, Dr. D. Grigal is experienced in work with soils, Drs. P. Morrow and W. Mattson are experienced with insects and insect herbivory, and Drs. P. Regal, J. Tester and D. Siniff are experienced in mammal studies. In addition, Tilman does modelling, and Siniff is an experienced statistician.

The Co-principal Investigators for this project, David Tilman and John Tester, are both permanent, full-time tenured faculty of the University of Minnesota. We are both aware of the long-term commitment that we are making. By serving as project leaders for the duration of this project, we will provide long-term continuity to this research. Additional continuity will come from the large number of scientists working on this project, and the long-term monitoring and experimentation that we propose. We anticipate that over the next 5 to 10 years, some of the scientists working on this project may complete their studies, and that others may join in the research to investigate new problems. We will especially encourage scientists from outside the University of Minnesota to join in this research, by inviting them to give seminars to our group, encouraging that sabatical leaves be taken at Cedar Creek, by providing "seed money" to initiate projects at Cedar Creek (this program is already underway), and by inviting them to attend our Annual Meeting. We have included funds in our budget for these purposes.

Our cumulative skills and experience, as evidenced by the vitae at the end of this proposal, will allow us to effectively pursue the research proposed herein. We realize that we are proposing a major research program, and we are eager for it to begin.

V. PROPOSED RESEARCH

INTRODUCTION

We believe that the field of ecology is at a crossroads. The last 15 years have seen a great increase in our knowledge of population growth, pairwise interspecific interactions, evolutionary ecology, optimal foraging, energy flow, nutrient budgets and cycling, and species diversity patterns. However, each of these advances has been gained by ignoring or greatly simplifying either higher or lower level phenomena. One portion of a system has been studied in great depth and other portions, even though they impinge on it, have been ignored or treated as if they were constant. We believe that the next major synthesis in ecology will be the integration of the principles and processes of population and community ecology into the framework of the whole ecosystem.

Most of current population ecology theory is based on pairwise interactions between species - interactions such as competition, predation, herbivory, parasitism and mutualism. There have been numerous attempts to extend such simple approaches to whole communities. However, almost all of these attempts have ignored long-term, indirect, and feedback effects. As several recent papers have shown (Holt 1977; Lynch 1978), the long-term effect of interactions among three or more species may be qualitatively different than the short-term mechanism of pairwise interactions. The difference comes from the indirect feedback of other species (and processes) on pairwise interactions. Figure 1 illustrates one such hypothetical situation. Species A and B are direct competitors with each other. In years when species C is rare or absent, this direct effect predominates. However, when the density of species C is high, the indirect effect of species A on B via species C outweighs the direct effect. The strong competitive interaction between species A and C and between species C and B means that the total, long-term effect of species A on B is positive, the opposite of the negative (competitive) direct effect. Thus an interaction which was competitive when studied in isolation could functionally behave as if it were mutualism in a natural community. This is only one of numerous ways in which the indirect and feedback effects of other species may modify the total effect of one species on another.

Ecology has reached the point where a sufficient amount is known about the direct, pairwise interactions of species. Syntheses of these approaches with information on whole system processes must now be attempted. Population and community ecology can be greatly strengthened by consideration of the long-term effects, the indirect effects and the feedback effects that the ecosystem approach emphasizes. Similarly, ecosystem ecology can be strengthened by detailed studies of the dynamics of interactions among individual species that play such a key role in the processes of productivity, energy flow and nutrient cycling. We believe this synthesis will only be possible when long-term experimental research combines population, community and ecosystem perspectives.

This synthesis will require a marraige of what Orians (1980) has called the micro and macro approaches in ecology. Orians (1980) stated: "We have been slow to

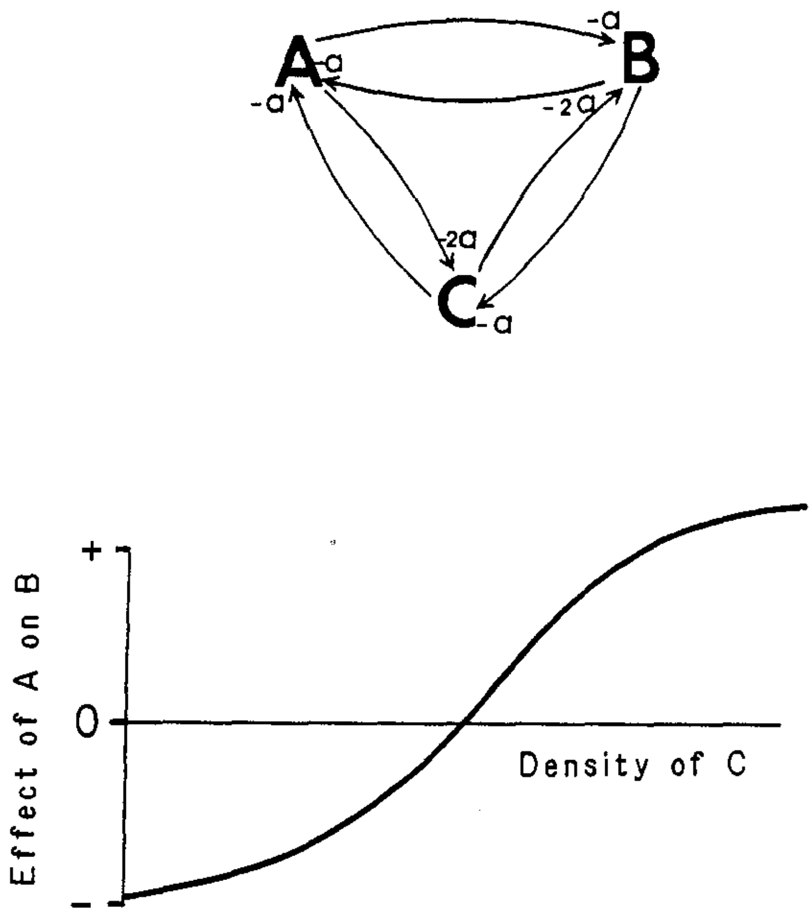


Figure 1. (Upper) In pairwise interactions, species A, B, and C are direct competitors with each other. However, when all three species are interacting, each species affects another species in two ways: directly through competition, and indirectly through its effect on the third species. (Lower) The relative importance of direct and indirect effects depends on the strength of interaction between species and on the densities of the species. When species C is absent, the effect of species A on B is negative (competitive). However, as the density of species C increases, the total effect of species A on B can become positive because the indirect effect of A on B through C outweighs the direct effect. (See Holt 1977).

develop better ways of integrating the two areas because, until very recently, we had little microecology worth using as building blocks for imaginative macroecological models. This is no longer true, and much is to be done." The experiments outlined in this proposal include long-term studies of both large scale and small scale unmanipulated and manipulated plots. The large-scale plots will provide information on whole system, long-term responses, while the small-scale plots will provide information on many of the micro-processes that are influencing the long-term plots. Several of the small-scale plot experiments are designed around a "micro to macro" theory - a theory of multispecies resource competition. This theory is based on the consumer-resource and niche theories of MacArthur (1972), Maguire (1973), Leon and Tumpson (1975), Abrosov (1975), Tilman (1980, 1981 c), and others. As developed in Tilman (1981c), this theory extends the simple consumer-resource approach to include the interactions of numerous consumers and resources in both spatially and temporally structured habitats. The theory is thus one of what may become a large set of theories joining micro and macro views of ecology. Only carefully-controlled, long-term observation and experimentation will provide the detailed data sets needed to test and hone these theories. Only such data will be able to suggest new approaches to be taken in increasing our understanding of and in developing predictive theories of the structure of the natural world.

This micro theory of resource competition (Maguire 1973; Tilman 1980, 1981a,b,c, see Figure 2) can be used to illustrate the need for a synthesis of population and ecosystem perspectives. The micro view of resource competition suggests that the outcome of competition between species can be predicted using information on the resource requirements of each species and the rates of supply of these resources in a particular habitat. However, it does not include information on the factors controlling the availability of resources nor the processes leading to changes in the budgets of different nutrients. Thus, the micro theory has the potential to provide a short-term view of change in plant community composition,

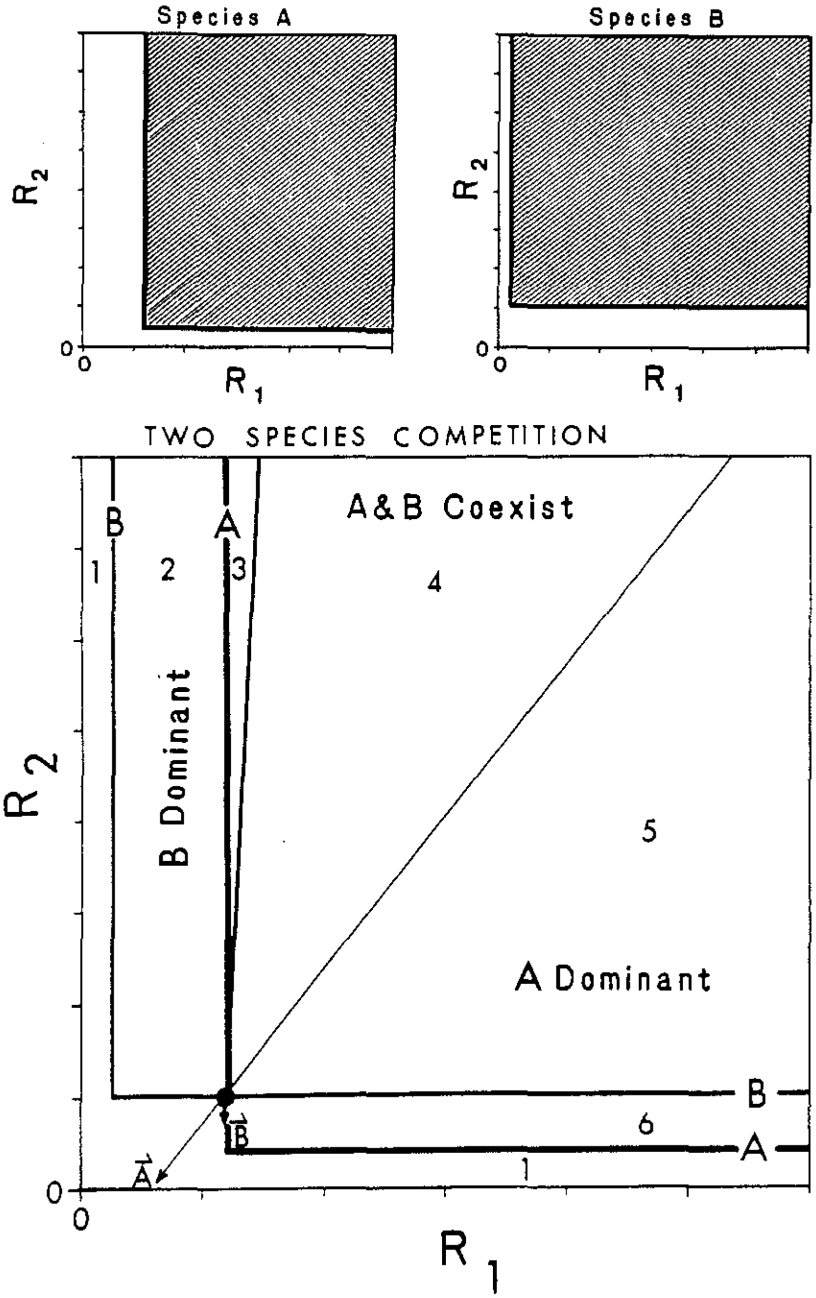
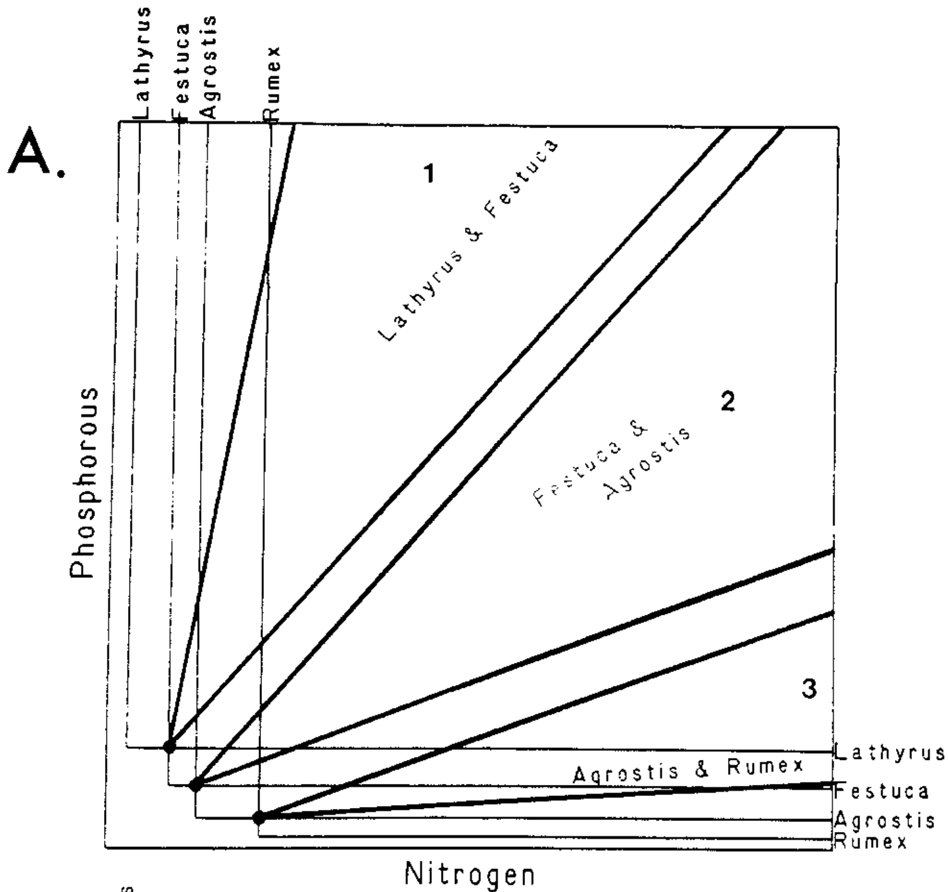


Figure 2. The upper parts of this figure show the requirements of two plant species for two limiting resources. The thick line in each figure is a growth isocline for each species -- i.e., a line along which the resource-dependent reproduction of each species just balances its mortality rate. If a habitat had resource availabilities that fell on the isocline, the population density of the species would not change. If a habitat had resource availabilities that fell in the shaded region, the population density of the species would increase. (Lower figure) The point at which these two isoclines cross is a two-species equilibrium point, shown with a dot. These two species will stably coexist in a habitat which has the resource availabilities at this point. Habitats which have resource supply points that fall in the region labeled "A & B Coexist" will eventually have their resource availabilities reduced down to this point by the consumption of both species. The boundaries between the region of coexistence and regions in which only one species is dominant are determined by the consumption characteristics of the species. Habitats which have resource supply points that fall in the region numbered 1 will lead to extinction of both species. For regions 2 and 3, species B will be dominant. In region 4, both species will stably coexist. In regions 5 and 6, species A will be dominant. See Tilman (1980) for more details.

but could only provide a long-term perspective if it were to be combined with an ecosystem level study of nutrient dynamics.

This example may be more concrete by considering four species of terrestrial plants which naturally compete for two limiting soil nutrients, nitrogen and phosphorous. Given the information on the resource requirements of these species in Figure 3A (from Tilman 1981c), it is possible to predict, in theory, the outcome of competition among them in any given habitat. If a habitat had relatively high rates of supply of phosphorous and low rates of supply of nitrogen, such as at point 1 in Figure 3A, it would be predicted to be dominated by the legume, Lathyrus and the grass, Festuca. A habitat which was more nitrogen rich but more phosphorous poor, such as at point 2, would be predicted to be dominated by Festuca and Agrostis, both grasses. An even more nitrogen rich but phosphorous poor habitat would be predicted to be dominated by Agrostis and an herb, Rumex. The long-term outcome of the fertilization experiments performed in the Rothamsted Park Grass Experiments support these generalizations (once soil pH is controlled for; Tilman 1981c). Thus, a simple, population-level theory is at least potentially able to predict local patterns of species abundances based on the resource requirements of the dominant species.

However, this population-level model cannot predict, by itself, what might happen to such communities under natural conditions. Fertilization imposes fixed, constant rates of supply of nutrients which tend to override the natural rates of supply, and is thus a useful experimental tool. Under natural conditions, all of the processes affecting nutrient supply and loss to the system, as well as those affecting nutrient cycling within the system would have to be understoood in order to use the micro theory to predict the direction and rate of community change. Consider Figure 3B. Let us say that a field has rates of supply of N and P that put it at point 1. Let us also admit that the field will have spatial heterogeneity, so that we cannot represent the field by a single point, but must use a probability distribution, which can be represented in the figure as the



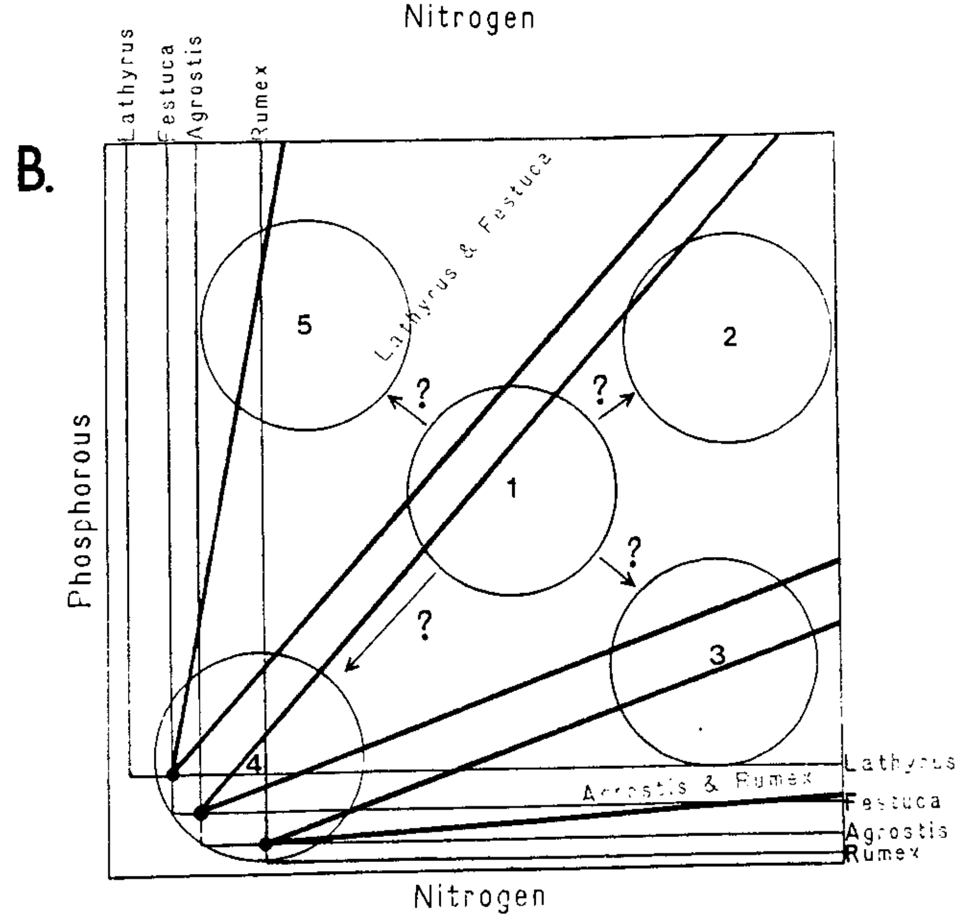


Figure 3. (Upper) Competition for N and P by four species of terrestrial plants occurring in the Rothamsted Park Grass Experiments (from Tilman 1981c). The isoclines and consumption vectors of the species define regions in which various pairs of species may coexist.
(Lower) The circle around the number 1 represents the microsite to microsite spatial variation in resource supply habitat 1. How will the rates of supply (and the amount of spatial variance) change in this habitat through time?

circle encompassing the number 1. This would include some percent (let us say 99%) of the point to point spatial variation in resource supply in the field. Theory would predict that Agrostis and Festuca should be dominant in this habitat, but that there would be sufficient spatial heterogeneity for Lathyrus to coexist with these species in this field at this time.

What, though, would happen in this field through time? What pattern would succession take? Even if we were to ignore many other important processes for the sake of this discussion, it should be clear from Figure 3B that the micro theory is incapable of making a prediction. Only when it is combined with a knowledge of the processes determining the budgets and supply rates of the limiting nutrients would any long-term predictions be possible. If the processes controlling nutrient budgets were to lead to an accumulation of both N and P in the soils, the nutrient supply probability distribution would move toward the distribution numbered 2 in Figure 3B. If nitrogen were to accumulate but phosphorous to decrease, it would move toward the distribution numbered 3, etc. Each of these changes would have an effect on which species should be dominant in the system and on the number of species that could possibly coexist (Tilman 1980, 1981c). To see the possibility of the effect on diversity, note that all four species can coexist in habitat 4, whereas only two species can coexist in habitat 2 of Figure 3B.

This simple example illustrates an important -- and unexplored -- interface between the population and ecosystem perspectives. There are other such interfaces that have been insufficiently studied. For example, consider the short-term direct effects of herbivory on plant reproduction -- a process often studied by population ecologists, versus the long-term effects of herbivory on nutrient cycling -- a process often studied by ecosystem ecologists. Are the short-term "costs" of herbivory outweighed by the possible long-term "benefits" of nutrient cycling? How do changes in the supply rates of various nutrients caused by herbivory influence competitive interactions among plant species? If the growth rate of a plant and its herbivore load both increase under favorable nutrient conditions, which effect, if either, would predominate in determining the dominance of the plant species in the community? How do such direct, indirect, and feedback effects interact to determine the rate and direction of succession?

The research that we propose will be performed within the context of the natural secondary successional sequence that occurs at Cedar Creek. We believe that a detailed, long-term study of succession is the ideal framework within which a synthesis of population and ecosystem approaches can develop. Succession is a long-term process which results from numerous short-term changes. Succession includes numerous direct, indirect, and feedback effects. It is impossible to divorce succession from a consideration of plant life history characteristics, from the population processes of competition and herbivory, or from the ecosystem processes of productivity, soil development, nutrient cycling and disturbance. The patterns and causes of the process of succession are the major theme unifying the work that we propose. Our experiments and observations are designed to provide a multi-faceted view of succession from evolutionary, population, community and ecosystem perspectives. We believe that our studies can provide a synthesis of these approaches and that they will demonstrate that all of these viewpoints must be combined to gain a meaningful understanding of the natural world.

In addition, we believe that the long-term research that we propose will allow us to address a whole series of related questions which ecologists have not been able to address because of the short-term nature of most research projects. Many of these questions will be addressed using information from the long-term monitoring that we propose. For instance, how does climatic variability affect the species composition and diversity of plant communities? Of herbivore communities? The rate and direction of succession? How does it influence productivity, or nutrient budgets and cycles? Are the effects great when viewed on a population level but minimal when viewed on an ecosystem level? Are the effects decreased or increased in systems with different levels of productivity (such as will be caused by some of our manipulations or in areas of different successional age?)

Another question is to what extent may a temperate ecosystem be assumed to be at steady state? Ecologists often assume that any fluctuations are small and center around some steady state level. Yet profound changes in the ecology of North America have taken place since the end of the last glaciation and even since the height of the Prairie Period of warm dry climate some 5000-8000 B.P. Changes in the ranges of some species are taking place now (Davis 1976, Wright 1976, 1977, Amundson and Wright 1979). M. Davis stresses that many ecologists tend to think that species interactions structure communities, whereas poleoecologists tend to see climate structuring communities. Studies such as we are proposing should bring us closer to a middle ground. The descriptive studies of the effects of weather on patterns of primary production and on the responses of networks of organisms in the food chain should comprise a unique data set of general ecological interest and significance.

How important is climatic stability in determining the diversity of communities? The balancing act by which a pyramid of consumers remains atop a fluctuating base of resources may not be so simple as an energy flow model may suggest. Knowing how resources are used during harsh seasons and years is no doubt essential to understanding carrying capacities, community dynamics, and community structure. A particular resource that is little used by any of several species in most years might be fiercely contested in years when other important resources are absent. Thus, the nature and frequency of such bottlenecks could have an effect on species diversity that would not be revealed in a study of niche overlap during good years. Unfortunately, the lack of long-term research in ecology means that ecologists currently have only anecdotal stories, and not the data needed to evaluate such effects. For instance, R. Foster tells of a year on Barro Colorado Island, Panama, when an early rain caused premature flowering, but many pollinators were not similarly stimulated by the rain. Since there was little pollination there was little subsequent fruit production. Dead mammals were found on the trails and some normally shy animals would even rush into the dining room to take food. A simple report of early flowering would not have revealed the effects of the premature event along the food chain. If detailed studies had been in progress a more exact idea may have been gained of the effects of seasonal variability on community composition and structure.

Our proposed research includes studies of the biology of a variety of the major species chosen from several trophic levels in each study site, as well as studies of species diversity, dominance-diversity patterns, disturbance, productivity, litter accumulation, rates of nutrient supply, loss and cycling, etc. This research will bridge the gap between the short-term, potentially predictive approach of population and community ecology and the more synthetic approach of ecosystem studies. To date, ecology has produced some excellent "micro" studies and some excellent "macro" studies, but it will require a major research effort to integrate the collection of such sets of information on one site over a sufficiently long period of time to provide the data needed for this synthesis.

The research proposed herein includes detailed, long-term monitoring of meterological events and ecosystem processes repeated in a set of three habitats from a natural secondary successional sequence at Cedar Creek. These habitats are: a newly abandoned field, a 25 year old field, and an annually-burned mature oak savannah. We will make detailed, long-term observational studies of the population dynamics of many plants and herbivores in these successional stages. In addition to such observations on these permanent study sites, we will perform numerous experimental manipulations. These will include application of mineral fertilizers in various rates and proportions, imposed disturbance of microsites, and manipulations of insect and mammal herbivores. These experimental treatments will provide insight into the processes controlling the structure of these communities. In addition, the use of three different successional stages will allow us to determine the relative importance of these processes throughout succession, and to determine the response of different successional stages to various natural and imposed disturbances.

In each of the successional areas, we will have two sets of plots for our studies: a set of nine large (0.5 hectare) plots for long-term monitoring of unmanipulated and manipulated areas, and a set of five small "microplots" which will receive numerous manipulations. All of the principal investigators will work jointly on the large plots. Various teams of investigators will coordinate specific studies in the microplots. The monitoring performed in these large plots will be coordinated with that at other LTER's so that the data we collect can be of maximal usefulness in cross-site comparative studies. It will be made readily available for use both within the group of investigators on this project and to other interested scientists by coordinating our computer storage and retrieval methods with those of other LTER sites.

In analyzing our data, we will be looking for patterns that may exist among parameters such as productivity, diversity, soil nutrient status, and annual and long-term climatic variability. Our own preliminary studies, studies performed elsewhere, and several recent theories all lead us to believe that we will see such patterns. One of the major advantages for performing our work within the context of a network of LTER sites is the ability to do cross-site comparative studies. Such studies will allow us to determine the generality of such patterns. For instance, the Rothamsted experiments revealed that a given increase in plant productivity led to the same decrease in plant species richness, independent of the year or species composition of the plots (Tilman 1981c). Might the correlational and experimental data from Cedar Creek and the correlational data from Konza Prairie, Andrews Experimental Forest, and other LTER sites show the same relationship? Might the diversity of some taxonomic groups be related to the amount of seasonal climatic variance of the LTER network sites? How do the processes of soil development and change depend on climate? These and many other questions can be addressed with the data collected by the LTER sites. The network will allow an unprecedented opportunity for syntheses.

Our microplot experiments are designed to test a variety of hypotheses that have been put forward to explain the patterns likely to be observed in the larger plots. More such plots will be added as hypotheses develop. We plan to study these microplots for at least 4 years, and to evaluate at that time if further work on them would be useful.

The approaches taken in these experiments reflect our belief that major insights into the relationships among primary production, succession, and structure and function in natural ecosystems will only come from long-term observation and experimentation on a variety of micro and macro processes in both natural and manipulated communities. In the following sections of this proposal we will first outline our experimental design and then describe the reasons for these experiments and the general methods that we will use. For each aspect of the proposed research, at least some members of our group have had previous research experience addressing similar questions and using similar techniques. For that reason, for brevity, and because it will be necessary for all LTER sites to coordinate methods, we will not present detailed descriptions of our methods in the following sections.

PERMANENT STUDY AREAS

Introduction

The sandy, nutrient poor soils of Cedar Creek are ideal for experiments on productivity, diversity and succession because of their relatively rich natural flora and because of the changes in soil fertility easily induced by fertilization. The scheduled abandonment of farmland since the founding of Cedar Creek as a natural area has provided a complete series of fields ranging in age from one year post abandonment to 45 years post abandonment, as well as extensive areas of oak savannah which have not been used for grazing for the last 45 years. From this array of sites of different successional ages, we have chosen three for our permanent plots.

The newly abandoned site will be created on land that was last farmed in 1971. Portions of this 35 hectare field have been used in Tilman's experiments for the last three years, and have been mapped for soil chemistry and floral composition. Nutrient enrichment experiments, a N:Mg ratio gradient experiment, and disturbance experiments have been performed in the area. A 0.1 hectare area has had all naturally disturbed sites (mainly from gophers) mapped, the soil nutrient status of the sites recorded at the time of disturbance, and the successional sequence on the disturbed sites recorded for one year. The site is thus relatively well studied, with a large background data set, and a complete herbarium collection including many seedlings. To create the newly abandoned field, a 8.0 hectare square will be disked thoroughly twice each month from July 15 to October 15 during the first year of these experiments. The initial disking will be delayed until the middle of July so that pre-disturbance species composition and soil characteristics can be determined. This information on past history will be useful in seperating field effects from experimental effects in the successional sequence in the newly abandoned field. In addition, it will allow determination of the extent of convergence on past patterns after a major disturbance.

The second successional stage will be a 25 year post-abandonment field on a soil type similar to the first area. Fields of this age at Cedar Creek have been invaded by choke cherry and black cherry, and have scattered oak saplings. Except for the annuals common on very nutrient poor soils or in recently disturbed areas, the flora of 25 year-old fields is mainly herbaceous perennials and grasses. The survey of Cedar Creek soils (Grigal et al. 1974) has allowed us to chose several approximately 25 year old fields which have parent soils similar to the newly abandoned old field. Further surveying of these possible sites will allow us to choose one with the greatest floral and topographic uniformity.

The third successional stage will be a mature oak savannah. The best developed oak savannah is located in areas that naturally burned in the past (including a natural wildfire in 1956), and which have been periodically burned since the inception of Cedar Creek Natural History Area. We will locate our study site in a 21 hectare area that has been subject to annual burns for the last 17 years. We will continue the annual burning. Within this area, we will chose as topographically uniform an area as possible for our permanent plots. In each of the nine permanent plots, we will have one 10 x 10 m area which is protected from the annual fire. We realize the importance of fire in these communities. However, we cannot study all important processes simultaneously. We hope to gain some insight into the role of fire from the nine 10 x 10 m plots with fire excluded, and later look at the interactions between fire, nutrients ano herbivory in determining the structure of these communities.

Design of Permanent Plots.

The long-term research to be performed at Cedar Creek will focus on 27 permanent study plots. Each 0.5 hectare (70 x 70 m) plot will be divided into 49 permanently marked subplots of 100 m^2 using color-coded aluminum stakes. The coded stakes will make it easy for an investigator to quickly determine location within any plot. Some subplots will be further subdivided for long-term monitoring of selected species and processes. The nine plots at each of the three successional stages represent triplicates of each of the following: (a) unmanipulated plots; (b) plots receiving a complete mineral fertilizer applied at a low rate; and (c) plots receiving the same complete mineral fertilizer applied at a high rate. These nine plots will be laid out in the field in a complete Latin Square design. Because each row and each column of a Latin square is a complete block, it is possible to allow for and determine the magnitude of row and column field effects. To facilitate such an analysis, the rows (or columns) will be located parallel (or perpendicular) to any observed gradients in the fields.

The complete mineral fertilizer will contain all essential trace elements and will be blended to have the macronutrients N, Mg, Ca, K and P in the proportion naturally occurring in the soil and vegetation of each site. This will be determined by a thorough preliminary soil nutrient analysis for each site, as well as by sampling of foliage of the dominant plants in the sites. By balancing the fertilizer to the proportions of nutrients found in the soils and plants of each site, primary productivity can be increased with less an effect on the nutrient status of individual plants. Other experiments, described in detail in a later section, are designed to determine the relative competitive abilities of plants for different proportions of N, P and Mg. We will use commercially available, slow-release fertilizers, which we will blend to our specifications. The fertilizer will be applied by broadcast-spread, backpack-mounted fertilizer spreaders, such as used in forestry. Uniform coverage can be assured by fertilizing each plot with four light treatments applied in a criss-cross manner. To prevent aereal drift of fertilizer, plots will only be fertilized on calm days. A 10 m walkway will seperate each of the 0.5 hectare plots to provide access to the sites and to minimize surface runoff movement of fertilizer.

To allow baseline information to be collected on the plots before manipulation, none of the plots will be fertilized until September of the first field season. Fertilizer will be applied twice each year, once in spring (May) and once in late summer (September). Experience gained from fertilizing natural vegetation at Cedar Creek has indicated that fertilization during the drier summer months often damages foliage and may kill some species. However, the rapid percolation of the sandy soils at Cedar Creek requires fertilization twice a year.

Design of Micro-plots.

As we perform long-term monitoring in the 27 large plots, we will also be exploring a variety of population, community, ecosystem and evolutionary questions. Some of these questions will be answered directly using the monitoring information that we will collect uniformly throughout the 27 plots (as described in a later section). Other questions will require additional sampling in some or all of the plots. However, some of the hypotheses of interest to us can only be tested by additional experimental work. To answer these questions, we are proposing a set of five small-scale experimental manipulations, termed "microplots", to be performed in each of the three successional stages. The micro-plot treatments will be (1) various ratios of N:P fertilization; (2) various ratios of N:Mg fertilization, (3) application of deionized water and other essential mineral elements; (4) insect and mammal removal; and (5) interactions between disturbance regime and soil nitrogen. The experimental design for these microplots is briefly outlined below.

1) N:P Ratios.

These experiments are designed to determine the effects of different relative supply rates of N and P on the plant species composition of small, replicated plots. The experiments will consist of a factorial, randomized block which is replicated four times. Each block will contain 9 microplots which are 25 m^2 in area. The treatments for the microplots within one of the blocks will be (a) no fertilization for one microplot; (b) fertilization with all nutrients except N and P for one microplot; and (c) fertilization of the seven remaining microplots with all nutrients other than N and P and with N and P in various ratios ranging from low N and high P to high N and low P. Each of the microplots will be seperated by a 2 m wide walkway, giving a total area for this manipulation of 0.2 hectare. Fertilizers will be applied using a small broadcast spreader with the same timing and general methods as for the large scale plots.

2) N:Mg Ratios.

These experiments are designed to determine the effects of different relative rates of supply of nitrogen and magnesium on plant species composition. They will be performed in a manner analagous to that used for the N:P experiments, with all but one of the microplots in a block receiving all nutrients except N and Mg, and with seven of the microplots in a block receiving various ratios of N and Mg.

3) Water and Other Nutrients.

Deionized water and mineral nutrients other than N, P and Mg will be added singly in a replicated block design as used for the N:P and N:Mg experiments described above, except that 2 x 2 m microplots will be used. One of the microplots within a block will be unmanipulated, one will be watered bi-weekly with deionized water, and the other seven will receive one of the following essential plant mineral nutrients: K, Ca, S, B, Fe, Mn, Mo. Each block will be replicated four times.

4) Herbivore Removal.

Insects and mammals are the major herbivores at Cedar Creek. This is a three factor experiment designed to determine the effects of insect and mammal herbivory on plant communities of different levels of productivity. The experiment will include two levels of plant productivity (unfertilized and fertilized plots), and insect removal, mammal removal and removal of both herbivore groups. Of the four blocks used in these experiments, two will be unfertilized and two will be fertilized. Within each block there will be four treatments: (a) unmanipulated; (b) insects removed via periodic application of insecticide; (c) mammals removed via fencing and snap, pitfall and buried traps; and (d) both insects and mammals removed. These four treatments will each occupy a 10 x 10 m microplot, making the complete experiment, including 2 m walkways, occupy 0.25 hectare.

5) Disturbance and Nitrogen.

This set of microplots is designed to look at the process of microsite succession in the various successional stages of Cedar Creek. In these experiments, we will create sets of newly disturbed microsites at various times of the year and observe the species succession on these sites. Each set of disturbed sites will include both large (0.7 m^2) and small (0.1 m^2) disturbances, with adjacent disturbed sites of the same size being randomly assigned to one of the three following groups: (1) unfertilized; (2) fertilized with all nutrients except nitrogen; (3) fertilized with only nitrogen. Four such sets of disturbed sites will be created at a given time, and the process will be repeated at three different times during the season. Microsite succession in these plots will be followed at least through the second year after disturbance. Because of the intense efforts required for these experiments, we will perform them first in the 25 year post abandonment field, two years later in the mature oak savannah areas, and finally in the four year old community that will have developed on the "newly disturbed" site.

These five sets of microplots, when combined with the large plots in each of the three successional stages, will provide a unique data set of unusual experimental richness. It will allow the researchers at Cedar Creek, those at other LTER sites, and other interested ecologists to explore theories of succession, plant community structure, nutrient competition, soil development and nutrient cycling, herbivory and coevolution in much greater depth than ever before possible. The data generated should spark new approaches to ecological theory, and lead to syntheses of the now disparate approaches of population, community, ecosystem and evolutionary ecology. In the following pages we detail some of the methods we will use and some of the reasons for proposing this long-term experimental and observational research as we discuss specific questions that may be addressed with the data to be collected. However, we might note that the experiments are likely to generate a much more varied array of questions than those which follow.

PLANTS AND PRIMARY PRODUCTION PROCESSES

Succession

Ecologists have long been intrigued by plant succession because the repeatability of the successional sequence in an area suggests that a set of general underlying processes are controlling the sequence. Because succession refers to the changes that occur in ecological communities after a disturbance provides open space, succession can be seen to be a pervasive process in communities. All natural communities are being perturbed on various spatial and temporal scales. Successional processes can be considered to apply to the dynamics of change following an event as small as the death of a single individual plant, and to the changes following such major disturbances as fire, erosion, landslides, glacial recession, and agricultural land use. From the pioneering work of Cowles (1899) and Cooper (1913) arose one of the first major ecological theories, the theory of succession proposed by Clements (1916). The simplicity, completeness and apparent purpose contained in Clement's theory were sufficiently satisfying to ecologists that it survived numerous attacks (e.g. Gleason 1917, 1927; Egler 1954), remaining the most commonly held view of succession until the question was re-explored in papers by McCormick (1968), Odum (1969), Drury and Nisbet (1973), Colinvaux (1973), Horn (1974), Connell and Slatyer (1977), and others. The cause or causes of successional patterns are now a matter of debate, but the importance of the process in determining the structure of natural communities is not.

Re-examination of the causes of successional patterns has led to numerous competing hypotheses. Among these are the "facilitation" hypothesis of Clements, the initial floristic composition model of Egler (1954), the differential tolerance model and the differential colonization and inhibition model (Connell and Slatyer 1977), and the "resource ratio model" (implied by Crocker and Major 1955 and Lawrence et al. 1967; formalized in Tilman 1981c). All of these models share certain assumptions, with the major distinctions among the models being the emphasis placed on the relative importance of certain processes.

The facilitation hypothesis, which stresses that each species modifies the habitat in ways that favor succeeding species (see Odum 1969), has received considerable criticism (McCormick 1968; Colinvaux 1973; and others). In its extreme form, the facilitation hypothesis treats an ecosystem as an organism which is acting with a goal or purpose. The evolutionary improbability of such interrelationships has led many workers to reject this hypothesis, at least in its extreme form. However, numerous studies of succession do suggest that at least the initial changes in species composition take place because of changes in the habitat caused by the early colonists (see review in Connell and Slatyer 1977). If such changes are recognized as an unavoidable consequence of the growth of the earlier species, the evolutionary objection to the facilitation hypothesis is removed. However, the question of the importance of such species-induced environmental changes on the successional pattern remains. The differential colonization and inhibition hypothesis suggests that the successional sequence is a reflection of the life history characteristics of the various plant species. Those plants which are short-lived and rapid colonists will, on average, dominate a site initially. They will be replaced by longer-lived species which are poorer colonists, but which can hold the site for a longer period of time because of their longer life span. The resource ratio hypothesis states that the relative availability of limiting resources is changing throughout succession, and that the species sequence observed during succession reflects species which are better competitors for particular ratios. The work of Crocker and Major (1955) and Lawrence et al. (1967) on Glacier Bay primary succession suggested that the two most important limiting resources for plants were nitrogen and light. At the time of glacial recession, the substrate was a high light but very low nitrogen habitat. It was dominated by annuals and perennials capable of growth on a low nitrogen soil and by nitrogen-fixing alders. Such plants are specialized on habitats with a high ratio of light to nitrogen. As soil nitrogen levels increased, the area became increasingly dominated by species that were superior competitors for light by virtue of their height but required higher nitrogen levels, i.e., by species specializing on habitats with a low ratio of light to nitrogen. This example of the theory of resource ratio succession is illustrated in Figure 4 (from Tilman, 1981c).

The detailed, long-term nature of the observations and experiments we propose for three different successional stages at Cedar Creek would allow us to document the processes of succession and test the various theories that have been advanced to explain the process. We will follow the soil processes of litter accumulation, profile development, textural change, and changes in pH and in the total, available

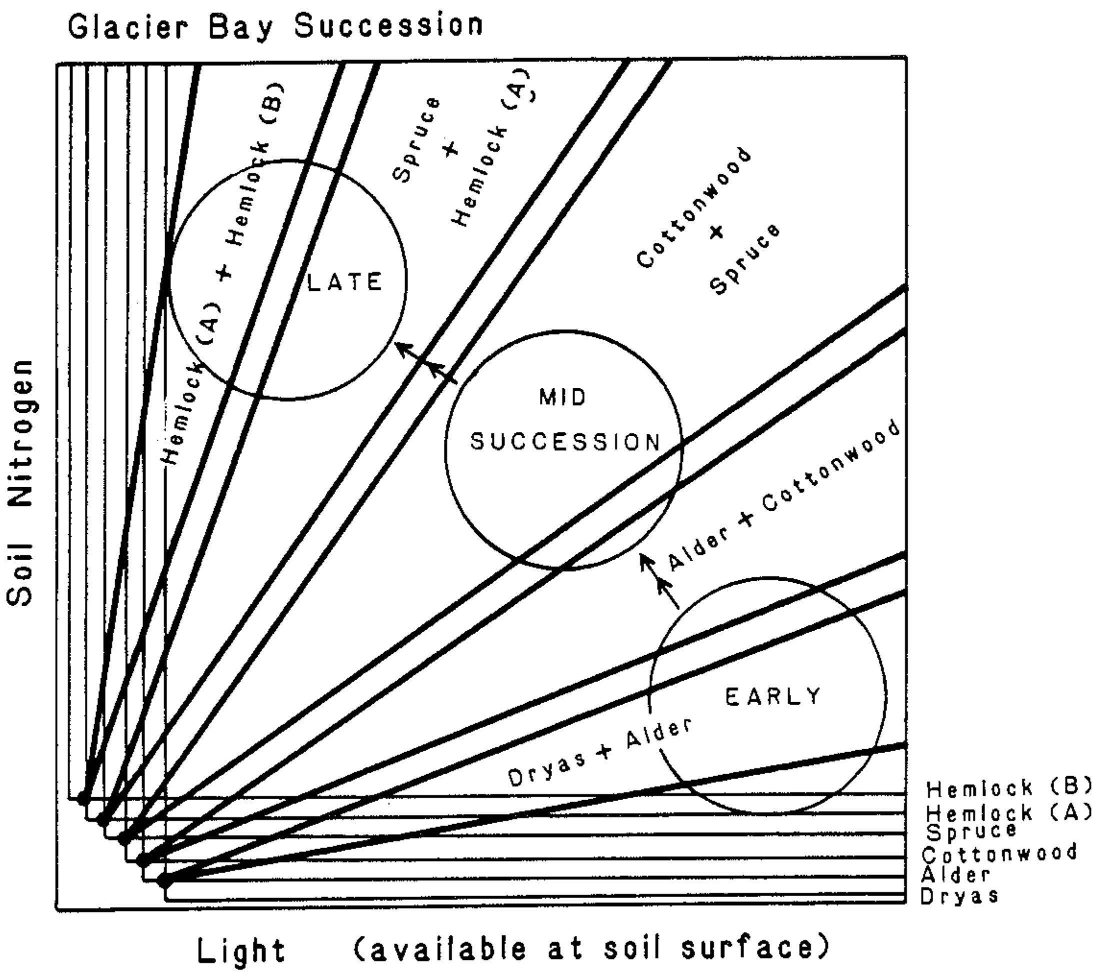


Figure 4. Hypothesized light and nitrogen requirements of major plants observed in the successional sequence at Glacier Bay, Alaska. Processes of nitrogen fixation and soil development are suggested to lead to an increase in soil nitrogen through succession. This allows an increase in plant biomass, which leads to decreased light availability for seedlings and for plants of small stature. The successional sequence from Dryas and alder to spruce and hemlock is hypothesized to be the result of different requirements of these species for light and nitrogen, and biotically-imposed changes in the soil nutrient status. Through succession, the habitat changes from one with high light and low nitrogen to one with low available light and high nitrogen.

and mineralizable forms of various plant nutrients. We will monitor rates and patterns of nutrient movement and cycling for the major nutrients throughout our study in our three study sites and thus know how this process changes with succession. We will follow rates of herbivory on dominant species and determine, in our micro plots, how herbivore removal influences the rate and direction of succession.

The large scale disturbance of our newly abandoned site will allow us to determine the role of the seed bank in the initial vegetation of the area, as well as the role of immigration from adjacent areas. Our small-scale microplot disturbances will allow us to determine the importance of seed banking versus immigration in microsite succession. Preliminary experimental work performed last summer at Cedar Creek in a 10 year old field suggests that sites disturbed in late autumn or in early spring are dominated by seed bank species whereas sites disturbed in summer are heavily colonized by plants with small, wind-born seeds, mainly composites. We will sample soils from our sites to determine what plant species are in the seed bank. Some species which we know occur in later successional stages are absent in early stages. We will "seed in" such species in small plots to determine if lack of a seed source was the only reason for absence. By following the dynamics of our carefully monitored permanent plots, we will be able to observe the process of local species replacement that is the most basic element of succession.

By observing the changes in species composition in the fertilized plots, we will be able to deduce the relative requirements of species for light versus nutrients. The microplot experiments with different ratios of N:P and N:Mg will allow us to determine the effects of changes in the relative abundance of these nutrients on species composition and will suggest if different species are specialized on different ratios of these nutrients. The long-term fertilization experiments performed at the Rothamsted Station in England (Lawes and Gilbert 1880) suggest that the ratio of N:P can be an important determinant of species composition. This is illustrated in Figure 5 (from Tilman 1981c). Seven of the 8 dominant plants in the Rothamsted plots seem to have maximal population density at a particular ratio of N:P. The species which does not fit this pattern, Holcus lanatus, dominates plots given complete fertilization--in which light is the major limiting resource.

If dominance on a resource ratio gradient is caused by differing competitive abilities of species for limiting resource, it should be possible to predict the ratio at which each species will be dominant from information on their nutrient physiology (see Tilman 1976; Tilman 1977, 1980, 1981a, b for examples with freshwater algae). Sand culture greenhouse experiments with several of the early successional Cedar Creek species performed last year by Tilman (manuscript in preparation) revealed major differences in nitrogen-limited and magnesium-limited growth curves for Rumex acetosella and Crepis tectorum. The results of an initial set of nitrogen limited greenhouse competition experiments showed Rumex to be a superior nitrogen competitor, in apparent agreement with its low nitrogen requirement for growth. (Such experiments are discussed in a latter section.)

Several recent papers have emphasized how little is known about the role of herbivores in succession (Connell and Slatyer 1977; Drury and Nisbet 1973). Our animal exclosure experiments will allow us to determine the effects of removal of insects, removal of mammals, and removal of both on plant species succession. By monitoring changes in plant species composition and soil nutrient processes in adjacent manipulated and control areas, we will obtain evidence on the importance of herbivory in the successional process. The experimental studies of Lubchenco (1978) clearly demonstrated the importance of an herbivore in determining the diversity, species composition, and successional pattern in a community of intertidal plants. Our initial herbivore removal experiments will allow us to determine how herbivory influences the rate and direction of succession. Once this major effect is documented, we will design other microplot experiments to test hypotheses such as:

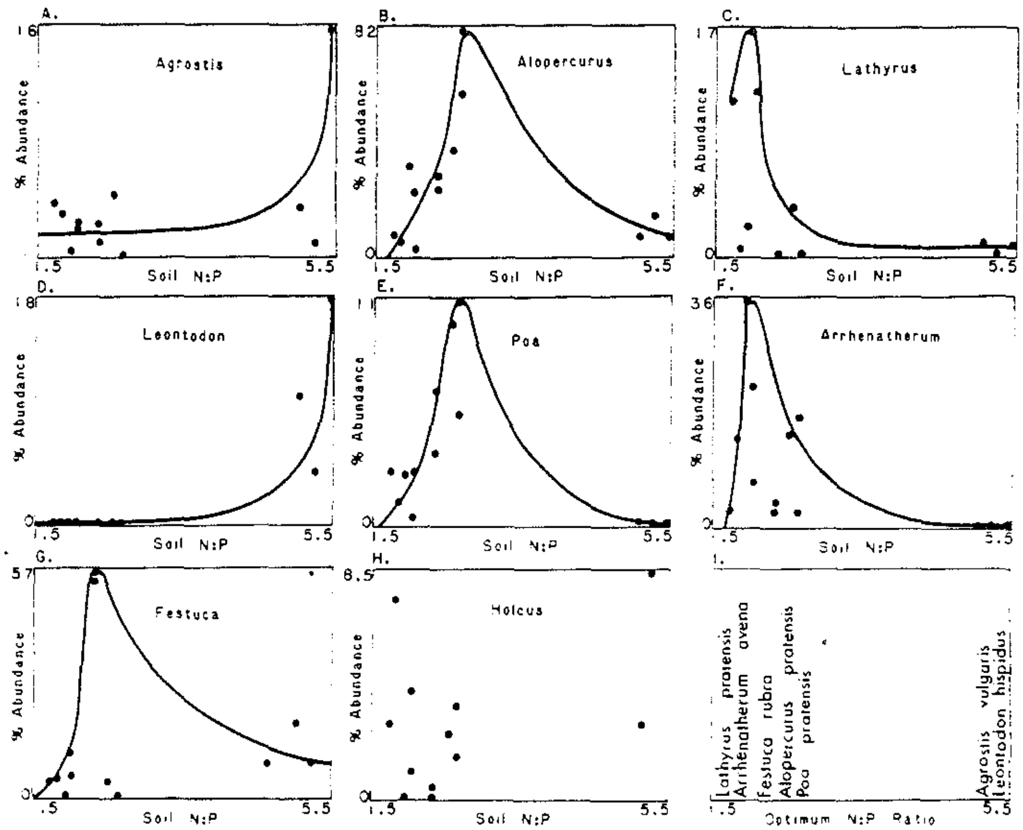


Figure 5. The various parts of this figure show the relative abundance of the 8 dominant plant species in the Park Grass Experiments performed at Rothamsted, England, for the last 125 years. Note that different species have their maximal abundance at different ratios of soil N:P. This is consistent with the theory presented in Figures 2 and 3. The only exception is Holcus lanatus, a grass which is a superior competitor for light (and open sites), but apparently a poor competitor for both N and P.

(1) To what extent does the effect of herbivory on succession depend on the species preferences of the herbivores?

(2) Is the major effect of herbivory on succession from feeding or from nutrient cycling?

(3) Do all the dominant herbivore species respond similarly to increased rates of plant productivity, or are some herbivore species limited by nitrogen (protein) while others are energy limited?

(4) If the nutritional status of plants is a major cause of herbivore preferences, does the differential response of plant species to fertilization cause different rates of herbivory? If this is so, are the plant species which are initially favored by fertilization the same as the species that eventually dominate an area, or does the long-term effect of increasing herbivore population densities eventually eliminate such species?

There have been several observations of the effects of differential herbivory on community composition. One of the more interesting comes from Harper (1969):

> Generalizing from the controlled experiments and the results of the post Myxomatosis surveys, the effects of rabbit removal appear to be (1) the release and demonstration of hitherto unsuspected floristic richness in the rabbit-grazed communities: species which in the past had been regularly nibbled and suppressed, flowered and showed their identity ...

In some of our preliminary studies of old field succession, we observed that the evening primrose (Oenothera biennis) was dominant in an area one year. The next spring, following heavy insect attack on emerging plants, evening primrose was not dominant. We hypothesize that herbivore population levels may have built up during the first year of the study and were sufficiently high early in the next season to eliminate the plants at the time of emergence. Such an effect of cumulative herbivore load could be an important cause of successional sequences.

Soil Nutrient Heterogeneity, Productivity and Plant Community Structure

After preliminary experiments in 1978, an old field fertilization study was started in the spring of 1979 at Cedar Creek by D. Tilman and M. McKone. The area chosen for the study had a fine Sartell sand soil, with a pH of 4.6, total N of 0.04%, undetectably low levels of Mg, 0.2 meq Ca/100 g, 0.1 meq K/100 g and 260 ppm extractable P. The low availability of essential nutrients, except P, was reflected in the low standing crop in the old field, which had areas of vegetation-free soil. N, P, K, Mg, and Ca were added at two times during the season to 0.25 m^2 plots in a partial factorial design with from one to four nutrients added at a time.

In early September, 78 plots were clipped to the ground, plants were sorted to species, and the biomass and height of each species determined. Analysis of these results (using t-tests) indicated that, of all the nutrients added singly, only nitrogen had a significant effect. The plots receiving nitrogen alone showed significantly lower species richness and a significantly increased rate of primary productivity. Of all the plots receiving multiple nutrients, only those with N and Mg had higher biomass than those receiving only N. Thus, these fertilization experiments demonstrated that primarily N and secondarily Mg influenced productivity and diversity in this old field community.

In the spring of 1980, an adjacent area in this same old field was thoroughly disked, and then divided into 36 plots. Using a complete Latin Square design, the plots were assigned to one of six treatment groups, including no fertilization and fertilization with various ratios of N and Mg. Analysis of the first years results, obtained by early July and late August clips of small quadrats through each plot, revealed a tendency for the plots with greater productivity to have lower species diversity, as measured by the Shannon index, H'. There seemed to be some separation of species in response to the N:Mg gradient, with _Ambrosia artemisiifolia_ performing best at intermediate ratios of N:Mg, the legume _Vicia villosia_ performing best under conditions of low N:Mg ratios, and the grasses _Agrostis hyemalis_, _Setaria viridis_, and _Setaria lutescens_ performing best at high N:Mg ratios.

The results that we obtained in this work are not unique. In both temperate and tropical regions, in grasslands, forests, lakes, rivers and oceans, the addition of limiting nutrients to plant communities has two repeatedly observed effects. Plant productivity increases and plant species richness decreases (see, for instance, Lawes and Gilbert 1880; Lawes, Gilbert and Masters 1882; Brenchley and Warington 1958; Fischer 1960; Milton 1934, 1940, 1947; Steeman-Nielson 1954; Willis and Yemm 1961; Willis 1963; Bakelaar and Odum 1978; Kirchner 1977; Mellinger and McMaughton 1975; Patrick 1963, 1967; Thurston 1969; Williams 1964; Tilman, 1981c). Highly enriched communities become dominated by a few species, with many formerly abundant species going extinct. This is part of a broader relationship between species diversity and nutrient richness that is revealed by a comparison of undisturbed plant communities. Within a geographic region, extremely nutrient poor and nutrient rich habitats generally have low plant species richness, with moderately nutrient poor habitats having the highest species richness (Ashton 1977; Al-Mufti et al. 1977; Beadle 1966; Blasco 1971; Grime 1973; Holdridge et al. 1971; Huston 1979; Patten 1962; Schindler 1977; Young 1934). Such trends in three natural communities are illustrated in Figure 6 (from Tilman 1981c). These observational and experimental studies illustrate the possible critical importance of nutrient availability in determining the species richness and composition of plant communities.

The Park Grass Experiments at Rothamsted, England, begun in 1856 and still in operation today, are probably the most long-term ecological experiments ever performed. An 8 acre pasture that had been used for grazing for the previous ca. 200 years was divided into 20 plots, two serving as controls, the others receiving a particular fertilizer treatment once each year (Lawes and Gilbert 1880). Although started as an agricultural experiment to determine the effects of various types of fertilization on the yield of hay, Lawes and Gilbert (1880) observed such dramatic changes in species composition during the first few years that they concluded that the experiments were of greater interest to the "botanist, vegetable physiologist and the chemist than to the farmer." In 1862, Lawes, Gilbert, and

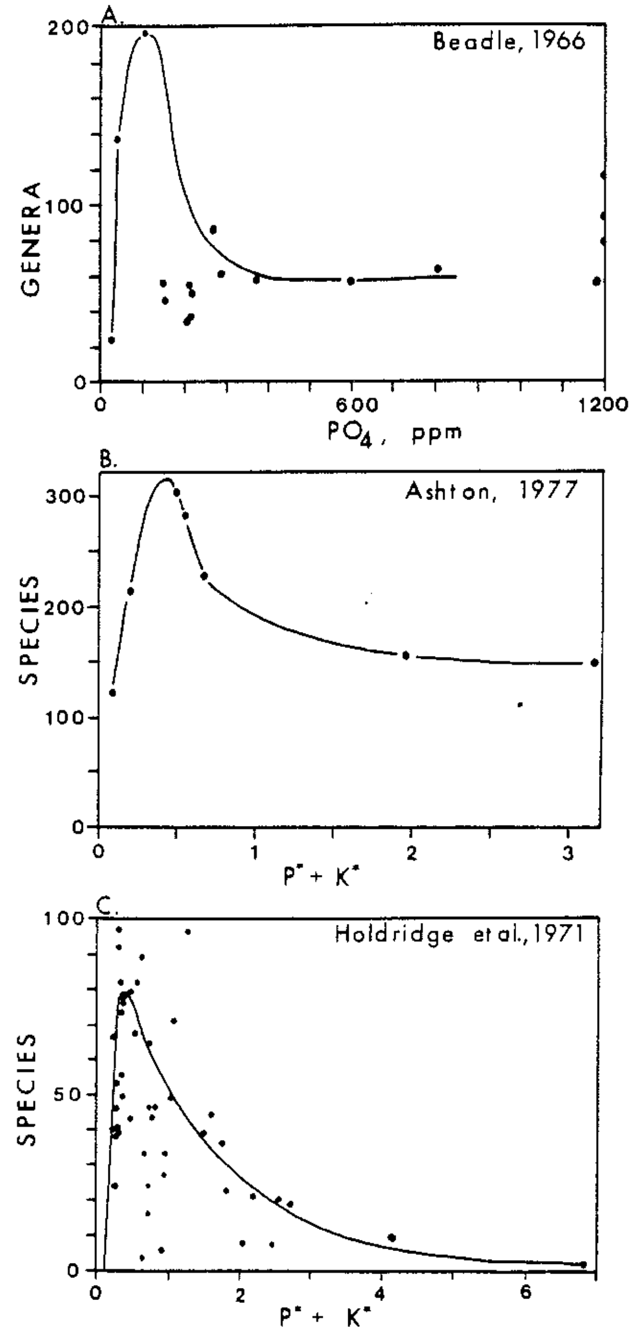


Figure 6. Species (or genera) richness in relation to soil nutrient levels from correlational studies in three different habitats. Part A is for Australian plants in relation to soil phosphate, with the data from Beadle (1966). Part B is for Malaysian rainforest species in relation to soil phosphate and potassium, with the data from Ashton (1977). Part C is for Costa Rican forests in relation to phosphate and potassium with the data from Holdridge et al. (1971). The curves shown are hand-drawn to the data (from Tilman 1981c).

Masters (1882) made their first quantitative survey of the species composition of the plots, and these botanical surveys were repeated eleven times in the next 100 years.

The Rothamsted experiments revealed that nutrient addition to a regularly mowed grass community had dramatic effects on species composition within a period of 3 to 5 years, and that the effects, most notably exclusion of plant species, have continued to this day (Thurston 1969). This is illustrated in Fig. 7 (from Tilman, 1981c) for two of the experimental treatments used at Rothamsted. Parts A and B of Figure 7 show species diversity ($H' = -\sum p_i \ln p_i$) and species evenness or equitability ($J = H'/\ln S$) in unfertilized control plots from initiation of the experiments to the last published information. Throughout the 100-year period, the unfertilized plots showed no significant changes in species richness, species diversity, evenness or species composition. They maintained richness of ca. 40 species, and evenness of ca. 0.7. Parts C and D show the plots receiving complete mineral fertilization, for which species richness fell from ca. 40 to ca. 3 or 4 species per plot, with the community changed from one with many co-dominant species to one dominated by a single species, Holcus lanatus. Areas receiving partial fertilization also had changes in species diversity and species composition. For example, the areas fertilized with all nutrients except nitrogen became increasingly dominated by nitrogen-fixing legumes, whereas the areas fertilized only with nitrogen became dominated by grasses, with almost all nitrogen-fixing species being displaced. Similarly, there were observable long-term effects of other types of fertilization on species composition, diversity and evenness. Interestingly, the plots that had the most dramatic changes in species composition and species diversity were those in which a given pattern of fertilization resulted in the largest change in primary productivity (Tilman 1981c).

As already mentioned, other studies have consistently demonstrated that fertilization results in decreased species diversity and changes in species composition (Milton 1947; Willis and Yemm 1961; Mellinger and McNaughton 1975;

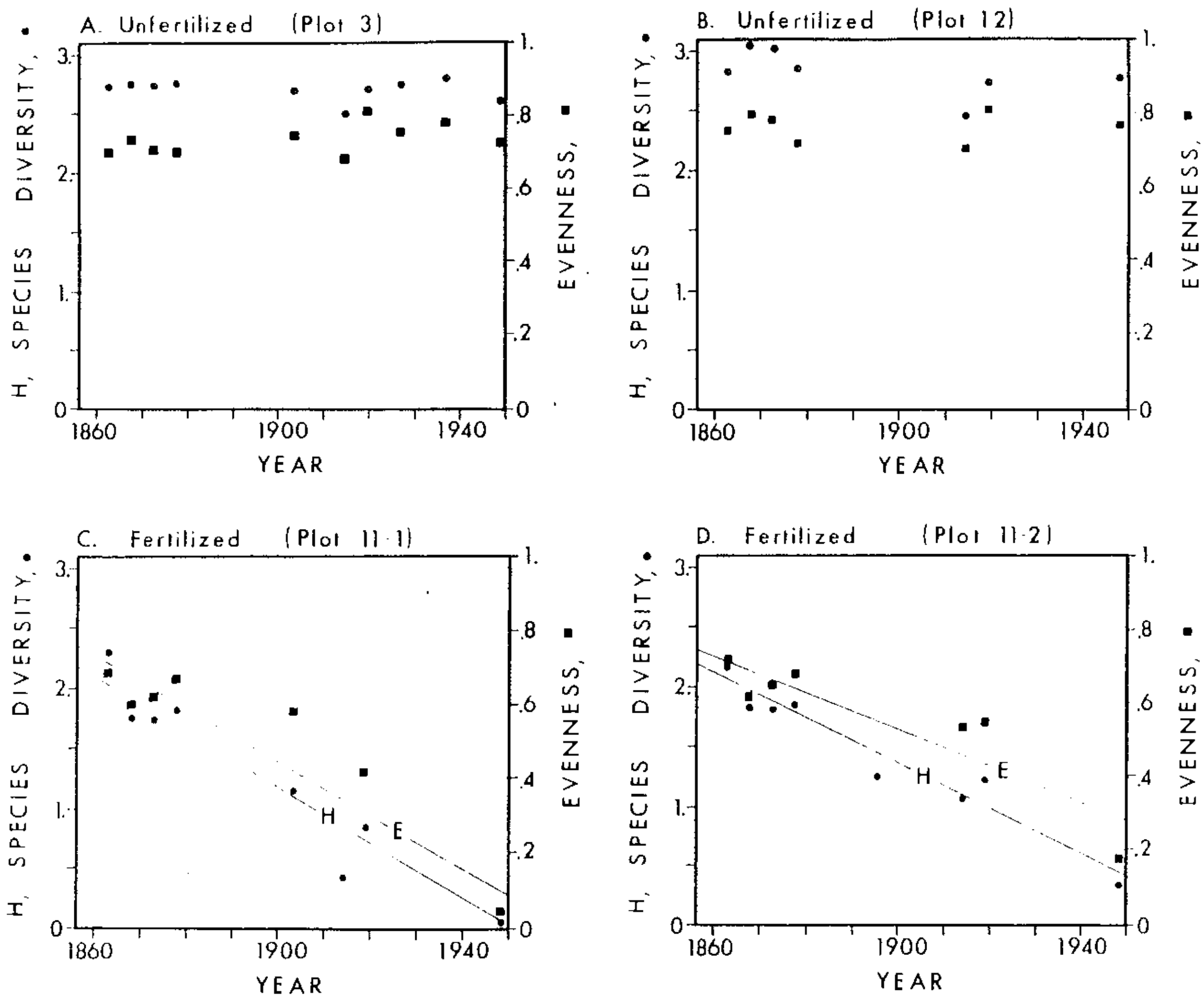


Figure 7. Species diversity (Shannon index) and evenness or equitability index in two unfertilized plots (parts A and B) and in two plots receiving complete mineral fertilizer (parts C and D) in the long-term experiments performed at Rothamsted, England from 1856 to the present time. Note that there was no significant change in diversity in the unfertilized plots, but that diversity decreased dramatically in the plots receiving complete fertilization.

Kirchner 1977; Bakelaar and Odum 1978). However, with the exception of a few short-term studies, these experiments have looked only at the effects of changes in productivity on the producer community itself, and have ignored any ramifications of the experimental manipulations on higher trophic levels. Additionally, there have been no attempts to measure the spatial heterogeneity of soil nutrients in these plots, even though it has long been suggested that soil nutrient spatial heterogeneity may be important in determining the diversity and non-random structure of plant communities (e.g., Snaydon 1962).

Because of the importance of soil nitrogen and magnesium in our experimental plots at Cedar Creek, we mapped the availability of these two nutrients in a 12 x 12 m grid near our experimental area. Figure 8, A and B show contour plots of total nitrogen and extractable magnesium within a 12 x 12 m area chosen for its topographic uniformity. Part C of this figure shows the relative availability of these two nutrients in this grid, i.e., the ratio of N:Mg. There are definite patches of high and low N:Mg ratios in this plot which may be influencing the local pattern of species composition and succession.

The results of our preliminary experiments are useful in evaluating several competing theories of the role of nutrients, productivity and disturbance in determining the composition and diversity of plant communities. One theory of nutrient competition in spatially heterogeneous habitats (Tilman 1981c) predicts that maximal species richness should occur in relatively nutrient poor habitats, and that areas that are either more nutrient rich or more nutrient poor should have lower diversity. That theory also suggests a quantitative dependence of species richness on the spatial heterogeneity of soil nutrients. However, this and other approaches to plant community structure (e.g., Grubb 1977; Huston 1979; Connell 1978; Hubbell 1979; Lubchenco 1978; Platt and Weis 1977; Rosenzweig 1971) can only be tested, extended and modified when there is an adequate observational and experimental data base. The extensive, long-term studies of soil nutrient heterogeneity, plant community composition, productivity and herbivore population

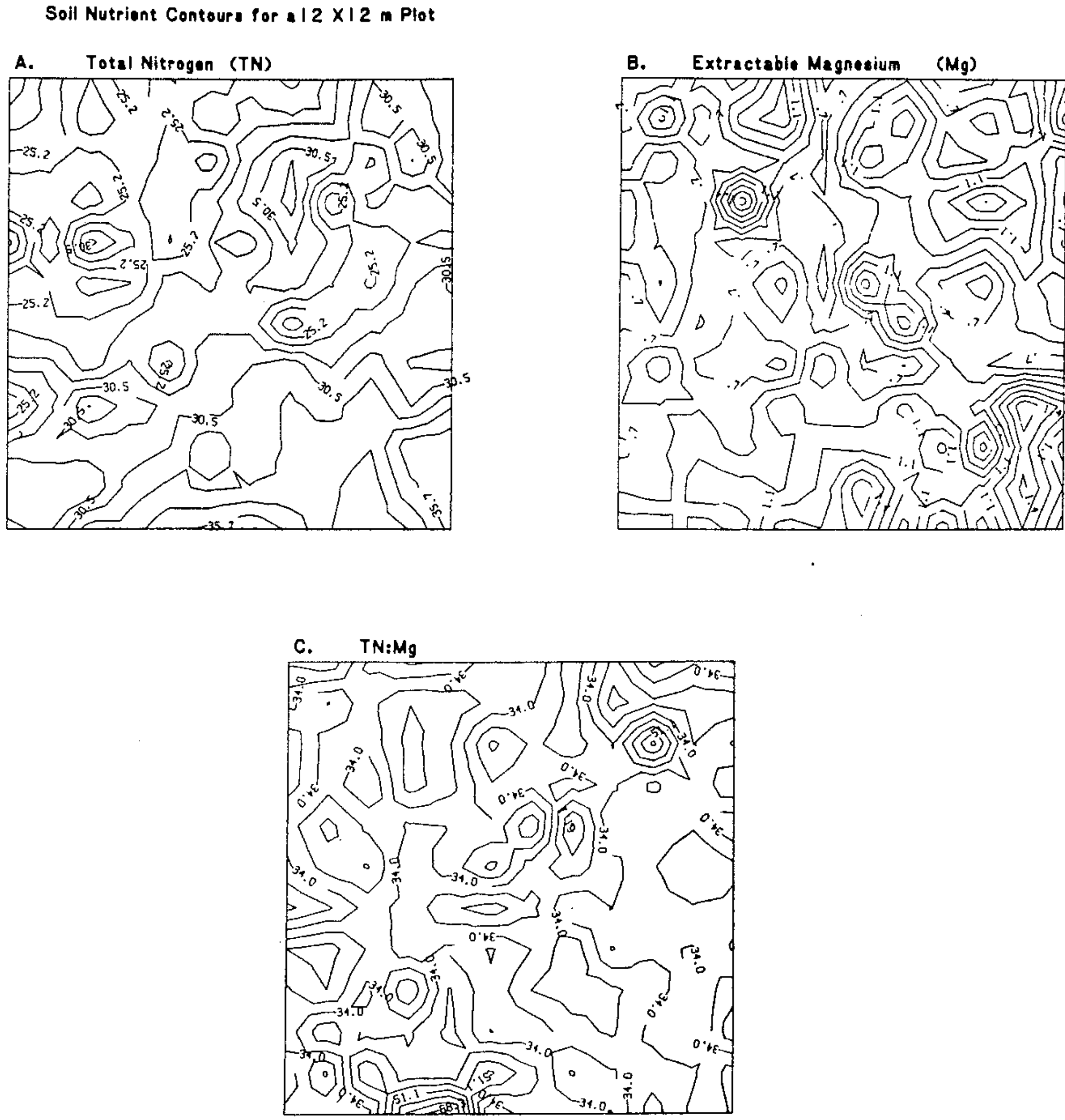


Figure 8. Soil spatial heterogeneity in the amounts of total nitrogen (TN) and extractable magnesium (Mg), for a 12 x 12 m plot at Cedar Creek Natural History Area. Contours are computer-fit to a grid of 144 evenly-spaced data points. May the 2 fold difference in the ratio of TN to Mg allow coexistence of more species than there are limiting resources as suggested by some theories?

dynamics in the 27 permanent plots in three successional areas at Cedar Creek will provide an invaluable data base. In addition, the more intensive microplot studies of N:P ratios, N:Mg ratios and microsite succession, combined with nutrient physiology and nutrient competition studies in the greenhouse, will provide insights into the possible mechanisms controlling species abundance.

Soil Processes and Nutrient Budgets

We are interested in the processes of soil development and modification during succession, and in the differences in these processes in response to differences in primary productivity. This aspect of our study will involve long-term monitoring of soil characteristics in our 27 permanent 0.5 hectare plots. Using lysimeters and standard techniques of soil analysis, such as discussed in Grigal and Grizzard (1975), McColl and Grigal (1977), and Grigal (1979), we will monitor litterfall and accumulation, nutrient loss from leaching and erosion, and nutrient additions from biological fixation and from wet and dry precipitation. (See the Long-Term Monitoring section of this proposal). In addition, we will periodically determine extractable and available levels of nutrients and particle-size distributions from various depths in the soil profile. Use of the Soil Science Department's Inductively-Coupled Plasma Spectrophotometer allows simultaneous, inexpensive and accurate measurement of all important nutrients except N, which will be determined with either Kehldehl or persulfate digestion techniques. Soil samples will be obtained twice from nine fixed localities within each of the 27 permanent plots during the first year of study, and annually afterwards. In addition, we will sample one locality in each of the 27 permanent sites once a year for depth profile determinations. After techniques are finalized and this sampling program is in operation, we will have an additional intensive sampling program to determine soil heterogeneity within the unmanipulated plots. In analyzing these data we will look for relationships between soil characteristics and local plant community structure. We will perform one such intensive sampling program per year, starting in the newly abandonded field, followed the next year by the 25 year old field, and then by the mature oak savannah. This intensive study of small-scale spatial heterogeneity will also allow us to determine the dependence of microsite community changes on past soil chemistry in these three successional stages.

Vegetation Studies.

A variety of plot sizes will be used to estimate the density of plants in the 27 permanent plots. Nine uniformly-spaced 1 m^2 subplots will be completely censused to species level twice each year in each of the 27 permanent plots. Each subplot will be photographed at the time it is censused. These samples should provide good estimates of the abundance (expressed as % cover and/or as stems/m^2) of mosses, lichens, grasses, and other herbaceous plants in the various plots. Each of these 1 m^2 subplots will be adjacent to the spot where the annual soil samples will be collected. Thus it will be possible to relate changes in soil chemistry with changes in plant community structure, and to explore broad patterns in soil and vegetation relationships within and between plots and treatments. Nested around each of the 1 m^2 subplots will be a 100 m^2 subplot. The densities of various larger perennial herbaceous and woody plants, including seedlings, will be determined in these areas twice each year, at the same time that the smaller plots are sampled. Finally, for all 27 permanent plots, all woody plants larger than 1 cm diameter at ground level will be individually marked and their survivorship followed year to year for the duration of this project. Although not all of the plants are easily identified to species level, we have a complete herbarium collection from Cedar Creek for lichens (with over 50,000 specimens) and for vascular plants including seedlings. Species lists have been prepared for various habitats and faculty with the necessary taxanomic skills are participating in this project.

Because variations in the timing and intensity of events such as bud break, flowering, fruit set and fruit fall are of importance to herbivores, pollinators and frugivores, the phenology of selected plants in the 12 permanent plots will be closely monitored. Many of the phenological studies will be qualitative, recording plants larger than 1 cm diameter at ground level will be individually marked and their survivorship followed year to year for the duration of this project. Although not all of the plants are easily identified to species level, we have a complete herbarium collection from Cedar Creek for lichens (with over 50,000 specimens) and for vascular plants including seedlings. Species lists have been prepared for various habitats and faculty with the necessary taxanomic skills are participating in this project.

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Primary Productivity and Plant Nutrient Analysis.

Rates of primary productivity will be estimated in the 27 permanent plots using the above ground biomass accural method. For the newly abandoned field and the 25 year old field, which lack woody plants, 4 different sets of 1 m^2 rectangles per 0.5 hectare plot will be cut to ground level at three different times of the year, each year. The plant material (after sorting to species) and litter will be dried and weighed. Soil samples will be collected from each clipped area. Similar quadrats will be used to estimate rates of productivity of the non-woody component of the oak savannah site. In addition, there will be annual measurements of selected woody plants, combined with regressions such as used by Whittaker and Woodwell (1968, 1969) to estimate total rates of primary productivity. The plant and soil samples from the clipped 1 m^2 subplots in each permanent 0.5 hectare plot will provide additional information for the vegetation and herbivore aspects of this study. Determinations of tissue protein, nitrogen, P, K, Mg, and fiber will be made on homogenized samples for the 6 to 8 major species in each study site. These analysis, performed by the Soil Chemistry Laboratory, will be useful in interpreting both soil-plant and plant-herbivore relationships.

Life History, Nutrient Physiology, and Competition.

Greenhouse experiments in progress are using sand culture methods to determine the nutrient requirements of selected old field plants. The studies to date have concentrated on the nitrogen and magnesium dependence of growth of Crepis tectorum (Compositae) and Rumex acetosella (Polygonaceae), both common species in the old field plots at Cedar Creek. Such information may prove useful in predicting the outcome of competition among species under various conditions of nutrient limitation (Tilman 1977, 1980, 1981 a,b). It may thus be useful in understanding the pattern of abundance of these species at Cedar Creek in relation to soil nutrient status and to predict the effect of fertilization on the relative abundance of these species. Moreover, the greenhouse studies done to data indicate that soil nutrient levels influence many aspects of the life history of these species, including the ratio of male to female flowers on a plant, seed size, percent germination, and growth form. We propose growing the 6 to 8 most abundant annual plants in the old fields under controlled greenhouse conditions to determine their nutrient requirements, the nutrient dependence of various aspects of their life histories, and the nutrient dependence of interspecific competition. For these same species, we will determine the dispersal abilities of seeds (Werner and Platt 1977) and germination characteristics (see Werner and Rioux 1977; Gross and Werner 1981) so that we may include in our analyses the interactions of competition for nutrients and competition for open (disturbed) sites. These experiments are designed to provide the life history information needed to interpret the microplot disturbance experiments.

This more detailed information on the biology of individual species will be of critical importance in evaluating various hypotheses concerning the role of small-scale disturbances and soil nutrient heterogeneity in determining the structure of plant communities and the successional sequence. In addition, the data will be useful in elucidating the mechanism whereby fertilization influences species composition and diversity.

In proposing these experiments we wish to stress that we consider nutrient and open site competition to be only a few of numerous processes that can influence the species composition and diversity of natural plant communities. Differences in the positions of the root systems of plants, the nutrient uptake mechanisms used by plants, the times of maximal growth during the season, and other processes are also of central importance in determining the structure of plant communities. We wish to start this aspect of our research with studies of the mechanisms influencing nutrient competition and open site competition because these are processes that may be easily incorporated into a mechanistic theory of community function. Knowledge of these processes will allow us to determine to what extent observed patterns can and cannot be explained by these processes. As such, it will help us focus our future research as our understanding of succession develops.

SECONDARY PRODUCERS

Introduction.

As food fluctuates between abundance and scarcity in good or bad years or in response to fertilization, the secondary producers can be expected to respond in their demography, behavior, or both. In addition, responses can also be influenced by the nutritional quality of the food resource (McNeil and Southwood 1978; White 1978; Mattson 1980). We propose to examine the effects of fluctuations in productivity and food quality upon selected species of insects and mammals, and to monitor browsing and grazing intensity for other species.

Arthropod Studies

The effects of plant associations upon arthropod populations are often difficult to predict from knowledge of host preferences of the arthropods, the autoecology of the plants, and similar, parochial information. Atsatt and O'Dowd (1976), in summarizing some of the effects of plant associations on (primarily) their herbivore populations, note that most plants deter herbivores with chemicals that are not instantly lethal, but are feeding deterrents, and that the effectiveness of these deterrents will be conditional on the presence of stimuli from other plants. Little work has focused on the effects of associations of endemic plant species on their associated arthropod populations. Most studies have examined imported plants and their pests, many of which are also imported, often without their co-adapted natural enemy fauna (Simmonds et al. 1976; Wilson and Huffaker 1976; Kroh and Beaver 1978).

In attempting to predict whether plant associations will be more or less susceptible to insect attack, arguments regarding the diversity and stability of communities are of little help (Goodman 1975; Southwood and Way 1970; Van Emden 1965; Van Emden and Williams 1974; Way 1966). Recognition of this problem has led in recent years to attempts to redefine the terms "diversity" (e.g. Pielou 1966, 1975; Peet 1974, 1975; Goodman 1975) and "stability," or to replace them with different terms (Hurlburt 1971; Holling 1973; Westman 1978). Definitions of diversity have focused on (a) the number of species in a community (species richness) and (b) the relative numbers of individuals in each species (species evenness). The most glaring omission from quantitative indices of diversity based on these parameters is any accomodation for the similarity among the species invovled. This aspect of diversity has only been briefly addressed (Pielou 1975: 17-18). Pielou defines an index of diversity which, for equivalent richness and evenness components, gives higher diversity to a group of unrelated plants than to a group of closely related plants.

Diversity among plant species might be an important component in affecting susceptibility to colonization and subsequent fluctuations of herbivore populations. For example, related plants frequently share a characteristic group of secondary compounds which prevent herbivory by most insects (Ehrlich and Raven 1964; Whittaker and Feeny 1971). Those insects which have overcome these defenses typically can feed on a number of members of the plant family, and even use those secondary compounds as cues for location of the plants (Beck 1974; Dethier 1970; Feeny 1976). A corollary concept is the notion of "resource concentration" (Root 1973, 1975), which suggests that as a host plant species becomes more concentrated, the herbivores that feed on that species are more likely to find it and remain there.

The effects of fertilization and of weather variation on our study plots are likely to result in changes in species richness and evenness in primary productivity, and in the nutritional quality of various plant species. With respect to understanding the response of insect herbivore populations to these changes, the critical questions are:

a) How are herbivore load, rates of colonization by herbivores and predator/prey ratios affected by such changes in diversity, productivity and food quality.

b) Under which conditions does the least and the most herbivory occur?

Arthropod populations on quadrats within the experimental and control plots will be estimated by observations (Smith et al. 1976; Mayse et al. 1978) and by various collection methods suitable for the habitats involved (including sweep netting, pit-fall traps, tangle-foot paper and vacuuming). Herbivory levels will be determined by collection of leaf materials and measuring amounts eaten with an optical leaf area meter as well as by observations of feeding rate and calculation from known insect densities. The sites on which we make our observations of insect herbivory will be adjacent to those which are clipped for productivity studies. The three-times-per-season clipping of quadrats for the productivity studies will provide information on the density and nutritional status of various plant species, as well as productivity rates. This information will be used in analyzing the herbivory studies. Information on nutritional status of these plants is especially important because of the reported relationships between plant nutrition and herbivore growth rates (Feeney 1970; White 1978; McNeil and Southwood 1978; Mattson 1980), as well as the effect of fertilization on rates of herbivory (e.g., Carrow and Betts 1973; Mattson 1980) as often observed in agriculture.

In addition, our analysis will explore the general effects of arthropod herbivores on plants in the different successional stages. The relationship between damage and yield (of both vegetative and reproductive portions of the plants), and between the numbers of arthropods and plant productivity will be assessed for the different successional stages.

Small mammals.

The most common mammals on the study plots are likely to be small rodents, 13-lined ground squirrels (Citellus tridecemlineatus) and pocket gophers (Geomys bursarius). Food items utilized by these species include vegetative material, seeds and insects. We will attempt to determine the role of these species in the transfer of energy, and the cycling of nutrients, in the three successional stages and to determine the effects of fertilizing on these processes.

The relationship between an herbivore and its food supply can be addressed from three points of view, as discussed by Krebs and Myers (1974):

1. Does the herbivore exhibit a clear pattern of preference for and avoidance of specific plants?
2. How does the foraging affect the habitat, with reference to plant growth and cover for the herbivore?
3. Is there evidence that food quality and/or quantity are limiting the herbivore population?

In addition, questions of optimal foraging strategy must be considered because of the patchy nature of the environment of the study plots (see Kamil and Sargent 1981 for general review of foraging behavior).

Numerous investigators have examined the relationship between food and changes in population density of small mammals (see Finerty 1980 for review of these theories). It may be that "food shortages" reported as limiting populations might actually be the lack of one or more essential nutrients (Pitelka 1964, Schultz 1964). Botkin et al. (1973) suggested that the quantity of sodium that could be obtained during grazing of aquatic plants in summer might be limiting to moose populations on Isle Royale in Lake Superior. Grant et al. (1977) and Abramsky and Tracy (1979) reported that certain species of small mammals increased in density on short grass prairie fertilized with nitrogen. They did not, however, consider the physiological basis for the observed increases.

It is important to realize that forage limitations are not always conspicuous (Grange 1965). For example, lemmings may sometimes feed copiously to compensate for some nutrient deficiency, and this may be a contributing but not determining factor in lemming cycles (Grant 1978).

The impacts of small mammals on primary production, succession, and other aspects of ecosystem structure and function are not well known, although Golley (1973), Golley et al. (1975) and Chew (1978) have addressed this in a general way. Such effects must be considered in terms of digging and soil structure, nutrient cycling, plant growth, species composition of vegetation, consumption and dispersion of seeds, and influence on decomposition of litter. Golley et al. (1975) predict that these impacts will be high in grassland, moderate in forest and low in agricultural ecosystems.

Stimulation of plants by grazing has been shown to be significant in the extreme environments of the Arctic. Marsden (1964) suggests that because vegetative decay is extremely slow in the Arctic the conversion of vegetation into lemming flesh and droppings is probably essential to plant growth. Grass production in a tundra site from which lemmings had been excluded declined while in similar areas where grazing by lemmings occured the production usually increased. Lemmings also can influence plant composition by reducing litter and by burrowing (Dennis and Johnson, 1970) and grazing can stimulate shoot production (Bliss et al, 1973).

Krebs and Myers (1974) have pointed out the synchrony between lemming density and nutrient levels. During years of peak lemming density, levels of phosophorus, nitrogen, calcium, potassium and sodium (but not magnesium) were found at their highest concentrations in the forage (Piper 1964, Aumann 1965). An important question here is whether the nutrient levels in the vegetation are the cause of or the result of changes in the lemming density. Observations by Krebs and Myers (1974), Mullen (1968) and Pitelka (1973) suggest that the correlation between plant nutrient peaks and lemming population peaks may be more an example of lemmings affecting the plants than of the plants determining the density of lemmings.

The role of toxic compounds in plants must also be considered in evaluating the relationship between grazing mammals and their forage species. Small amounts of plant toxins consumed by rodents may have adverse effects, including inhibition of protein synthesis, growth and reproduction (Freeland 1974). At present little information is available on what is toxic (Batzli and Pitelka, 1975). Evaluation of this matter is difficult because, as Schlesinger (1976) has pointed out, no statistically significant correlation has been found between food preferences and the frequency of food appearing in the stomach, the quantity of food appearing in the stomach, or an index comparing feeding behavior to the natural occurrence of plants in the field. In addition, there is no clear evidence that decreased relative availability of preferred foods results in increased consumption of toxic plants (Batzli and Pitelka 1975).

Although not necessarily related to the question of toxicity, secondary plant compounds might play a significant role in mammal population dynamics and in forage consumption by mammals. Berger et al. (1977) found that 2 naturally occurring cinnamic acids, and their related vinyl phenols, inhibited reproduction in Microtus montanus. These compounds increased in salt grass, the primary forage, near the end of the vegetative growing season, which coincided with the end of the breeding season. When a group from a non-breeding winter population was given fresh grass all the females became pregnant. Negus and Berger (1977) suggest that the voles may cue breeding from the secondary plant compounds thus timing reproductive effort to maximum food availability.

Methods: Relationships between small mammals and the permanent 0.5 hectare experimental plots in the three successional areas will be evaluated by live trapping, marking and releasing animals in the experimental plots and adjoining areas, and by intensive monitoring of the movements and activity of selected individuals for short periods of time by telemetry. Emphasis will be on determining the response of mammalian grazers to the fertilization experiments and on determining the effects of the grazing on primary productivity. Mammals will be trapped for 5 consecutive nights at approximately 8-week intervals beginning in early spring and ending in late fall. Longworth live traps and pitfall traps will be utilized in a 7m x 7m grid pattern because different segments of small mammal populations are caught by these different techniques (Boonstra and Krebs 1978, Beacham and Krebs 1980). Pocket gophers will be captured with live traps set in active burrow systems (Baker and Williams 1972). Demographic parameters will be determined using methods similar to those described by Smolen et al. (1980). Preliminary estimates of population densities for the various treatments in the large permanent plots will be developed using direct enumeration (Hilborn et al. 1976), the Jolly Stochastic Model (Jolly 1965) or the Zippin Regression Model (Zippin 1956).

Sex, age (adult, subadult or juvenile), reproductive status and weight of each live trapped animal will be determined by external examination. Information on diets will be periodically obtained from microscopic examination of stomach contents of animals captured from nearby areas using the method developed by Hansen and Ueckert (1970). Fecal material will be collected from each captured individual if available in the trap and will be analyzed by the method of Flinders and Hansen (1972).

Of all the small mammal herbivores in the Cedar Creek study sites, the pocket gopher, Geomys bursarius, is probably the most important because of its commonness, its rate of herbivory, and the numerous small-scale disturbances that it creates. Our monitoring of disturbance processes in the 27 permanent 0.5 hectare plots will provide an index of its feeding activities in relation to variations in productivity. Although we will initially exclude pocket gophers from our microplot studies of N:P and M:Mg fertilization, we will introduce radio-tagged pocket gophers into these plots in the third year so that we may monitor the gopher's use of a patchily-distributed food source. Such monitoring will make use of an antenna grid interfaced with an automatic scanning receiver and microprocessor (Kuechle et al 1979). By periodically following the foraging of gophers through a full season in a field in which the species composition and plant nutritional status of 36 adjacent 5 x 5 m treatments is known, we will be able to monitor the seasonal progression of preferred food types, and infer much about the effects of gopher herbivory on plant species composition and succession in our three successional areas. In the next year, we will extend such studies to other small mammal herbivores such as Citellus, Peromyscus and Microtus, again obtaining a full season of data on habitat use patterns in relation to species composition and plant nutritional status.

If our census and movement data indicate that the small mammals present on each large-scale (0.5 hectare) experimental plot constitute a distinct population we may be able to model energy transfer. Grant et al. (1977) and French et al. (1976) attempted to measure energy flow from grassland vegetation to small mammals using data obtained at International Biological Program sites. We will be collecting somewhat similar data at Cedar Creek and will utilize their modeling approach when possible.

Foraging by larger herbivorous mammals

In all of our permanent plots, we will obtain estimates of larger herbivore (deer, rabbits, hare) activities by periodic surveys of browsing. The anticipated low frequency of herbivory in the study sites by such larger herbivores would make more detailed studies too expensive for the probable return. However, in the mature oak savannah, gray squirrels (Sciurus carolinensis) are an important herbivore whose foraging patterns are currently being studied at Cedar Creek by Dr. Regal. We propose to continue a portion of these studies to observe the long-term interactions between these herbivores and the oaks in our oak-savannah site.

The radio telemetry system at Cedar Creek (Cochran et al. 1965; see also Appendix A) provides a unique opportunity to continuously monitor the behavior of selected species and to study behavioral reorganization resulting from fluctuations in plant productivity. A central concern of the research in progress is movement patterns in relation to optimal foraging (Regal 1978, Connolly 1979). We are especially interested in extending this through less intense, but long term studies on individuals to determine how they behave during years of food scarcity. Current work reveals that individuals often pass by patches of good food, apparently because of constraints of social organization. Will their behavior more closely correspond to simple optimal foraging models in years of scarce food than it does in years with mast seed crops?

Additionally, mast seed crops are characteristic of the oaks in our area. Are such crops a strategy for saturating predators in some years and "starving" them in others as Janzen (1976) has argued for bamboos and other plants? We may be able to gain insight into this question since we will be monitoring the production, consumption and destruction rates of acorns, as well as the population response of squirrels. The ca. three year mast crop cycle makes this question attractive in a ten year study.

Foraging by birds.

We will monitor bird foraging in our permanent plots by periodic song and visual censuses. These censuses will be a minor additional effort for our sampling program, but will allow us to record patterns of bird habitat use with respect to succession and in response to changes in primary productivity. Such information may later be integrated with studies of seed dispersal, seed predation, and insect predation in these areas.

TERTIARY PRODUCTION

We are well aware that the studies proposed do not directly involve tertiary levels of production. While some research on raptors and mammalian predators has been done at Cedar Creek using telemetry (see Appendix A) we feel such studies are beyond the scope of the proposed research at the present time. Capture and monitoring of wary and highly mobile predators is prohibitively costly in terms of manpower and the potential for integrating data on raptors into our analyses based on 0.5 ha. plots is remote. However, our periodic arthropod sampling will allow us to determine the relative abundances of various predatory and parasitic insects in our sites, and we will obtain data on small mammal predation on insects.

SUMMARY OF PROPOSED RESEARCH

We believe that major advances in ecological understanding can only come when micro views of population processes are combined with macro views of whole system processes. The detailed research that we propose combines information on the direct effects of species on each other with information on long-term, indirect and feedback effects in natural and manipulated communities. We believe that the study of succession provides the ideal framework for a synthesis of population, community and ecosystem perspectives into a mechanistically-based, potentially predictive theory of the structure and function of natural ecosystems. We are intrigued by succession because the process of community change reflects the long-term outcome of numerous direct, indirect and feedback effects, and can be understood only by a synthesis of numerous approaches. Our long-term research in sites from three different periods in the natural secondary successional sequence at Cedar Creek will provide the experimental and observational data needed to test numerous hypotheses concerning succession and ecosystem structure. Moreover, by performing these studies within the framework of a network of LTER sites, we will be able to address a series of broad, synthetic questions on a geographic scale which was previously impossible.

VI. LONG-TERM MONITORING

We have already described the types of information that will be collected in our long-term research projects in the permanent study sites at Cedar Creek. Much of this information is identical to that which is suggested in "Long-Term Ecological Research - Concept Statement and Measurement Needs," the T.I.E. report to the National Science Foundation. We propose to expand the monitoring of physical and biotic parameters which has been occurring at Cedar Creek since the 1940's to include the additional information suggested in the T.I.E. report. We agree with the statement in the T.I.E. report that such environmental data must be collected in a nationally consistent manner, and we are eager to participate in workshops that would establish the standard set of methods to be used. Our budget includes funds for the collection of the information already discussed and that listed below. In addition, we could easily monitor other processes or parameters if they are being monitored at other Long-Term Ecological Reserves.

A. Macroclimate Data

A weather station was established at Cedar Creek in 1955 using funds provided in part by the National Science Foundation. The following parameters have been monitored regularly since that time:

Air temperature in open field and forest (hourly)

Soil temperature at 50 cm in open field and forest (hourly)

Wind velocity (continuous)

Wind direction (continuous)

Precipitation (daily)

Snow depth (daily)

Solar radiation (continuous)

Data have been recored on strip charts using Esterline-Angus and Honeywell logging equipment, with subsequent transfer by hand to standard U.S. Department of Commerce Weather Bureau forms. These forms consitute the permanent weather records for Cedar Creek Natural History Area.

Installation of the Nova 2/10 computer at the laboratory provides the potential for updating this weather recording system, and for the collection of more complete and valuable weather data for ongoing and new research projects. It is proposed that the weather recording system be updated and modified so that all data would be recorded by the compouter on magnetic tape. This would eliminate many hours of tedious data transfer required by the present system and would provide more complete and readily available weather records.

Some of the transducers currently in use can be modified to provide data suitable for computer recording. Some of the transducers will need to be replaced. A program must be written for the Nova 2/10 to provide for data recording at Cedar Creek. Tabulation and printing of the weather records will be done with the University of Minnesota Control Data Cyber 74 computer system on the Twin Cities campus. Programs must be prepared for this purpose.

B. Atmospheric Chemical Measurements:

We will join the National Atmospheric Deposition Program and use their standardized techniques for collecting information on both wet and dry chemical inputs to Cedar Creek Natural History Area. Estimates of atmospheric nutrient inputs would be combined with measurements of rates of nutrient fixation, mineralization and loss in the soils to provide a more complete evaluation of nutrient supply and cycling. We would monitor atmospheric CO_2, which could be compared with earlier work on CO_2 at Cedar Creek (Reiners 1968). Continuous monitoring of CO_2, SO_2, NO_x and ozone would be easily integrated with the continuous monitoring and storage on magnetic tape of meteorolgoical data.

C. Geological Mapping

Small scale topographic maps have been prepared, and there have been several aerial surveys of Cedar Creek. Archive quality black and white photographic prints have been prepared from the early aerial surveys of Cedar Creek, but a more recent survey, taken with color film, should be preserved with archivel quality color prints, such as those prepared with the Cibachrome process. Aerial survey work should be repeated approximately every 5 years at the same time in the growing season, and the resulting color prints and slides should be of archivel quality.

D. Soil Mapping

A detailed mapping of the soils of Cedar Creek was completed in 1974 (Grigal, et al., 1974). The report included a discussion of the physiography and glacial history of the Anoka Sand Plain upon which Cedar Creek is located, a description and mapping of the area's major soil series, and a detailed analytical description of nine major soil pedons sampled at Cedar Creek. For each site, Ca, Mg, K, Na, cation exchange capacity, base saturation percent, total C, total N, extractable P, pH, mineral content and particle size distribution were determined for at least two depths each in the A, B, and C horizons. The general vegetational cover associated with each soil type was also recorded. Our soil nutrient sampling schedule will be much more complete than suggested in the T.I.E. guidelines. Because of the direct causal relationship between soil moisture and soil nutrient availability, we will also monitor soil moisture and soil water movement patterns in our permanent plots.

E. Vegetation Inventory

The postglacial vegetation history of Cedar Creek was elucidated by Cushing (1963) who examined pollen in the sediments of Cedar Bog Lake. Pierce (1954) determined, through interview and land survey records, the pre-settlement vegetation of Cedar Creek. Each year since Cedar Creek was formed in 1942, the resident manager of Cedar Creek has updated land use maps. By combining aereal survey photos with field work, a detailed mapping of the vegetational communities has been completed for 560 hectares of the 2185 hectares included in the Cedar Creek Natural History Area. We propose that the entire area be mapped in similar detail to provide a base for present and future studies. The variety of habitats and the different patterns of land-use on the tracts within the Cedar Creek Natural History Area have created a complex mosaic of vegetation. This pattern must be recorded as soon as possible to provide a base against which future changes can be measured. The Resident Biologist will be responsible for completing the field work and cartography using the available base maps and vegetation classification system.

F. Phenology

In coordination with those working on the vegetation of the permanent plots, the Resident Biologist will initiate a system of monitoring phenological patterns on an annual basis. The system will be based primarily on characters utilized in other studies in Minnesota (Hodson, 1951; Kotar, 1967; Hansen, personal communication).

Timing and intensity of events such as bud swelling, bud bursting, flowering, pollination, leafing out, seed ripening, seed fall, foliage change and leaf fall will be monitored for selected species. To provide continuity in phenological monitoring, individual perennial plants will be marked and changes in their development will be recorded throughout the study.

G. Plant Collection:

The plant collection for Cedar Creek is in good condition and the monograph by J. W. Moore titled, "A catalog of the flora of Cedar Creek Natural History Area, Anoka and Isanti Countries, Minnesota," published in 1973 provides a sound base for vegetation studies. However, few collections have been made in recent years and a number of species not represented in the collection have been discovered. The Resident Biologist will be responsible for updating and maintaining the plant collection and for assisting investigators working with the flora of the area.

H. Faunal Inventory:

Reference collections of the birds and mammals of Cedar Creek are available at the Bell Museum of Natural History and checklists have been prepared. Numerous studies of birds and mammals of Cedar Creek have already provided estimates of the densities of various species. The detailed studies of invertebrate and vertebrate herbivores, predators, and parasites at the 27 permanent plots will provide a much more complete inventory of the fauna of Cedar Creek.

I. Effects of Disturbance:

One of the major natural disturbances at Cedar Creek has been fire. For the last 17 years, different areas at Cedar Creek have been subjected to various patterns of controlled spring burning. Some tracts have been burned annually and others have been burned on a 2, 5 or 7 year cycle. Moreover, a natural fire swept Cedar Creek in 1956, and the extent of the burn and some of its ecological effects have been documented. In conjunction with our work in the annually-burned oak savannah, we will periodically survey the vegetation of adjacent areas experiencing a different burn cycle. Effects of periodic droughts can be documented by our permanent plot studies. Other types of disturbance occur on a smaller spatial scale. Events such as gopher and badger digging, insect outbreaks, tree falls, etc., will be recorded as they occur in our permanent plots.

J. Long-Term Data Collection and Access:

It is our plan to collect all of the data from these studies in a manner that will maximize the chance that it will be used by all interested investigators, both at the time of collection and in the future. We wish to avoid the loss of raw data that often accompanies publication, and will insist that all doing research at Cedar Creek provide clearly labeled tables of all raw data. Each year such raw data will be analyzed by each investigator, tabulated, and published as an Annual Report in the Field Biology Program's Occasional Papers. Thus, not only will the data be analyzed in papers published by the investigators at Cedar Creek, but all the data will be available for others to use in future re-analysis of the research being done at Cedar Creek. It will be the duty of the Resident Biologist to coordinate the tabulation, documentation and dispersal of the Cedar Creek data set. Much of the data will be initially entered into a portable Texas Instruments data terminal with 40K of bubble memory that is currently available for Cedar Creek researchers. From the T.I. data terminal, the data will be easily transferred for permanent storage on tape. We currently have all the computer facilities we need for such data storage and retrieval at Cedar Creek, and we have a professional staff who are well trained in working with large data sets. The ease of operation of the bubble memory data terminal, its ability to be telephone interfaced both with the Cedar Creek compouter and the main University of Minnesota computers means that investigators will have easy access to data and to programs for data analyses. We wish to stress that such data systems cannot substitute for long-term storage of data in widely circulated annual reports or for its timely analysis and formal publication. The publication records of the investigators on this project indicate that these data will not be collected in vain!

VII. INITIAL RESEARCH SCHEDULE BASED ON 1 JANUARY 1982 STARTING DATE

October, 1981. (Earlier depending on date of notification of approval).

Hold organizational meeting of research personnel as soon as funding is certain. Have background discussions and discuss new developments. Finalize a detailed plan for coordinating research during the first field season. Draft this plan as a short report, to be sent to the External Advisory Committee. Begin field surveys to choose the exact areas to be used for the experimental plots. Initiate procedures (advertising, interviews, etc.) for hiring research personnel, especially resident biologist.

January, 1982. Funding begins. Hire resident biologist and computer programmer. As soon as resident biologist is hired, hold a meeting of all research personnel with the External Advisory Committee to discuss and extend the research plans. Start attending meetings of the LTER Coordinating Committee. Order necessary equipment. Establish formats for data collection and storage. Clearly define duties of various research personnel. Establish procedures to assure that all necessary data are collected in a timely manner using standard techniques.

February, 1982. Review status of insect, small mammal, and plant collections at Cedar Creek. Familarize new personnel with collections. Establish priorities for enlarging collections and for verification via the Herbarium in the Botany Department, the Insect Collection in the Department of Entomology, Fisheries, and Wildlife, and the Mammal collection in the Bell

Museum. Work on weather monitoring equipment, including computer interface. Mark trees and saplings in all sites for long-term monitoring.

<u>March-April, 1982</u>. Hire technician (junior scientist). Install permanent aluminum stakes in all of the plots and subplots in the three study areas. Fence areas. Install sheet metal barriers around microplots to exclude gophers and small mammals, and trap microplot areas to remove resident animals.

<u>May-September, 1982</u>. Begin intensive field studies on plots. Make vegetation measurements, phenological studies, continue building plant and insect reference collections. Perform soil chemistries, population monitoring, etc. In May, bring in three outside scientists (other than those on Review Panel) to present seminars and visit Cedar Creek sites. In September, do first fertilizations.

<u>October-March, 1983</u>. Continue winter studies. Review procedures for data collection, compilation. Analyze first year's data. Build portable telemetry system. Prepare first Annual Report. Hold Annual Meeting (March) and finalize Annual Report. In Annual Meeting, finalize detailed research plans for the 1983 field season, the first season with manipulations.

<u>April-September, 1983</u>. Perform manipulations of both large scale and microplots. Continue monitoring of plots, etc.

<u>October-March, 1984</u>. Continue winter studies. Compile and analyze data. Prepare first draft of the second Annual Report, hold annual meeting, and finalize the second Annual Report. Prepare detailed research plan for the coming field season.

VIII. ADMINISTRATION

We believe that sound administration at Cedar Creek and close coordination with other LTER projects will be the keys to success of the proposed investigations. Administration and coordination duties will be shared by Drs. Tilman and Tester. During the first two years, each will take a sabbatical leave from the University so that full time can be devoted to the project. From January 1, 1981 through September 14, 1982 Dr. Tester will be free of all teaching and committee assignments and will be the project director, with an office at Cedar Creek. Dr. Tilman will be on sabbatical leave from September 15, 1982 until September 14, 1983 and will serve as full-time project director during this period. We will both participate in broad administrative decisions and planning at all times, but feel the sabbatical arrangements described above will provide the well defined and effective leadership necessary for successful initiation of an LTER program at Cedar Creek. Beginning in Year 3, administration, which should be somewhat simpler, will be handled jointly by Tilman and Tester. Immediate supervision of field and laboratory work will be carried out by the Resident Biologist, who will have had two years of experience on the project.

In addition to the administrative schedule outlined above, the teaching schedules of several of the investigators are such that they will be able to devote almost full-time efforts to research during the crucial periods of initiation of this project. Dr. Tilman's teaching schedule for January to June, 1982, includes only one course, a small-enrollment field course that will be taught one day a week at Cedar Creek. In addition, Dr. P. Werner will be on sabbatical leave during the 1981-1982 academic year, and will spend the late spring and summer of this period at Cedar Creek. The average teaching load of faculty at Minnesota is two formal courses per year plus seminars. This means that faculty have one academic quarter plus the summer months to pursue research full-time. Tilman and Tester will use this time for Cedar Creek work.

The proposed research requires coordination and integration at several different levels. First, data being collected at Cedar Creek must be consistent with data collected at other LTER sites. Second, data collected by the various researchers at Cedar Creek must be obtained in a manner that maximizes their utility to all workers. Third, activities of the researchers at Cedar Creek must be coordinated to eliminate possible conflicts in site usage and in usage of shared personnel and equipment.

To coordinate our research activities with those at other LTER sites, we have allocated funds for visits to other LTER sites and to attend intersite coordination meetings.

Throughout the project the PI's will work together in short and long range coordination of research, administration of personnel, and allocation of funds. Day to day operations will be directed by one person as described above.

Conflicts over site usage, allocation of funds for various aspects of the research project, etc., will be resolved through monthly meetings of all research personnel, including all investigators, graduate student research assistants and technicians. These meetings will not only resolve conflicts, but will allow for monthly discussions of research progress, syntheses of research activities, and planning of extensions and modifications of research projects.

IX. EXTERNAL REVIEW COMMITTEE

Four scientists with expertise in our areas of interest, and who have demonstrated a broadly synthetic approach to ecology, will serve as an External Advisory Committee. Because the numerous meetings with personnel from other LTER sites will provide us with input from these scientists, we will chose for our committee scientists who are not directly involved in any of the funded L.T.E.R. projects. To date, we have contacted the following scientists, who have indicated a willingness to serve on our committee: Dr. Bassett Maguire, Department of Zoology, University of Texas; Dr. James MacMahon, Department of Biology, Utah State University, Dr. William Reiners, Department of Biology, Dartmouth, and Dr. Lee Eberhardt, Ecosystems Department, Pacific Northwest Laboratory.

X. ANNUAL WORKSHOP

In March of each year we will hold a two or three day workshop to discuss, synthesize, and integrate research, and to finalize the next field season's activities. The workshop will be attended by the faculty, graduate student research assistants, and other personnel working on the project. In addition, we will invite all scientists conducting research at Cedar Creek, other interested researchers, including those of other LTER sites, the External Advisory Committee and NSF personnel.

The workshop will consist of research reports and discussion followed by discussion and planning of future research activities. Project personnel will then write up the ideas and plans generated. With about 30 people in attendance, there will be ample time for discussing interrelationships among various workers' results, planning of future research activities to answer questions raised by the past year's activities, and coordination of research with that being conducted at other LTER sites. At least 3 weeks before the workshop, the first draft of the Annual Report will be distributed to all participants and to all other LTER sites. The Annual Report will contain a summary of each presentation to be given at the workshop and a compilation, properly annotated, of the data collected during the last year. It will also contain a copy of all manuscripts prepared during the last year which resulted from the work at Cedar Creek.

A member of the staff will record the discussions during the meetings. Subgroups will be formed to pursue syntheses that arise from the discussions. These subgroups, which may include scientists from other LTER sites, members of the External Advisory Committee and other interested researchers, will prepare reports summarizing their ideas. These reports will be included in the final form of the Annual Report.

Through the mechanism of both large and small group discussions in an annual workshop, we will prepare an Annual Report that summarizes the research being done at Cedar Creek, provides the data collected during the last year, and summarizes the syntheses and extensions of the data and recommendations of the next year's research activities. After professional editing, the Annual Report will be published as an occasional paper of the Field Biology Program, and distributed to other LTER sites, other interested scientists and numerous libraries. For inclusion in the Annual Report, all data must first be compiled and entered into a computer data bank, to be run by the Senior Computer Programmer, as stated in the proposal.

By inviting personnel from outside the University of Minnesota to annual meetings, we will provide a mechanism which will allow others to be aware of and use the data already collected and which should allow others to develop interests in pursuing research at Cedar Creek. Interest will also be generated by our publications, by papers that we will present at scientific meetings, and from seminars given at other institutions.

XI. SEMINAR PROGRAM

In May of each year, we will invite three outside scientists to give seminars at Minnesota and to visit Cedar Creek. The scientists will be chosen for the relevance of their work to that being done at Cedar Creek. Additionally, the Department of Ecology and Behavioral Biology brings in about 15 to 20 outside speakers annually who will also have the opportunity to learn of Cedar Creek.

BIBLIOGRAPHY

Abramsky, Z., and C.R. Tracy. 1979. Population biology of a "noncycling" population of prairie voles and a hypothesis on the role of migration in regulating microtine cycles. Ecol. 60:349-361.

Abrosov, N.S. 1975. Theoretical investigation of the mechanism of regulation of the species structure of a community of autotrophic organisms. Ekologiya 6:5-14. (Translated in Soviet Journal of Ecology, 1975, pp. 491-497.)

Al-Mufti, M., C. Sudes, S. Furness, J. Grime, and S. Band. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. J. Ecol. 65:759-792.

Amundson, D., and H.E. Wright, Jr. 1979. Forest changes in Minnesota at the end of the pleistocene. Ecol. Monogr. 49:1-16.

Ashton, P. 1977. A contribution of rainforest research to evolutionary theory. Ann. Missouri Bot. Gar. 64:694-705.

Atsatt, P.R., and D.J. O'Dowd. 1976. Plant defense guilds. Science 193:24-29.

Aumann, G.D. 1965. Microtus abundance and soil sodium levels. J. Mammal. 46:594-604.

Bakelaar, R., and E. Odum. 1978. Community and population level responses to fertilization in an old-field ecosystem. Ecol. 59:660-671.

Baker, R.J. and S.L. Williams. 1972. A live trap for pocket gophers. J. Wildl. Management 36:1320-1322.

Batzli, G.O. and F.A. Pitelka. 1975. Vole cycles: test of another hypothesis. Am. Nat. 109:482-87.

Beachman, T.D. and C.J. Krebs. 1980. Pitfall versus live-trap enumeration of fluctuating populations of Microtus townsendii. J. Mamm. 61(3):486-499.

Beadle, N. 1966. Soil phosphate and its role in molding segments of the Australian flora and vegetation, with special reference to xeromorphy and sclerophylly. Ecol. 47:992-1007.

Beck, S.D. 1974. Theoretical aspects of host plant specificity in insects. Proc. Summer Inst. on Biological Control of Plant Insects and Diseases. U. Miss. Press, Jackson. Pp. 290-311.

Bell, D., and F. Johnson. 1975. Phenological patterns in the trees of the streamside forest. Bull. Torrey Bot. Club 102:187-193.

Berger, P.J., E.A. Sanders, P.D. Gardner, and N.C. Negus. 1977. Phenolic plant compounds functioning as reproductive inhibitors in Microtus montanus. Science 195:575-77.

Blasco, D. 1971. Composition y distribucion del fitoplancton en la region del afloramiento de las costas peruanas. Invest. Pesq. 35:61-112.

Bliss, L.C., G.M. Courtin, D.L. Pattie, R.R. Rieve, D.W.A. Whitfield, and P. Widden. 1973. Arctic tundra ecosystems. Annu. Rev. Ecol. Syst. 4:359-99.

Boonstra, R. and C.J. Krebs. 1978. Pitfall trapping of Microtus townsendii. J. Mamm. 59(1):136-148.

Botkin, D.B., P.A. Jordan, A.S. Dominski, H.S. Lowendorf, and G.E. Hutchinson. 1973. Sodium dynamics in a northern ecosystem (moose, wolves, plants). Proc. Natl. Acad. Sci. U.S.A. 70:2745-48.

Brenchley, W., and K. Warington. 1958. The Park Grass Plots at Rothamsted. Rothamsted Expt. Stn. Harpenden, U.K.

Carrow, J.R. and R.E. Betts. 1973. Effects of different foliar-applied nitrogen fertilizers on balsam wooly aphid. Can. J. For. Res. 3:122-139.

Chew, R.M. 1978. The impact of small mammals on ecosystem structure and function. In D.P. Snyder (ed.) Population of small mammals under natural conditions. Pymatuning Lab. Ecology, Univ. Pittsburgh, 5:167-180.

Clements, F.E. 1916. Plant Succession. Carnigie Inst. Wash. Pub. 242.

Cochran, W.A., D.W. Warner, J.R. Tester, and V.B. Kuechle. 1965. Automatic radio-tracking system for monitoring animal movements. BioSci. 15:98-100.

Colinvaux, P.A. 1973. Introduction to Ecology. Wiley, N.Y. 621 pp.

Connell, J. 1978. Diversity in tropical rainforests and coral reefs. Science 199:1302-1310.

Connell, J.H. and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Amer. Natur. 111:1110-1144.

Connolly, M.S. 1979. Time-tables in home range usage by gray squirrels (Sciurus carolinensis). J. Mamm. 60:814-817.

Cooper, W.S. 1913. The climax forest of Isle Royale, Lake Superior, and its development. Bot. Gaz. 55:1-44; 115-140; 189-235.

Cowles, H.C. 1899. The ecological relations of the vegetation on sand dunes of Lake Michigan. Bot. Gaz. 27:97-117; 167-202; 281-308; 361-391.

Crocker, R. and J. Major. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. J. Ecol. 43:427-448.

Cushing, E.J. 1963. Late Wisconsin pollen stratigraphy of east-central Minnesota. Ph.D. Thesis. University of Minnesota, Minneapolis.

Davis, M. 1976. Pleistocene biogeography of temperate deciduous forests. Geosci. and Man 13:13-26.

Dennis, J., and P.L. Johnson. 1970. Shoot and rhizome-root standing crops of tundra vegetation at Barrow, Alaska. Arct. Alp. Res. 2:253-66.

Dethier, V.G. 1970. Chemical interactions between plants and insects. In: E. Sandheimer and T.B. Simeone, eds. Chemical Ecology. Academic Press, NY. P. 83-102.

Drury, W.H. and I.T. Nisbet. 1973. Succession. J. Arnold Arboretum 54:331-368.

Egler, F.E. 1954. Vegetation science concepts. 1. Initial floristic composition - a factor in old field development. Vegetatio 4:412-417.

Ehrlich, P.R., and P.H. Raven. 1964. Butterflies and plants: a study in co-evolution. Evol. 18:586-608.

Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51:565-581.

Feeny, P. 1976. Plant apparency and chemical defense. In: J.W. Wallace and R.L. Mansell, eds. Biochemical Interaction Between Plants and Insects. Plenum, New York. Pp. 1-40.

Finerty, J.P. 1980. The population ecology of cycles in small mammals. Yale Univ. Press. 234 pp.

Fischer, A. 1960. Latitudinal variation in organic diversity. Evol. 14:54-81.

Flinders, J.T. and R.M. Hansen. 1972. Diets and habitats of jackrabbits in northeastern Colorado. Range Sci. Dept., Sci. Series No. 12. Colo. State Univ., Ft. Collins, Colo.

Freeland, W.J. 1974. Vole cycles: another hypothesis. Am. Nat. 108:238-45.

French, N.R., W.E. Grant, W. Grodzinski and D.M. Swift. 1976. Small mammal energetics in grassland ecosystems. Ecol. Mono. 46:201-220.

Gleason, H.A. 1927. The individualistic concept of the plant association. Bull. Torrey Bot. Club 53:7-26.

Gleason, H.A. 1917. The structure and development of the plant association. Bull. Torrey Bot. Club 43:463-481.

Golley, F.B. 1973. Impact of small mammals on primary production. In J.A. Gessaman (ed.). Ecological energetics of homeotherms. Utah State Univ. Press, Mono. Series 20:142-147.

Golley, F.B., L. Ryszkowski, and J.T. Sokur. 1975. The role of small mammals in temperate forests, grasslands and cultivated fields. Pp. 223-241, in Small mammals: their productivity and population dynamics (F.B. Golley, K. Petrusewicz, and L. Ryszkowski, eds.). Internatl. Biol. Programme. Cambridge Univ. Press, 5:1-451.

Goodman, D. 1975. The theory of diversity-stability relationships in ecology. Quart. Rev. Biol. 50:237-266.

Grange, W.B. 1965. Fire and tree growth relationships to snowshoe rabbits. Proc. Annu. Tall Timbers Fire Ecol. Conf. 4:110-25.

Grant, P.R. 1978. Dispersal in relation to carrying capacity. Proc. Natl. Acad. Sci. U.S.A. 75:2854-58.

Grant, W.E., H.R. French, and D.M. Swift. 1977. Response of a small mammal community to water and nitrogen treatments in a shortgrass prairie ecosystem. J. Mamm. 58:637-652.

Grigal, D.F. 1979. Extractable soil nutrients and permafrost under adjacent forest types in interior Alaska. Northwest Sci., 53:43-50.

Grigal, D.F. and T. Grizzard. 1975. Analysis of litterfal in a deciduous forest on Walker Branch Watershed, Tennessee: Data stratification by two alternative methods. Amer. Midl. Nat., 94:361-369.

Grigal, D.F., L.M. Chamberlain, H.R. Finney, D.V. Wroblewski, and E.R. Gross. 1974. Soil of the Cedar Creek Natural History Area. Univ. Minn. Agric. Expt. Stn. Rept. 123, 47 p.

Grime, J. 1973. Control of species diversity in herbaceous vegetation. J. Environ. Mgmt. 1:151-167.

Gross, K.L., and P.A. Werner. 1981. Colonization by four biennial plant species in patchy environments: implications for local species abundances. Ecology, in press.

Grubb, P. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52:107-145.

Hansen, R.M. and D.N. Veckert. 1970. Dietary similarity of some primary consumers. Ecology 51:640-648.

Harper, J.L. 1969. The role of predation in vegetational diversity. In "Diversity and Stability in Ecological Systems," Brookhaven Symposium in Biology 22:48-62.

Hilborn, R., J.A. Redfield and C.J. Krebs. 1976. On the reliability of enumeration for mark and recapture census of voles. Canadian J. Zool. 54:1019-1024.

Hodson, A.C. 1951. How go the seasons? Minn. Farm and Home Sci. 3:15.

Holdridge, L., W. Grenke, W. Hathaway, T. Liang, and J. Tosi, Jr. 1971. Forest Environments in Tropical Life Zones: A Pilot Study. Pergamon Press, Oxford.

Holling, C.S. 1973. Resilience and stability of ecological systems. BioSci. 28:705-710.

Holt, R.D. 1977. Predation, apparent competition, and the structure of prey communities. Theorectical Population Biology 12:197-229.

Horn, H.S. 1974. The ecology of secondary succession. Annu. Rev. Ecol. Syst. 5:25-37.

Hubbell, S.P. 1979. Tree dispersion, abundance and diversity in a tropical dry forest. Science 203:1299-1309.

Hurlburt, S.A. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecol. 52:577-586.

Huston, M. 1979. A general hypothesis of species diversity. Amer. Nat. 113:81-101.

Janzen, D. 1976. Why bamboos wait so long to flower. Ann. Rev. Ecol. Syst. 7:347-371.

Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration - stochastic model. Biometricka 52:225-247.

Kirchner, T. 1977. The effects of resource enrichment on the diversity of plants and arthropods in a short grass prairie. Ecol. 58:1334-1344.

Kotar, J. 1967. Phenological study of 35 tree and shrub species of Itasca State Park and some geographic comparisons. M.S. Rept., Dept. Forestry, Univ. Minn. 55 p.

Krebs, C.J., and J.H. Myers. 1974. Population cycles in small mammals. Adv. Ecol. Res. 8:267-399.

Kroh, G.C., and D.L. Beaver. 1978. Insect response to mixture and monoculture patches of Michigan old-field annual herbs. Oecol. 31:269-275.

Kuechle, V.B., R.A. Reichle, K.E. Zinnel and M.J. Ross. 1979. Use of a microprocessor to locate fish in experimental channels. Intl. Conf. Wildlife Biotelemetry 2:33-39.

Lawes, J., and J. Gilbert. 1880. Agricultural, botanical and chemical results of experiments on the mixed herbage of permanent grassland, conducted for many years in succession on the same land. I. Phil. Trans. Roy. Soc. 171:189-416.

Lawes, J., J. Gilbert, and M. Masters. 1882. Agricultural, botanical and chemical results of epxeriments on the mixed herbage of permanent grasslands, conducted for many years on the same land. II. Phil. Trans. Roy. Soc. 173:1181-1413.

Lawrence, D.B., R.E. Schoenike, A. Quispel and G. Bond. 1967. The role of Dryas drummondi in vegetation development following ice recession at Glacier Bay, Alaska, with special reference to its nitrogen fixation by root nodules. J. Ecol. 55:793-813.

Leon, J. and D. Tumpson. 1975. Competition between two species for two complementary or substitutable resources. J. Theor. Biol. 50:185-201.

Lieth, A. 1974. Phenology and Seasonality Modeling. Springer-Verlag. New York.

Lindeman, R.L. 1942. The trophic-dynamic aspects of ecology. Ecol. 23:399-418.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of food preference and algal competitive abilities. Amer. Nat. 112-23-39.

Lynch, M. 1978. Complex interactions between natural coexploiters Daphnia and Ceriodaphnia. Ecol. 59:552-564.

MacArthur, R.H. 1972. Geographical Ecology. Harper and Row, New York. 269 p.

Maguire, B. 1973. Niche response structure and the analytical potentials of its relationship to the habitat. Amer. Natur. 107:213-246.

Marsden, W. 1964. The Lemming Year. Chatto & Windus, London.

Mattson, W.J. 1980. Herbivory in relation to plant nitrogen content. Ann. Rev. Ecol. Sys. 11:119-161.

Mayse, M.A., M. Kogan, and P.W. Price. 1978. Sampling abundances of soybean arthropods: comparison of methods. J. Econ. Ent. 71:135-141.

McColl, J.G. and D.F. Grigal. 1977. Nutrient changes following a forest wildfire in northeastern Minnesota: Effects of watersheds with differing soils. Oikos, 28:105-112.

McCormick, J. 1968. Succession. pp. 22-35 in VIA 1. Student publication, Graduate School of Fine Arts, University of Pennsylvania, Philadelphia.

McKone, M. 1980. The effect of nutrients on competition among old field plants. M.S. Thesis, University of Minnesota.

McNeil, S. and T.R.E. Southwood. 1978. The role of nitrogen in the development of insect/plant relationships. In Biochemical Aspects of Plant and Animal Coevolution, ed. J.B. Harborne, pp. 77-98. Academic, London.

Mellinger, M., and S. McNaughton. 1975. Structure and function of successional vascular plant communities in central New York. Ecol. Mono. 34:161-182.

Milton, W. 1934. The effect of controlled grazing and manuring on natural hill pastures. Welsh J. Agric. 11:126-132.

Milton, W. 1940. The effect of manuring, grazing and curring on the yield, botanical, and chemical composition of natural hill vegetation. J. Ecol. 28:326-356.

Milton, W. 1947. The yield, botanical and chemical composition of natural hill herbsge under manuring, controlled grazing and hay conditions. I. Yield and botanical. J. Ecol. 35:65-89.

Mullen, D.A. 1968. Reproduction in brown lemmings (Lemmus trimucronatus) and its relevance to their cycle of abundance. Univ. Calif. Publs. Zool. 85:1-24.

Negus, N.C. and P.J. Berger. 1977. Experimental triggering of reproduction in a natural population of Microtus montanus. Science 196:1230-31.

Odum, E.P. 1977. The emergence of ecology as a new integrative discipline. Science 195:1289-1293.

Odum, E.P. 1969. The strategy of ecosystem development. Science 164:262-270.

Orians, G.H. 1980. Micro and macro in ecological theory. Bioscience 30(2):79.

Patrick, R. 1963. The structure of diatom communities under varying ecological conditions. Ann. N.Y. Acad. Sci. 108:359-365.

Patrick, R. 1967. The effect of varying amounts and ratios of nitrogen and phosphate on algae blooms. Proc. 21st Ann. Industrial Waste Conf., Purdue Univ., Lafayette, Indiana. P. 41-51.

Patten, B. 1962. Species diversity of net phytoplankton of Raritan Bay. J. Mar. Sci. 20:57-75.

Peet, R.K. 1974. The measurement of species diversity. Ann. Rev. Ecol. Syst. 5:285-307.

Peet, R.K. 1975. Relative diversity indices. Ecol. 56:496-498.

Pielou, E.C. 1966. Species-diversity and pattern-diversity in the study of ecological succession. J. Theor. Biol. 10:370-383.

Pielou, E.C. 1975. Ecological Diversity. Wiley-Interscience. New York. 165 p.

Pieper, R.D. 1964. Production and chemical composition of arctic tundra vegetation and their relation to the lemming cycle. Ph.D. dissertation, Univ. of California, Berkeley.

Pierce, R.L. 1954. Vegetation cover types and the land use history of Cedar Creek Natural Reservation, Anoka and Isanti Counties, Minnesota. M.S. Thesis. Univ. of Minnesota.

Pitelka, F.A. 1964. The nutrient recovery hypothesis of Arctic microtine cycles. I. Introduction. In: A.J. Crisp, ed. Grazing in Terrestrial and Marine Environments, pp. 55-56. British Ecological Society, Blackwell Scientific Publications, Oxford.

Pitelka, F.A. 1973. Cyclic patterns in lemming populations near Barrow, Alaska. In: M.E. Britton, ed. Alaska Arctic Tundra. pp. 199-215. Tech. Pap. 25, Arct. Inst. N. Am. Wash.

Platt, W., and I. Weis. 1977. Resource partitioning and competition within a guild of fugitive prairie plants. Amer. Nat. 111:479-513.

Regal, P. 1978. Time based movement patterns in gray squirrels. NSF Proposal DEB 7818599 (funded 1979-1981).

Reiners, W.A. 1968. Carbon dioxide evolution from the floor of three Minnesota forests. Ecol. 49:471-483.

Root, R.B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (Brassica oleracea). Ecol. Mono. 43:95-124.

Root, R.B. 1975. Some consequences of ecosystem texture. In: S.A. Levin, ed. Ecosystem Analysis and Prediction. Soc. Ind. Appl. Math, Philadelphia. Pp. 83-97.

Rosenzweig, M. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. Sci. 171:385-387.

Schlesinger, W.H. 1976. Toxic foods and vole cycles: additional data. Am. Nat. 110:315-17.

Schindler, D. 1977. Evolution of phosphorus limitation in lakes. Sci. 195:260-262.

Schultz, A.M. 1964. The nutrient recovery hypothesis for Arctic microtine cycles. II. Ecosystem variables in relation to Arctic microtine cysles. In: A.J. Crisp, ed. Grazing in Terrestrial and Marine Environments, pp. 57-68. British Ecological Society, Blackwell Scientific Publications, Oxford.

Simmonds, F.J., J.M. Franz, and R.I. Sailer. 1976. History of biological control. In: C.B. Huffaker and P.S. Messenger, eds. Theory and Practice of Biological Control. Academic Press, New York. Pp. 17-39.

Smith, J.W., E.A. Stadelbacher, and C.W. Gantt. 1976. A comparison of techniques for sampling beneficial arthropod populations associated with cotton. Environ. Ent. 5:435-444.

Smolen, M.J., H.H. Genoways and R.J. Baker. 1980. Demographic and reproductive parameters of the yellow-cheeked pocket gopher (Pappogeomys castanops). J. Mamm. 61(2):224-236.

Snaydon, R.W. 1962. Micro-distribution of Trifolium repens L. and its relation to soil factors. J. Ecol. 50:133-143.

Southwood, T.R.E., and M.J. Way. 1970. Ecological background to pest management. In: R.L. Rabb and R.E. Guthrie, eds. Concepts of Pest Management. North Carolina State Univ. Press, Raleigh. Pp. 6-29.

Steeman-Neilson, E. 1954. On organic production in the oceans. J. Int. Coun. Stud. Sea 19:309-328.

Swain, P.C. 1979. The development of some bogs in eastern Minnesota. Ph.D. Thesis. Univ. Minnesota.

Thurston, J. 1969. The effect of liming and fertilizers on the botanical composition of permanent grassland, and on the yield of hay. In: I. Rorison, ed. Ecological Aspects of the Mineral Nutrition of Plants. Blackwell, Oxford. P. 3-10.

Tilman, D. 1976. Ecological competition between algae: experimental confirmation of resource-based competition theory. Science 192:463-465.

Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. Ecol. 58:338-348.

Tilman, D. 1980. Resources: a graphical-mechanistic approach to competition and predation. Amer. Nat. 116:362-393.

Tilman, D. 1981a. Experimental tests of resource competition theory using four species of Lake Michigan algae. Ecology, in press.

Tilman, D., M. Mattson, and S. Langer. 1981b. Competition and nutrient kinetics along a temperature gradient: an experimental tests of a mechanistic approach to niche theory. Limnol. Oceanogr., in press.

Tilman, D. 1981c. Resource Compeition and Community Structure. (A book solicited by the Princton Monograph series; currently undergoing final revisions).

van Emden, H.F. 1965. The role of unvultivated land in the biology of crop pests and beneficial insects. Sci. Hort. 17:126-136.

van Emden, H.F., and G.F. Williams. 1974. Insect stability and diversity agroecosystems. Ann. Rev. Ent. 19:455-475.

Way, M.J. 1966. The natural environment and integrated methods of pest control. J. Appl. Ecol. 3:29-32.

Werner, P.A. and W.J. Platt. 1977. Ecological relationships of co-occurring goldenrods (Solidago: Compositae). Amer. Natur. 110:959-971.

Werner, P.A. and R. Rioux. 1977. The biology of Canadian weeds. 24: Agropyron repens (L.) Beauv. Can. J. Plt. Sci. 57:905-919.

Westman, W.E. 1978. Measuring the inertia and resilience of ecosystems. BioSci. 28:705-710.

White, T.C.R. 1978. The importance of a relative shortage of food in animal ecology. Oecologia (Berl.) 33:71-86.

Whittaker, R.H., and P. Feeny. 1971. Allelochemics: chemical interactions between species. Science 171:757-770.

Whittaker, R.H., and G.M. Woodwell. 1968. Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. J. Ecol. 56:1-25.

Whittaker, R.H., and G.M. Woodwell. 1969. Structure, production and diversity of the oak-pine forest at Brookhaven, New York. J. Ecol. 57:157-174.

Williams, L. 1964. Possible relationships between plankton-diatom species numbers and water quality estimates. Ecol. 45:809-823.

Willis, A. 1963. Braunton Burrows: the effects on the vegetation of the addition of mineral nutrients to the dune soils. J. Ecol. 51:353-374.

Willis, A., and E. Yemm. 1961. Braunton Burrows: mineral nutrient status of the dune soils. J. Ecol. 49:377-390.

Wilson, F., and C.B. Huffaker. 1976. The philosophy, scope, and importance of biological control. In: C.B. Huffaker and P.S. Messenger, eds. Theory and Practice of Biological Control. Academic Press, New York. Pp. 3-15.

Wright, H.E., Jr. 1976. The dynamic nature of Holocene vegetation. Quant. Res. 6:581-596.

Wright, H.E., Jr. 1977. Quanternary vegetation history -- some comparisons between Europe and America. Ann. Rev. Earth Planet Sci. 5:123-158.

Young, V. 1934. Plant distribution as influenced by soil heterogeneity in the Cranberry Lake region of the Adirondack Mountains. Ecol. 15:154-196.

Zippin, C. 1956. An evaluation of the removal method of estimating animal populations. Biometrics 12:163-189.

Appendix A

CEDAR CREEK BIBLIOGRAPHY

Wilcox, A. N. 1937. The fate of the indigeneous. Proc. Minn. Acad. Sci., 5:15-23.

Buell, M. F. and H. F. Buell. 1941. Surface level fluctuations in Cedar Creek Bog, Minnesota. Ecol., 22:317-321.

Lindeman, R. L. 1941a. The developmental history of Cedar Creek Bog, Minnesota. Amer. Midl. Nat., 25:101-112.

Lindeman, R. L. 1941b. Seasonal food cycle dynamics in a senescent lake. Amer. Midl. Nat., 26:636-673.

Lindeman, R. L. 1942a. Experimental simulation of winter anaerobiosis in a senescent lake. Ecol., 23(4):1-13.

Lindeman, R. L. 1942b. The trophic-dynamic aspect of ecology. Ecol., 23(4):399-417.

Gunderson, H. L. 1948. Birds nesting in Cedar Creek Forest. Flicker, 20:81-82.

Conway, V. M. 1949. The bogs of central Minnesota. Ecol. Mono., 19: 173-206.

Gunderson, H. L. 1949. Mammals of Cedar Creek Forest, Anoka County, Minnesota. Flicker, 21:96-100.

Gunderson, H. L. 1950. A study of some small mammal populations at Cedar Creek Forest, Anoka County, Minnesota, Minn. Mus. Nat. Hist. Occas. Paper No. 4. 49 pp.

Gunderson, H. L. 1950. The flora and fauna of Cedar Creek Forest, Minnesota. Minn. Nat., 1:11.

Wilcox, A. N. 1950. The development of the Cedar Creek Natural History Area. Proc. Minn. Acad. Sci., 18:163-168.

Wilson, C. S. 1950. Water use problems and wildlife values. Minn. Dept. Cons. Bull., 3. 11 pp.

Pelton, J. F. 1951. Outline for ecological life history studies in tree, shrub, and stem succulents. Ecol., 32:334-343.

Pelton, J. F. 1953. Relation of certain vegetative characteristics of Stipa sparta to survival from defoliation, Butler Univ. Bot. Studies, 11:60-70.

Turnock, W. and D. B. Lawrence. 1953. Measurement of the level of ground water at the Cedar Creek Forest. 11pp (ditto)

Duncan, D. P. 1954. A study of some of the factors affecting the natural regeneration of tamarack (Latrix laricina) in Minnesota. Ecol. 35: 498-521.

Swain, F. M. and N. Prokopovich. 1954. Stratigraphic distribution of lipoid substances in Cedar Creek Bog, Minnesota. Bull. Geol. Soc. Amer., 65:1183-1198.

Breckenridge, W. J. 1956. Measurement of habitat niche of the least flycatcher. Wils. Bull., 68:47-51.

Swain, F. M. 1956. Stratigraphy of lake deposits in central and northern Minnesota. Bull. Amer. Assoc. Petrol. Geol., 40:600-653.

Lawrence, D. B., J. R. Bray and L. C. Pearson. 1957-58. Ecosystem studies at Cedar Creek Natural History Area. Proc. Minn. Acad. Sci., 25-26: 108-112.

Pearson, L. C. and D. B. Lawrence. 1958. Photosynthesis in aspen bark during winter months. Proc. Minn. Acad. Sci., 26:101-107.

Pearson, L. C. and D. B. Lawrence. 1958. Photosynthesis in aspen bark. Amer. J. Bot., 45:383-387.

Bray, J. R. 1959. An analysis of the possible recent changes in atmospheric carbon dioxide concentration. Tellus, 11(2).

Bray, J. R., D. B. Lawrence and L. C. Pearson. 1959. Primary production in some Minnesota terrestrial communities for 1957. Oikos, 10:38-49.

Swain, F. M., A. Blumentals and R. Miller. 1959. Stratigraphic distribution of amino acids in peats from Cedar Creek Bog, Minnesota, and Dismal Swamp, Virginia. Limno. and Oceano., 4:119-127.

Bray, J. R. 1960. The chlorophyll content of some native and managed plant communities in central Minnesota. Can. J. Bot., 38:313-333.

Lawrence, D. B., J. D. Ovington and J. R. Bray. 1960. Ecosystem studies at Cedar Creek Natural History Area, II. Proc. Minn. Acad. Sci., 28:16-19.

Bonde, A. N., J. D. Ives, and D. B. Lawrence. 1961. Ecosystem studies at Cedar Creek Natural History Area, III. Water use studies. Proc. Minn. Acad. Sci., 29:190-198.

Bray, J. R. and J. E. Sanger. 1961. Light reflectivity as an index of chlorophyll content and production potential of various kinds of vegetation. Minn. Acad. Sci., 29:222-226.

Nute, G. L. 1961. A tribute to Cedar Bog Bird Woman. Naturalist, 12(4):28-31.

Sakamoto, S. 1961. Arisaema triphyllum, jack-in-the-pulpit in Minnesota, especially at the Cedar Creek Natural History Area. Proc. Minn. Acad. Sci., 29:153-168.

Wertman, F. L. and D. B. Lawrence. 1961. Fruit and seed project of the Cedar Creek Natural History Area. Proc. Minn. Acad. Sci., 29:219-221.

Bray, J. R. 1962. Estimates of energy budgets for a Typha (cattail) marsh. Science, 136(3522):1119-1120.

Bray, J. R. 1962. The primary productivity of vegetation in central Minnesota, U.S.A., and its relationship to chlorophyll content and albedo. Sonderdruck Aus-Die Stoffproduktion der Pflanzendecke, 102-116.

Bray, J. R. 1962. Root production and the estimation of net productivity. Can. J. Bot., 41:65-72.

Bray, J. R. 1962. Use of non-area analytic data to determine species dispersion. Ecol., 43(2):328-333.

Swain, F. M. and G. Venters. 1962. Distribution of flavinoids and some other heterocyclic substances in lake sediments. Adv..Org. Geochem. Proc. Intl. Meet., Milan, pp. 1-6.

Lawrence, D. B. 1963. Natural areas primarily for research. Pages 3-6. College Natural Areas as Research and Teaching Facilities. The Nature Conservancy Research Publication No. 1, Washington, D. C. 32 pages.

Ovington, J. D., D. Heitkamp and D. B. Lawrence. 1963. Plant biomass and productivity of prairie, savanna, oakwood and maize field ecosystems in central Minnesota. Ecol., 44(1):52-63.

Paulsell, L. K. and D. B. Lawrence. 1963. Artificial frost apparatus. Ecol., 44:146-148.

Swain, F. M. 1963. Geochemistry of humus. Org. Geochem., pp. 87-147.

Warner, D. W. 1963. Fundamental problems in the use of telemetry in ecological studies. In L. E. Slater (ed.), Bio-telemetry. Pergamon Press, Oxford, pp. 15-24.

Warner, D. W. 1963. Space tracks, bioelectronics extends its frontiers. Nat. Hist., 62:8-15.

Gorham, E. and J. Sanger. 1964. Chlorophyll derivatives of woodland, swamp, and pond soils of Cedar Creek Natural History Area, Minnesota, U.S.A. 1-12 pp. In Y. Miyake and T. Koyama (eds.) Recent researches in the fields of hydrosphere, atmosphere and nuclear geochemistry. Maruzen Co., Tokyo.

Ovington, J. D. and D. B. Lawrence. 1964. Strontium 90 in maize field, cattail marsh and oakwood ecosystems. J. Appl. Ecol., 1:175-181.

Swain, F. M., G. W. Paulsen and F. Ting. 1964. Chlorinoid and flavinoid pigments from aquatic plants and associated lake and bay sediments. J. Sed. Petrol., 34(3):561-598.

Swain, F. M., G. Venteris and F. Ting. 1964. Relative abundance and order of stability of amino acids in some aquatic plants and associated freshwater sediments. J. Sed. Petrol., 34(1):25-45.

Tester, J. R., D. W. Warner and W. W. Cochran. 1964. A radio-tracking system for studying movements of deer. J. Wildl. Mgmt., 28(1):42-45.

Cochran, W. A., D. W. Warner, J. R. Tester and V. B. Kuechle. 1965. Automatic radio-tracking system for monitoring animal movements. BioSci., 15(2):98-100.

Frenzel, L. D. 1965. An estimate of winter utilization of the Cedar Creek Natural History Area by the white-tailed deer (Odocileus virginianus borealis). J. Minn. Acad. Sci., 32(2):98-100.

McKinney, F. 1965. An analysis of pair-formation in Anas crecca carolinensis. Bull. Ecol. Soc. Amer., 46(3):110-111 (Abstract).

McKinney, F. 1965. The displays of the American green-winged teal. Wils. Bull., 77(2):122-121.

Mech, L. D. 1965. A critical evaluation of the concept of home range. Bull. Ecol. Soc. Amer., 46(3):121 (Abstract).

Mech, L. D. 1965. Sodium pentobarbital as an anesthetic for raccoons. J. Mammal., 46(2):343-344.

Mech, L. D. and N. V. Anderson. 1965. Renal hypoplasia and compensatory hypertrophy in a raccoon. J. Mammal., 47(1):128-129.

Mech, L. D., V. B. Kuechle, D. W. Warner and J. R. Tester. 1965. A collar for attaching radio transmitters to rabbits, hares, and raccoons. J. Wildl. Mgmt., 29(4):898-902.

Ovington, J. D. 1965. Prairie savanna and oakwood ecosystems at Cedar Creek. In D. J. Crisp (ed.), Grazing in terrestrial and marine environments. Symp. Brit. Ecol. Soc., 41:43-53.

Siniff, D. B. and J. R. Tester. 1965. Computer analysis of animal-movement data obtained by telemetry. Biosci., 15(2):104-108.

Tester, J. R. 1965. Effects of a controlled burn on small mammals in a Minnesota oak-savanna. Amer. Midl. Nat., 74(1):240-243.

Tester, J. R. and K. L. Heezen. 1965. Deer response to a drive census determined by radio tracking. Biosci., 15(2)100-104.

Tester, J. R. and J. C. Moulton. 1965. Movements and activity of pen-raised white-tailed deer (Odocoileus virginianus) after release in unfamiliar habitat. Bull. Ecol. Soc. Amer., 46(3):121 (Abstract).

Tester. J. R. and D. B. Siniff. 1965. Aspects of animal movement and home range data obtained by telemetry. Trans. N. A. Wildl. and Nat. Res. Conf., 30:379-392.

Bray, J. R., J. E. Sanger and A. L. Archer. 1966. The visible albedo of surfaces in central Minnesota. Ecol., 47(4):524-531.

Idso, Sherwood B., D. G. Baker and D. M. Gates. 1966. The energy environment of plants. Adv. Agron., 18:171-218.

Mech, L. D., K. L. Heezen and D. B. Siniff. 1966. Onset and cessation of activity in cortontail rabbits and snowshoe hares in relation to sunset and sunrise. An. Beh., 14:410-413.

Mech, L. D., J. R. Tester and D. W. Warner. 1966. Fall daytime resting habits of raccoons as determined by telemetry. J. Mammal., 47(3): 450-466.

Mech, L. D. and F. Turkowski. 1966. Twenty-three raccoons in one winter den. J. Mammal., 47(3):529-530.

Nicholls, T. H. and D. W. Warner. 1966. Bio-telemetry - a valuable tool in bird study. Passenger Pigeon, 28(4):127-131.

Schneider, D. G., L. D. Mech and J. R. Tester. 1966. An eight-month radio-tracking study of raccoon families. Bull. Ecol. Soc. Amer., 37(3):149-150.

Tester, J. R. 1966. Automatic radio-tracking system for studying animal movement and behavior (motion picture). Bull. Ecol. Soc. Amer., 47(3):156.

Tester, J. R. 1966. Potentials of radio tracking in studies of vertebrate behavior. Engineering in medicine and biology. Proc. 19th Annl. Conf., 22:3.

Gorham, E. and J. Sanger. 1967. Plant pigments in woodland soils. Ecol., 48(2):306-308.

Gorham, E. and J. Sanger. 1967. Caloric values of organic matter in woodland, swamp, and lake soils. Ecol., 48(3):493-494.

Heezen, K. L. and J. R. Tester. 1967. Evaluation of radio-tracking by triangulation with special reference to deer movements. J. Wildl. Mgmt., 31(1):124-141.

Kuechle, V. B. 1967. Batteries for biotelemetry and other applications. BIAC Information Module M10.

McKinney, F. 1967. Breeding behavior of captive shovelers. Wildfowl Trust, Ann. Rept., 18:108-121.

Mech, L. D. 1967. Telemetry as a technique in the study of predation. J. Wildl. Mgmt., 31(3):492-496.

Ovington, J. D. and D. B. Lawrence. 1967. Comparative chlorophyll and energy studies of prairie, savanna, oakwood, and maize field ecosystems. Ecol., 48(4):515-524.

Sunquist, M. E. 1967. Effects of fire on raccoon behavior. J. Mammal., 48(4):673-674.

Tester, J. R. 1967. Status and value of biotelemetry in studies of vertebrate ecology. Congres Des. Biol. Du-Gibier, Beograd-Ljubljana, 7:195-199.

Tester, J. R., D. B. Siniff and O. J. Rongstad. 1967. Effects of radiation on behavior of unconfined raccoons and snowshoe hares determined by telemetry. Am. Zool., 7(4):404.

Buell, M. F., H. F. Buell and W. A. Reiners. 1968. Radial mat growth on Cedar Creek Bog, Minnesota. Ecol., 49(6):1198-1199.

Marshall, W. H. 1968. Utilization of the Cedar Creek Natural History Area. J. Minn. Acad. Sci., 35(1):57-61.

McKinney, F. 1968. Nest-building movements performed by male ducks. Wildfowl, 19:64-66.

Mech, L. D., D. Barnes, J. R. Tester. 1968. Seasonal weight changes, mortality, and population structure of raccoons in Minnesota. J. Mammal., 49(1):63-73.

Moen, A. N. 1968. The critical thermal environment: a new look at an old concept. Biosci., 18(11):1041-1043.

Moen, A. N. 1968. Energy exchange of white-tailed deer, western Minnesota. Ecol., 49(4):676-682.

Nicholls, T. H. 1968. A harness for attaching radio transmitters to large owls. Bird Banding, 39(3):209-214.

Reiners, W. A. and R. O. Anderson. 1968. CO_2 concentrations in forests along a topographic gradient. Amer. Midl. Nat., 80(1):111-117.

Reiners, W. A. 1968. Carbon dioxide evolution from the floor of three Minnesota forests. Ecol., 49(3):471-483.

Rongstad, O. J. 1968-69. A bullsnake encounter with young ground squirrels. J. Minn. Acad. Sci., 35(2 & 3):95-96.

Tester, J. R., F. McKinney and D. B. Siniff. 1968. Mortality of three species of ducks--Anas discors, A. crecca and A. clypeata--exposed to ionizing radiation. Radiat. Res., 33(2):364-369.

Turkowski, F. and L. D. Mech. 1968. An intensive analysis of the movements of a young male raccoon. J. Minn. Acad. Sci., 35(1):33-38.

Weaver, M. G. and R. L. Shaffer. 1968-69. Records of the higher fungi of Minnesota. J. Minn. Acad. Sci., 35(2 & 3):123-128.

Houseknecht, C. R. 1969. Denning habits of the striped skunk and the exposure potential for disease. Bull. Wildl. Disease Assoc., 5:302-306.

McKinney, F. 1969. The behavior of ducks. In Behaviour of domestic animals. E.S.E. Hafez (ed.), Chapter 18:593-626. Balliers, Tindall and Cassell, London.

Pratt, D. C. and E. Gorham. 1969. Occurrence of Athiohodaceae in woodland, swamp and pond soils. Ecol., 51(2).

Rongstad, O. J. and J. R. Tester. 1969. Movements and habitat use of white-tailed deer in Minnesota. J. Wildl. Mgmt., 33(2):366-379.

Schladweiler, J. L. and G. L. Storm. 1969. Den-use by mink. J. Wildl. Mgmt., 33(4):1025-1026.

Siniff, D. B. and C. R. Jessen. 1969. A simulation model of animal movement patterns. Adv. Ecol. Res., 6:185-219.

Sunquist, M. E., G. G. Montgomery and G. L. Storm. 1969. Movements of a blind raccoon. J. Mammal., 50(1):145-147.

Hessler, E. W., J. R. Tester, D. B. Siniff and M. M. Nelson. 1970. A biotelemetry study of survival of pen-reared pheasants released in selected habitats. J. Wildl. Mgmt., 34(2):267-274.

Houseknecht, C. R. 1970. Biotelemetry as a technique in disease ecology studies. J. Wildl. Diseases, 6:414-417.

Houseknecht, C. R. and R. A. Huempfner. 1970. A red fox-striped skunk encounter. Amer. Midl. Nat., 83(1):304-306.

Irving, F. D. 1970. Field instruction in prescribed burning techinques at the University of Minnesota. Proc. Ann. Tall Timbers Fire Ecol. Conf., August. pp. 323-331.

McKinney, F. 1970. Displays of four species of blue-winged ducks. The Living Bird, 9:39-64.

Montgomery, G. G., J. W. Lang and M. E. Sunquist. 1970. A raccoon moves her young. J. Mammal., 51(1):202-203.

Reiners, W. A. and N. M. Reiners. 1970. Energy and nutrient dynamics of forest floors in three Minnesota forests. J. Ecol., 58:497-519.

Sanger, J. E. and E. Gorham. 1970. The diversity of pigments in lake sediments and its ecological significance. Limno. and Oceano., 15:59-69.

Schnell, J. H. 1970. Rest site selection by radio-tagged raccoons. J. Minn. Acad. Sci., 36(2 & 3):83-88.

Gilmer, D. S., V. B. Kuechle and I. J. Ball. 1971. A device for monitoring radio-marked animals. J. Wildl. Mgmt., 35(4):829-832.

Henry, R. A., R. C. Johnson, B. B. Bohlool and E. L. Schmidt. 1971. Detection and leptospira in soil and water by immunofluorescence straining. Appl. Microbiol., 21:953-956.

Rongstad, O. J. and J. R. Tester. 1971. Behavior and maternal relations of young snowshoe hares. J. Wildl. Mgmt., 35(2):338-346.

Sanderson, G. C., L. D. Mech and J. H. Schnell. 1971. A contribution to a bibliography of the raccoon (Procyon lotor). U.S. Atomic Energy Commission, Division of Tech. Info., 82 pp.

Sanger, J. E. 1971. Identification and quantitative measurement of plant pigments in soil humus layers. Ecol., 52(6):959-963.

Sanger, J. E. 1971. Quantitative investigations of leaf pigments from their inception in buds through autumn coloration to decomposition in falling leaves. Ecol., 52(6):1075-1089.

Schneider, D. G., L. D. Mech and J. R. Tester. 1971. Movements of female raccoons and their young as determined by radio tracking. An. Beh. Mono., 4(I):1-43.

Tester, J. R. 1971. Interpretation of ecological and behavioral data on wild animals obtained by telemetry with special reference to errors and uncertainties. In: Symp. of Biotelemetry, Pretoria, South Africa, November 1971, pp. 385-408.

Tester, J. R., D. B. Siniff and C. R. Jessen. 1971. Use of telemetry as means of studying spacing and behavior of animals. In: A. H. Esser (ed.), Behavior and environment, the use of space by animals and men. Plenum Press, New York, pp. 117-120.

Abraham, R. L. 1972. Mortality of mallards exposed to gamma radiation. Radiat. Res., 49:322-327.

Gorham, E. and D. C. Pratt. 1972. Influence of soil acidity on the occurrence of Athiorhodaceae. J. Minn. Acad. Sci., 38(1):2-4.

Nicholls, T. H. 1972. Barred owl habitat use as determined by radio telemetry. J. Wildl. Mgmt., 36(2):213-224.

Phillips, R. L., R. D. Andrews, G. L. Storm and R. A. Bishop. 1972. Dispersal and mortality of red foxes. J. Wildl. Mgmt., 36(2):237-248.

Reiners, W. A. 1972. Nutrient content of canopy through fall in three Minnesota forests. Oikos, 32:14-22.

Sargeant, A. B. 1972. Red fox spatial characteristcs in relation to waterfowl predation. J. Wildl. Mgmt., 36(2):225-236.

Sargeant, A. B. and D. W. Warner. 1972. Movements and denning habits of a badger. J. Mammal., 53(1):207-210.

Schladweiler, J. L. and J. R. Tester. 1972. Survival and behavior of hand-reared mallards released in the wild. J. Wildl. Mgmt., 36(4): 1118-1127.

Weaver, M. G. and R. L. Shaffer. 1972. Higher fungi of Minnesota, II. J. Minn. Acad. Sci., 38(1):46-52.

Andrews, R. D., G. L. Storm, R. L. Phillips and R. A. Bishop. 1973. Survival and movements of transplanted and adopted red fox pups. J. Wildl. Mgmt., 37(1):69-72.

Fuller, M. R. and J. R. Tester. 1973. An automatic radio tracking system for biotelemetry. Proc. Conf. on Raptor Conserv. Tech., March 22-25, 1973, Ft. Collins, CO. Raptor Res., 7(3/4):105-106.

Grigal, D. F., L. M. Chamberlain, H. R. Finney, D. V. Wroblewski and E. R. Goss. 1974. Soils of the Cedar Creek Natural History Area. Univ. Minn. Ag. Exper. Sta. Misc. Rept. 123:1-47.

Fuller, M. R., P. T. Redig and G. E. Duke. 1973. Raptor rehabitation and conservation in Minnesota. Loon, 45(2):50-55.

Gilmer, D. S., S. E. Miller and L. M. Cowardin. 1973. Analysis of radio-tracking data using digitized habitat maps. J. Wildl. Mgmt., 37(3):404-409.

McKinney, F. 1973. Ecoethological aspects of reproduction. In: Breeding biology of birds, pp. 6-21. D. S. Farner (ed.), Natl. Acad. Sci., Washington, D. C.

Moore, J. W. 1973. A catalog of the flora of Cedar Creek Natural History Area. Anoka and Isanti Counties, Minnesota. Bell Mus. Nat. Hist. Occas. Papers #12, 28 pp.

Preston, E. M. 1973. Computer simulated dynamics of a rabies-controlled fox population. J. Wildl. Mgmt., 37(4):501-512.

Sanger, J. E. and E. Gorham. 1973. A comparison of the abundance and diversity of fossil pigments in wetland peats and woodland humus layers. Ecol., 54(3):605-611.

Siniff, D. B. and V. B. Kuechle. 1973. Remote sensing of Antarctic biological resources, vertebrates. COSPAR Symposium: Approaches to earth survey problems through the use of space techniques. Konstanz, West Germany, P. Bock (ed.), pp. 65-74.

Storm, G. L. and G. G. Montgomery. 1973. Dispersal and social contact among red foxes: results from telemetry and computer simulation. In: Fox, M. W., Ecology and Social Behavior of Canids. Van Nostrand Reinhold Co., N.Y.

Thorkelson, J. and R. K. Maxwell. 1973. Design and testing of a heat transfer model of a raccoon (Procyan lotor) in a closed tree den. Ecol., 55(1):29-89.

Abraham, R. L. 1974. Vocalizations of the mallard (Anas platyrhynchos). Condor, 76(4):401-420.

Archibald, H. L. 1974. Directional differences in the sound intensity of ruffed grouse drumming. Auk, 91(3):517-521.

Burke, M. E., E. Gorham and D. C. Pratt. 1974. Distribution of purple photosynthetic bacteria in wetland and woodland habitats of central and northern Minnesota. J. Bacter., 117(2):826-833.

Forbes, J. E. and D. W. Warner. 1974. Behavior of a radio-tagged saw-whet owl. Auk, 91(4):783-795.

Fuller, M. R., T. H. Nicholls and J. R. Tester. 1974. Raptor conservation and management applications of bio-telemetry studies from Cedar Creek Natural History Area. In: F. N. Hamerstrom, et al. (eds.), Management of Raptors. Proc. Conf. on Raptor Conserv. Techn., Part 3, pp. 33-44.

Fuller, M. R. and J. R. Tester. 1974. An automatic radio tracking system for biotelemetry. Raptor Res., 7(3/4):103-104.

Gilmer, D. S., I. J. Ball, L. M. Cowardin and J. H. Riechmann. 1974. Effect of radio packages on ducks. J. Wildl. Mgmt., 38(2):243-252.

McKinney, F. 1974. The evolution of duck displays. In: Evolutionary Aspects of Behaviour. Niko Tinbergen Festschrift. Clarendon Press, Oxford.

Montgomery, G. G. 1974. Communication in red fox dyads: a computer simulation study. Smithsonian Contrib. Zool., Smithsonian Institution Press, Washington, D.C., 187:1-30.

Reiners, W. A. 1974. Foliage production by Thuja occidentailis L. from biomass and litter fall estimates. Amer. Midl. Nat., 92(2): 340-345.

Tester, J. R. and D. B. Siniff. 1974. Relevance of home range concepts of game biology. IX Intl. Cong. Game Biologist, Stockholm, pp. 287-296.

Archibald, H. L. 1975. Temporal patterns of spring space use by ruffed grouse. J. Wildl. Mgmt., 39(3):472-481.

Christenson, G. and M. R. Fuller. 1975. Food habits of two long-eared owl families in east-central Minnesota. Loon, 47(2):58-61.

Fuller, M. R. 1975. A technique for holding and handling raptors. J. Wildl. Mgmt., 39(4):824-825.

Gilmer, D. S., I. J. Ball, L. M. Cowardin, J. R. Riechmann and J. R. Tester. 1975. Habitat use and home range of mallards breeding in Minnesota. J. Wildl. Mgmt., 39(4):781-789.

Huempfner, R. A., S. J. Maxson, G. J. Erickson and R. F. Schuster. 1975. Recapturing radio-tagged grouse by nightlighting and snow-burrow netting. J. Wildl. Mgmt., 39(4):821-823.

Lammers, R. 1975. Ecology of the Tanypodinae in a Minnesota wetland. Verh. Intl. Verein. Limno., 19:3142-3148. Stuttgart, West Germany.

McKinney, F. 1975. The evolution of duck displays. In: Function and Evolution in Behaviour. Niko Tinbergen Festschrift. G. Baerends, C. Beer and A. Manning (eds.), Clarendon Press, Oxford.

Redig, P. T., M. R. Fuller and D. Evans. 1975. Techniques for determining some biomedical parameters of migrating raptors. Proc. Nor. Amer. Hawk Mig. Conf., Syracuse, NY

Storm, G. L. and G. G. Montgomery. 1975. Dispersal and social contact among red foxes: results from telemetry and computer simulation. In: The Wild Canids, M. W. Fox (ed.), pp. 237-246.

Sunquist, M. E. 1975. Winter activity of striped skunks (Mephitis mephitis) in east-central Minnesota. Amer. Midl. Nat., 92(2):434-446.

Archibald, H. L. 1976. Spring drumming patterns of ruffed grouse. Auk, 93(4):808-829.

Archibald, H. L. 1976. Spatial relationships of neighboring male ruffed grouse in spring. J. Wildl. Mgmt., 40(4):750-760.

Fuller, M. R. and G. S. Christenson. 1976. An evaluation of techniques for capturing raptors in east-central Minnesota. Raptor Res., 10(1):9-19.

Storm, G. L., R. D. Andrews, R. L. Phillips, R. A. Bishop, D. B. Siniff and J. R. Tester. 1976. Morphology, reproduction, dispersal and mortality of midwestern red fox populations. Wildl. Mono., No. 49, 82 pp.

Swanson, G. Q., V. B. Kuechle and A. B. Sargeant. 1976. A telemetry technique for monitoring diel waterfowl activity. J. Wildl. Mgmt., 40(1):187-190.

Archibald, H. L. 1977. Is the 10-year wildlife cycle induced by a lunar cycle? Wildl. Soc. Bull., 5(3):126-129.

Fuller, M. R., G. E. Duke and V. B. Kuechle. 1977. Semiconductor strain gauge sensing and telemetering of gastric motility in great-horned owls. Abstr. Fed. Proc., 36(3):462.

Maxson, S. J. 1977. Activity patterns of female ruffed grouse during the breeding season. Wils. Bull., 89(3):439-455.

Axelrod, F. N. and F. D. Irving. 1978. Some effects of prescribed fire at Cedar Creek Natural History Area. Minn. Acad. Sci., 44(2):9-11.

Houseknecht, C. R. and J. R. Tester. 1978. Denning habits of striped skunks (Mephitis mephitis) Amer. Midl. Nat., 100(2):424-430.

Maxson, S. J. 1978. A nesting study of ruffed grouse at the Cedar Creek Natural History Area, Minnesota. Loon, 50:25-30.

Maxson, S. J. 1978. Ruffed grouse use of supraorbital combs in displays. Condor, 80:240.

Maxson, S. J. 1978. Spring home range and habitat use by female ruffed grouse. J. Wildl. Mgmt., 42(1):61-71.

Maxson, S. J. 1978. Evidence of brood adoption by ruffed grouse. Wils. Bull., 90(1):132-133.

McKinney, F. 1978. Comparative approaches to social behavior in closely related species of birds. Adv. Study of Beh., 8:1-38.

McKinney, F. 1978. Social behavior of dabbling ducks in flight pens. Proc. 1st Intl. Birds in Captivity Symp., Seattle, Washington.

McKinney, F., J. Barrett and S. R. Derrickson. 1978. Rape among mallards. Science, 201:281-282.

Timm, R. M. and E. F. Cook. 1978. The effect of bot fly larvae on reproduction in white-footed mice, Peromyscus leucopus. Paper No. 9927, Scientific Journal Series, Univ. Minn. Ag. Exp. Sta., 7 pp.

Winter, J. D., V. B. Kuechle, D. B. Siniff and J. R. Tester. 1978. Equipment and methods for radio tracking freshwater fish. Univ. Minn. Ag. Exp. Sta., Misc. Rept. 152, 18 pp.

Gray, R. H. and J. M. Haynes. 1979. Spawning migration of adult chinook salmon carrying external and internal radio transmitters. J. Fish. Res. Board Can. 36:1060-1064.

Kuechle, V. B., D. P. DeMaster and D. B. Siniff. 1979. State of the art and needs of the earth platform. Proc. 13th Symp. Remote Sensing, Ann Arbor, MI. 15 pp.

Kuechle, V. B., R. A. Reichle, K. E. Zinnel and M. J. Ross. 1979. Use of a microprocessor to locate fish in experimental channels. 2nd Intl. Conf. Wildl. Biotelemetry, Laramie, Wyoming, pp. 33-39.

Ross, J. J., V. B. Kuechle, R. A. Reichle and D. B. Siniff. 1979. Automatic radio telemetry recording of fish temperature and depth. 2nd Intl. Conf. Wildl. Biotelemetry, Laramie, Wyoming, pp. 238-247.

Tester, J. R. 1979. Analysis of circadian rhythms of free-ranging mammals. Biotelemetry IV, Proc. 4th Intl. Symp. Biotelemetry, Garmisch-Partenkirchen, Germany, pp. 167-170.

Burns, J. T., K. M. CHeng, and F. McKinney. 1980. Forced copulation in captive mallards. I. Fertilization of eggs. Auk, (97):875-878.

Haarstad, J. 1980. The dragonflies of Cedar Creek Natural History Area. Unpbl. manusc. (being considered for Occasional Paper Series) (215 pp., 80 figures, 17 tables, 12 distribution maps, 26 plates).

Hilton, Jr., B. and J. M. Vesall. 1980. A preliminary report on the breeding behavior of the Blue Jay in Anoka County, Minnesota. Loon, 52:146-149.

Hoskinson, R. L. and J. R. Tester. 1980. Migration behavior of pronghorn in southeastern Idaho. J. Wildl. Mgmt., 44(1):132-144.

McMahon, G. L. and R. N. Johnson. 1980. Introduction of the wild turkey into the Carlos Avery Wildlife Management Area. In J. M. Sweeney, ed., Proc. of fourth natl. wild turkey symp. Arkansas Chapter of the Wildlife Society, Monticello, MN.

Williams, R. T. 1980. Utilization of the peatland methanogenic microflora. Peat as an Energy Alternative Symposium. Arlington, Virginia. December 1-3, 1980. Institute of Gas Technology. (in press)

STUDENT THESES

Chu, K. L. 1948. The upland plant communities of Cedar Creek Forest, Anoka County, Minnesota. M.S. Thesis, University of Minnesota.

Pierce, R. L. 1954. Vegetation cover types and the land use history of Cedar Creek Natural History Reservation, Anoka and Isanti Counties, Minnesota. M.S. Thesis, University of Minnesota.

Norberg, E. R. 1957. White-tailed deer movements and foraging on the Cedar Creek Forest, Minnesota. M.S. Thesis, University of Minnesota.

Cushing, E. J. 1963. Late Wisconsin pollen stratigraphy in east-central Minnesota. Ph.D. Thesis, University of Minnesota.

Heezen, K. L. 1965. Evaluation of animal location data obtained by triangulation with observations on winter and spring movements of white-tailed deer in Minnesota. M.S. Thesis, University of Minnesota.

Marotta, J. D. 1966. Factors associated with the vegetation pattern in an ecosystem in the Cedar Creek Natural History Area. M.S. Thesis, University of Minnesota.

Moen, A. N. 1966. Factors affecting the energy exchange and movement of white-tailed deer, western Minnesota. Ph.D. Thesis, University of Minnesota.

Moulton, J. C. 1966. Movement and activity of three white-tailed deer during the winter of 1964-65 in east-central Minnesota determined by telemetry. M.S. Thesis, University of Minnesota.

March, J. R. 1967. Dominance relations and territoriality behavior in captive shovelers (*Anas clypeata*). M.S. Thesis, University of Minnesota.

Siniff, D. B. 1967. A simulation model of animal movement patterns. Ph.D. Thesis, University of Minnesota.

Hessler, E. W. 1968. Survival of ring-necked pheasants released in selected habitats in Minnesota. M.S. Thesis, University of Minnesota.

Sanger, J. E. 1968. A quantitative study of leaf pigments from initiation in buds to decomposition in soils. Ph.D. Thesis, University of Minnesota.

Schneider, D. G. 1968. Movements of female raccoons and their young as determined by radio tracking. Ph.D. Thesis, University of Minnesota.

Schladweiler, J. 1969. Survival and behavior of hand-reared mallards. M.S. Thesis, University of Minnesota.

Sunquist, M. E. 1970. Winter activity of striped skunks (*Mephitis mephitis*) in east-central Minnesota. M.S. Thesis, University of Minnesota.

Abraham, R. 1971. An analysis of the mallard vocalization. M.S. Thesis, University of Minnesota.

Houseknecht, C. R. 1971. Movement, activity patterns and denning habits of striped skunks and the exposure potential for disease. Ph.D. Thesis, University of Minnesota.

Kaufmann, G. W. 1971. Behavior and ecology of the sora, *Porzana carolina*, and Virginia rail, *Rallus limicola*. Ph.D. Thesis, University of Minnesota.

Storm, G. L. 1972. Population dynamics of red foxes in north central United States. Ph.D. Thesis, University of Minnesota.

Swain, P. C. 1972. An analysis of morphological differences among oaks in selected Minnesota stands of the *Quercus borealis* - *Q. ellipsoidalis* complex. M.S. Thesis, University of Minnesota.

Thorkelson, J. 1972. Design and testing of a heat transfer model of a raccoon (*Procyon lotor*) in a closed tree den. Ph.D. Thesis, University of Minnesota.

Archibald, H. L. 1973. Spring drumming activity and space use of ruffed grouse. Ph.D. Thesis, University of Minnesota.

Barrett, J. 1973. Breeding behavior of captive mallards. M.S. Thesis, University of Minnesota.

Jones, J. A. 1973. Ecology of the mudminnow, *Umbra limi*, in Fish Lake (Anoka County), Minnesota. Ph.D. Thesis, Iowa State University.

Montgomery, G. G. 1973. Communication in red fox dyads: a computer simulation study. Ph.D. Thesis, University of Minnesota.

Nicholls, T. H. 1973. Ecology of barred owls as determined by an automatic radio-tracking system. Ph.D. Thesis, University of Minnesota.

Sanford, R. L. 1973. On the accuracy and optimization of tracking systems. Ph.D. Thesis, University of Minnesota.

Axelrod, A. N. 1974. The effects of varying frequencies of controlled burning on American hazel at the Cedar Creek Natural History Area. M.S. Thesis, University of Minnesota.

Maxson, S. J. 1974. Activity, home range and habitat usage of female ruffed grouse during the egg-laying, incubation, and early brood periods as determined by radio-telemetry. M.S. Thesis, University of Minnesota.

Stolen, P. D. 1974. Fall and winter movements and activity of muskrats in east-central Minnesota. M.S. Thesis, University of Minnesota.

Cliff, J. 1976. Small bird populations in relation to prescribed burning at Cedar Creek Natural History Area, Minnesota. M.S. Thesis, University of Minnesota.

Lampe, R. P. 1976. Aspects of the predatory strategy of the North American badger, Taxidea taxus. Ph.D. Thesis, University of Minnesota.

Bland, M. E. 1977. Daily and seasonal activity patterns in the eastern gray squirrel. Ph.D. Thesis, University of Minnesota.

Gull, J. 1977. Movement and dispersal patterns of immature gray squirrels (Sciurus carolinensis) in east-central Minnesota. M.S. Thesis, University of Minnesota.

Connolly, M. 1979. Biology rhythms and time patterns in the behavior, ecology and blood pressure of rodents. M.S. Thesis, University of Minnesota.

Fuller, M. R. 1979. Spatiotemporal ecology of four sympatric raptor species. Ph.D. Thesis, University of Minnesota.

Haarstad, J. 1980. Temporal organization in dragonfly communities. M.S. Thesis, University of Minnesota.

McKone, M. 1980. The effect of nutrients on competition among old field plants. M.S. Thesis, University of Minnesota.

Ribic. C. A. 1980. Fall movements and activity patters of sea otters (Enhydra lutris) in California, M.S. Thesis, University of Minnesota.

Zinnel, K. C. 1980. Behavior of walleye pike in channels as monitored by a micro-computer utilizing radio telemetry. M.S. Thesis, University of Minnesota.