LTER III.

FIRE, GRAZING AND CLIMATIC INTERACTIONS IN TALLGRASS PRAIRIE

--------------------LTER Researchers----------------------

Investigator	Department	Subject Area
John Briggs, Ph.D.	Biology	GIS, Data Management
Melissa Brown, B.A.	Biology	Field Coordinator
Scott Collins[1], Ph.D.	Botany (Univ. Oklahoma)	Plant Community Ecology
David Gibson[2], Ph.D.	Biology (Univ. West Florida)	Plant Community Ecology
Edward Evans[2], Ph.D.	Biology (Utah State Univ.)	Insect Ecology
David Hartnett, Ph.D.	Biology	Plant Population Ecology
Geoff Henebry, Ph.D.	Biology	Modeling
Barbara Hetrick, Ph.D.	Plant Pathology	Mycorrhizae
Donald Kaufman, Ph.D.	Biology	Mammalian Ecology
Cornell Kinderknecht, B.S.	Biology	Network and Data Management
Alan Knapp, Ph.D.	Biology	Plant Physiological Ecology
James Koelliker, Ph.D.	Civil Engineering	Hydrology
Chuck Martin, Ph.D.	Geography	Geomorphology
G.L. Macpherson, Ph.D.	Geology (Univ. Kansas)	Inorganic Geochemistry
Duane Nellis, Ph.D.	Geography	Remote Sensing/GIS
Jack Oviatt, Ph.D.	Geology	Geomorphology
Rosemary Ramundo, B.S.	Biology	Lab Coordinator
Charles Rice, Ph.D.	Agronomy	Soil Microbial Ecology
A. Paul Schwab, Ph.D.	Agronomy	Soil Chemistry
Tim Seastedt, Ph.D.	Biology	Ecosystem Studies
Cathy Tate, Ph.D.	Biology	Stream Ecology
Timothy Todd, M.S.	Plant Pathology	Nematology
John Tracy, Ph.D.	Civil Engineering	Hydrologic Modeling
John Zimmerman, Ph.D.	Biology	Avian Ecology

1. Subcontractor
2. Former full-time LTER researchers with on-going projects

A SATELLITE VIEW OF THE 1987 AND 1988 GROWING SEASONS ON KONZA PRAIRIE

This series of false color composites of SPOT HRV (3,2,1) illustrates how canopy reflectance on Konza Prairie changes during the growing season, and how these data can be used to elucidate ecological processes. Areas of dense, live vegetation appear bright red; note the dendritic projections of the riparian forests. Recently burned watersheds in May appear black while watersheds burned the previous year appear dark pink. Grazing effects on non-Konza land are clearly visible as a lighter strip along the left side of each image. Production on burned areas in 1987 exceeded that of unburned areas, while this pattern was reversed in 1988 (Fig. 12). Each pixel of an image represents a single value of canopy brightness in three wavelengths of a 20 x 20 m area. The digital form of the data permits transect sampling across individual watersheds to reveal topoedaphic influences on vegetation. Aggregate values from entire watersheds can measure treatment (burning and/or grazing) effects. We are developing procedures to correct these data radiometrically so that time series analyses and model calibration/validation are possible.

PROJECT SUMMARY

A multidisciplinary study of fire, grazing and fire-grazing interactions on population, community and ecosystem properties will be continued on Konza Prairie, a native tallgrass prairie site in northeastern Kansas. The proposed research builds and expands upon a ten-year study of fire frequency effects on tallgrass prairie. Previous and proposed LTER efforts will continue to provide long-term data and baseline studies such as those that spawned a series of intensive short-term experiments and manipulations supported by NSF, NASA, USGS and state funds. Results from these previous studies have been incorporated into current LTER measurements and questions. Our goal of the proposed research is to understand how grazing influences biotic and ecosystem processes and patterns imposed by fire frequency over the landscape mosaic, all of which are subjected to a variable (and possibly directional) climate regime. A new, landscape-level study linking surface and ground water chemistry will interface with ongoing measurements to provide a landscape emphasis to ecological research. Our new focus involves topoedaphic effects and landscape interactions influencing ecological phenomena; specifically, the relationship between geomorphic patterns and ecological constraints (fire and/or grazing) from the perspective of the individual organism to the watershed level. These efforts are necessary if ecologists are to integrate their research to scales where biotic processes may adequately be incorporated with climate models.

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Figure A. An annually-burned watershed is torched in mid April.

Results from Prior NSF Support (LTER grant BSR-8514327)

Mechanistic interpretations of the role of fire in the ecosystem dynamics of tallgrass prairie were essentially unknown and unstudied at the initiation of the Konza LTER. The 1986-1990 Konza Prairie efforts included an experimental emphasis that focused on the effects of fire on population, community and ecosystem processes of tallgrass prairie. To date, we have published or have in press over 100 peer-reviewed research articles and book chapters based largely on this five-year effort (1986 to date: see Appendix A). While most of these publications dealt with specific research projects, several syntheses of research have been presented (Knapp and Seastedt 1986, Seastedt et al. 1988a, Collins and Gibson 1990, Kaufman et al. 1990, Seastedt and Ramundo 1990, Tate in press).

A major effort initiated in 1986 was the conversion of the Konza LTER from a "product of the special interests of the individual Konza team members" (NSF Panel Summary, 1985), to an integrated study of factors controlling the grassland system. This effort emphasized belowground processes, hydrology, plant productivity, organic matter dynamics and nitrogen cycling. Brief accounts of the progress in these areas follow this overview; publications cited in the appendix attest to our productivity in these areas.

The CENTURY model (Parton et al. 1987), was modified by Ojima (1987 and unpubl. results) to address fire frequency questions in tallgrass prairie. The model used empirical data from Knapp (1984, 1985), Seastedt (1985, 1988) and Ojima (1987) to demonstrate that a combination of photosynthetic efficiencies of foliage and nitrogen availability to roots could control prairie NPP. Knapp (1985) demonstrated that photosynthetic efficiencies of dominant grasses were strongly influenced by the presence or absence of litter. Ojima et al. (1989, 1990) and Seastedt et al. (submitted) provided evidence that nitrogen availability to plants was controlled by soil C:N ratios which were, in turn, controlled by previous plant productivity. Thus, fire regime in ungrazed prairie controls both litter amounts and soil C:N ratios which, in turn, control NPP. The model predicts that the constraints imposed by fire have both short and long-term components. Short-term experiments have supported the predictions generated by the model (Seastedt et al. submitted) while LTER experiments are in place to evaluate long-term predictions. Similar hypotheses have been generated for soil organic matter and nitrogen dynamics, and preliminary results of field tests of the model support its predictions (Ojima et al. 1989). The CENTURY model therefore has become a focus for our synthetic efforts involving the ecosystem aspects of the LTER study. A full-time modeler was hired by the Konza Prairie LTER program in 1989 to provide leadership in this work.

Hydrologic studies completed include a model for water yield of the Konza Prairie drainage system, Kings Creek (Bartlett 1988). Four streams draining watersheds with different fire frequencies were gaged beginning in 1986. A simulated rainfall experiment was conducted to study fire effects on infiltration, overland flow and erosion rates (Duell 1990), and an analysis of fire effects on nonsaturated hydraulic conductivity of soils was completed (Klittich 1989). A major analysis of landscape and within-system controls on the temporal patterns and consequences of nitrogen availability in streams was also completed (Tate in press). The completion of a geomorphic map of Konza Prairie (Smith 1990) and the installation of soil lysimeters and ground water wells into various aquifers (a cooperative study with the USGS) has created a new research emphasis on the effects of prairie and agroecosystem management on water quality and quantity. Collectively, these studies enable Konza Prairie researchers to link a hydrologic model with similar efforts focused at vegetation-atmosphere interactions.

Studies of patterns and controls of population and community phenomena were the Konza LTER's initial focus when the project was funded in 1981, and efforts in these areas were not diminished during the

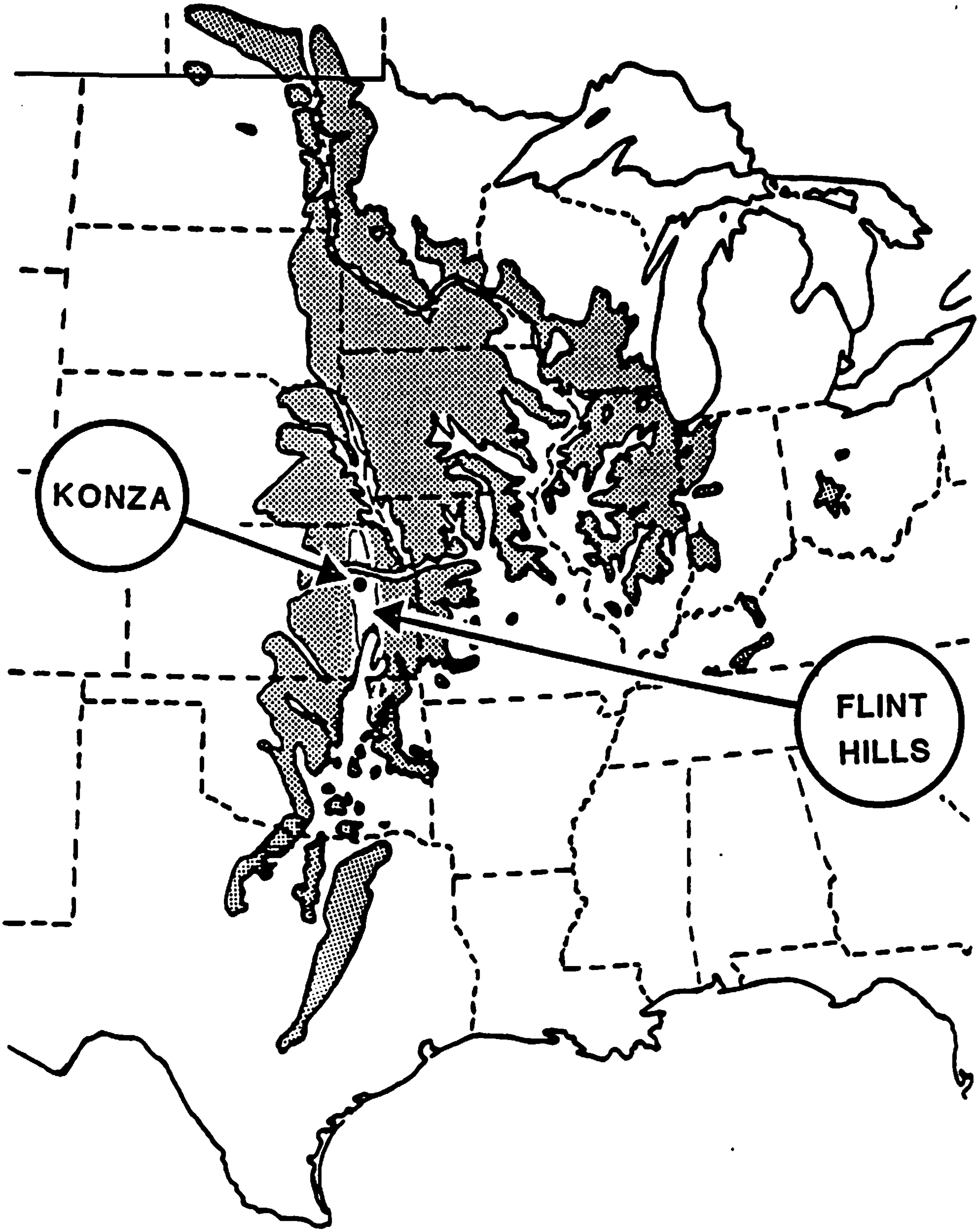


Figure B. Konza Prairie Research Natural Area is located in the Flint Hills region of northeastern Kansas. The tallgrass prairie biome, once the second largest biome in the 49 contiguous states, is now relegated to small remnants. As the Flint Hills were too steep and rocky to plow, this area still contains large expanses of native tallgrass prairie.

1986-1990 interval. Our approach to mechanistic interpretations of fire effects on tallgrass prairie is expressed by Huston et al.'s (1988) central hypothesis of ecosystem organization: spatially explicit interactions of individuals are the basis for correct mechanistic interpretation of ecological phenomena, even if the phenomenon of interest uses some aggregate of these interactions for more simplistic or proximate interpretations.

We have begun to explore the growth, reproductive and demographic response of individual grass and forb species that determine their patterns of abundance in relation to fire, soils and climate. Fire regime strongly influences the reproduction and population responses of the dominant grasses (Hulbert and Wilson 1983, Knapp and Hulbert 1986). The density and biomass of flowering tillers of the dominant C_4 grasses are increased significantly by spring burning, but their response to fire in a given year varies with past fire or climate patterns. For example, maximum enhancement of tiller growth and seed production by late spring fire occurs in mesic years that were preceded by a dry year or a long previous fire-free interval (Hulbert and Wilson 1983, Knapp and Hulbert 1986). In addition, Konza LTER studies offer exciting new science possibilities for interfacing remote sensing and geographic information systems for modeling impacts of bison grazing and longer-term watershed change.

Konza LTER studies have confirmed the importance of fire as a major influence on tallgrass prairie plant communities. The principal gradient of variation in plant community structure is related to time since fire and secondarily to topographic position (Gibson and Hulbert 1987). Communities on uplands are higher in species richness and diversity than lowlands, but the differences between them disappear with annual burning. Studies on the four year fire cycle showed that plant community characteristics such as biomass and life form composition shift in tandem with the fire cycle (Gibson 1988) in a similar manner to that observed for grasshoppers (Evans 1988a,b). Relative abundances of the dominant species, however, are more closely related to soil, topography, and annual climatic variation. Underlying the community response to the fire cycle is a landscape effect, resulting perhaps from prior large scale land-use practices. These landscape effects are important in the interpretation of the mechanisms determining the structure of plant communities on Konza (eg. Gibson and Hetrick 1988, Gibson 1989).

Patterns in plant community structure are a result of individualistic responses of plant species to fire frequency and topography (Gibson and Hulbert 1987). C_4 species and dominant grasses decrease in abundance with time since burning, whereas woody species increase (Bragg and Hulbert 1976). Changes in forb species abundances are variable, differing in both direction and magnitude along the principal fire/topographical gradients. The effects of fire on microclimate (Knapp 1984, Hulbert 1988) and species seed pools (Abrams 1988) have an important effect on the productivity and abundance of the dominant matrix-forming species and hence community structure (Collins and Gibson 1990). As a result, vegetation of infrequently burned prairie is more heterogeneous and species rich than frequently burned sites. Big bluestem remains the most abundant species under all fire and soil conditions, but its abundance is affected by annual climatic variation.

The influence of fire on prairie net primary productivity remains an active area of research. Initial studies focused on comparisons of long-term burned and unburned prairie (Abrams et al. 1986, Briggs et al. 1989). More recently, the effects of fire frequency have been evaluated in conjunction with predictions from the CENTURY model and with nitrogen enrichment experiments. These results demonstrate that the large production enhancement on infrequently burned sites results from the concurrent removal of light and nitrogen limitations to the system. We are now using remote sensing to evaluate whole watershed responses, and to test the extent to which topoedaphic factors control the within-watershed patterns (Briggs and Nellis 1989).

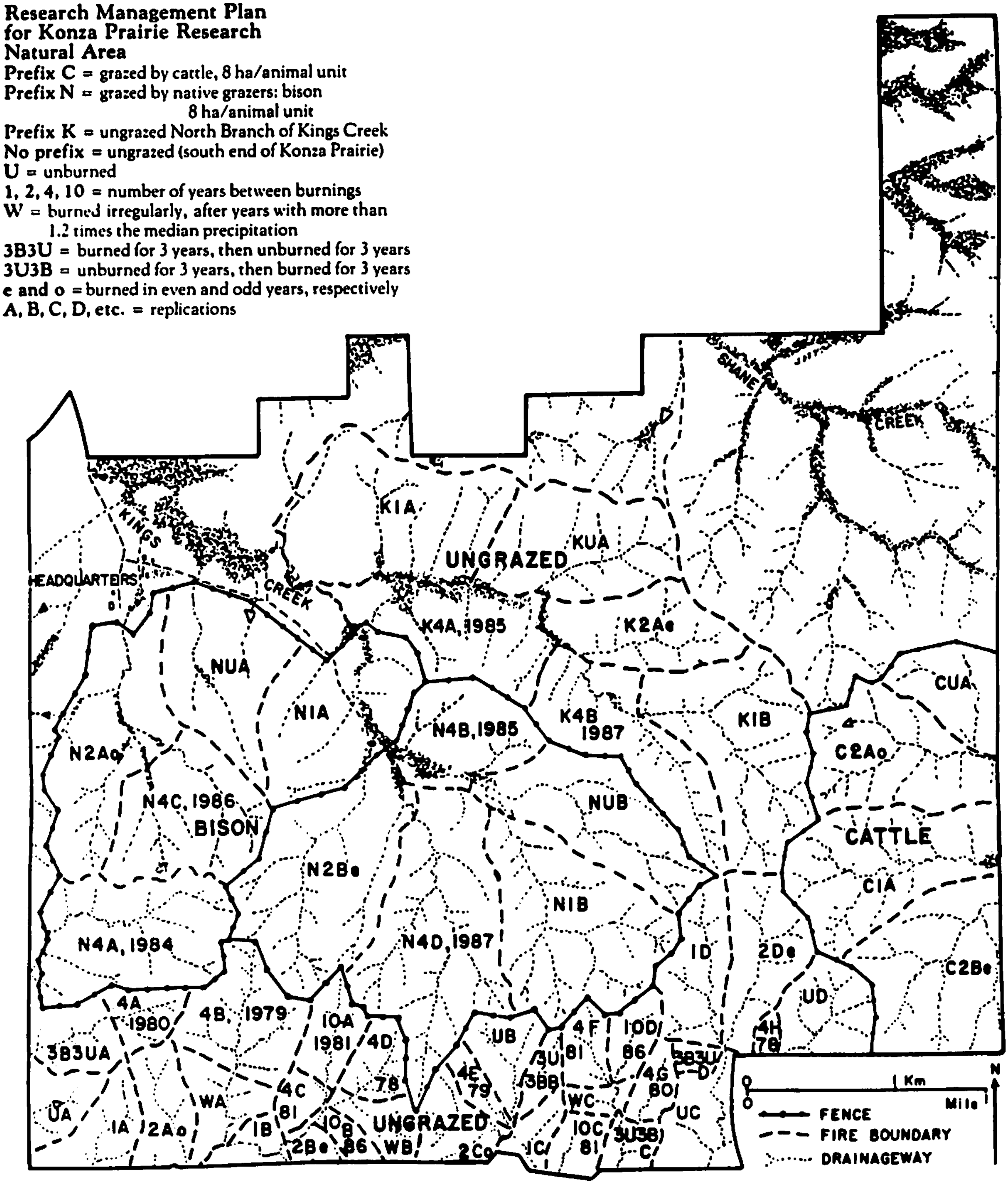


Figure C. A map of Konza Prairie illustrating its management units and watershed treatments. The southern portion of the research site was established in 1970, while the northern portion was added in 1980. Fire records have been maintained for all watersheds. A retrospective analysis of satellite images will allow us to use past years burning treatments to test current questions regarding fire frequency - climate interactions.

Research was expanded in 1986-1990 to include indices of belowground net primary productivity, and the interactions of soil biota with root dynamics. Hetrick et al. (1988a-d) demonstrated that the warm-season (C_4) prairie grasses are highly dependent on mycorrhizal symbiosis while the co-occcuring cool-season (C_3) grasses are not. They suggested that cool-season grasses evolved a more finely branched root system as an alternate strategy for nutrient acquisition since mycorrhizal fungi, like many microbes, are less metabotically active at the low soil temperatures. Thus, plant growth stimulation by spring burning may result from a maximization of potential mutualistic relationship between the fungus and the roots. Laboratory studies using bioassays (Hetrick et al. 1988a-d) and radioactive phosphorus (J. Hetrick 1989) indicated that big bluestem cannot efficiently obtain phosphorus without mycorrhizal roots. In subsequent studies Hetrick et al. (1989) have demonstrated that mycorrhizal dependence can influence the relative competitive abilities of warm- and cool-season grasses. These mycorrhizal effects are not solely nutritional as changes in root architecture and rooting strategy are also elicited by the symbiosis (Hetrick et al. 1988). Loss of symbiosis, as occurs under intensive simulated grazing (Hetrick et al. 1990), therefore, can profoundly affect species composition and productivity.

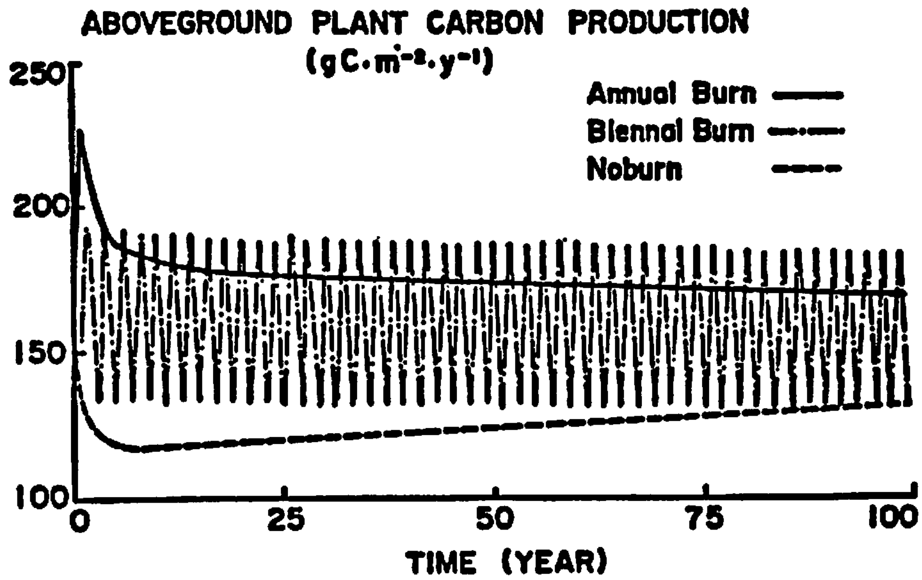
Root and rhizome biomass have been measured on experimental plots since 1986. These data are related to productivity by use of root windows which have been in operation since 1984 (Hayes and Seastedt 1987). Root windows, like mini-rhizotrons, provide somewhat biased estimates of growth and decay; however, relative treatment differences are not affected. Results to date (Ojima 1987, Seastedt et al. 1988a, 1989b) demonstrate both fire and grazing controls on root carbon and nitrogen amounts, with subsequent, measurable effects on soil microbial activity (Rice unpubl.) and soil fauna (Seastedt et al. 1988a, Todd unpubl.).

Studies of consumers demonstrated the complex relationships among fire frequency, topography and plant species composition for population densities and community structure (of both vertebrate and invertebrate groups). Interactions were demonstrated between above-ground (foliage) consumers and root-feeding organisms (Evans and Seastedt in press), including a "grazer maximization response", where intermediate levels of grazing by ungulates results in maximum densities of root-feeding arthropods (Seastedt et al. 1988b).

Studies of small mammals have provided the first detailed information on spatial and temporal variation in their population densities and community structure in tallgrass prairie. Yearly densities of common species varied several-fold during the last nine years. Short-term studies demonstrated that population responses of fire-negative species are due to emigration and not to direct mortality from fire (Clark and Kaufman submitted). Responses are probably related to removal of litter and standing dead vegetation (Kaufman et al. 1989). Distribution of small mammals also varied among topoedaphic sites with the effect of fire and population recovery following fire varying among sites (Kaufman et al. 1988). In similar fashion, Evans (1988a,b) demonstrated that species richness of the grasshopper fauna is correlated with local plant species richness and diversity. Overall, interspecific differences in habitat distribution suggest that individual species are adapted to different micro- to mesohabitats of the prairie mosaic that are created by topoedaphic conditions, fire and grazing.

Bison were added to Konza Prairie in autumn of 1987. Historically, large ungulate grazers were an essential component of North American grasslands, and the re-establishment of this species was an essential component of the original Konza Prairie management plan. Preliminary studies of the impacts of these organisms are underway, and grazing by this species will be a major component of new LTER research.

The 1986-1990 interval also saw our initial attempts to convert our two-dimensional (small-plot or plotless) models and questions into true watershed-level, landscape-related models and questions (e.g., Briggs et al. 1989, Schimel et al. submitted). This effort is necessary if ecological studies are to be useful in vegetation-



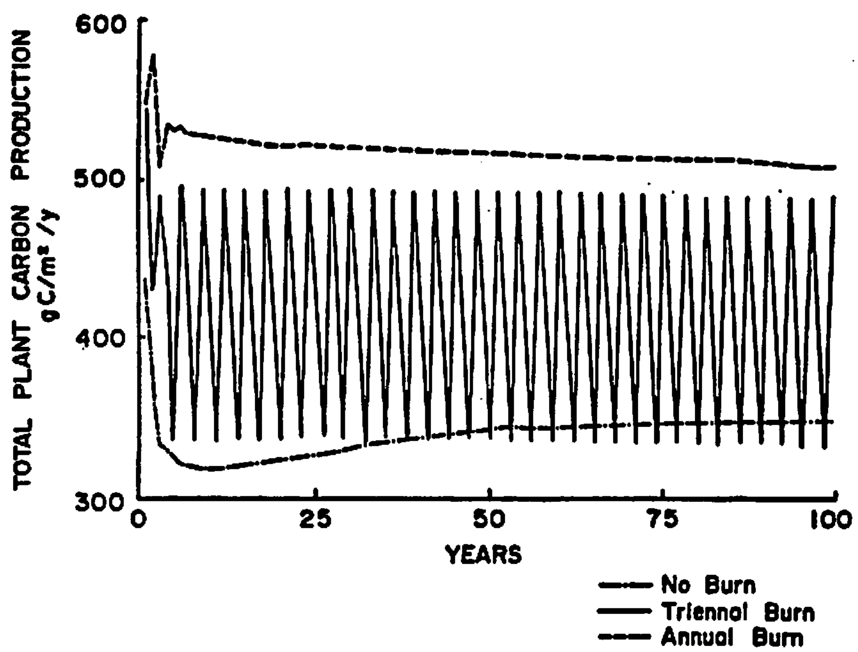
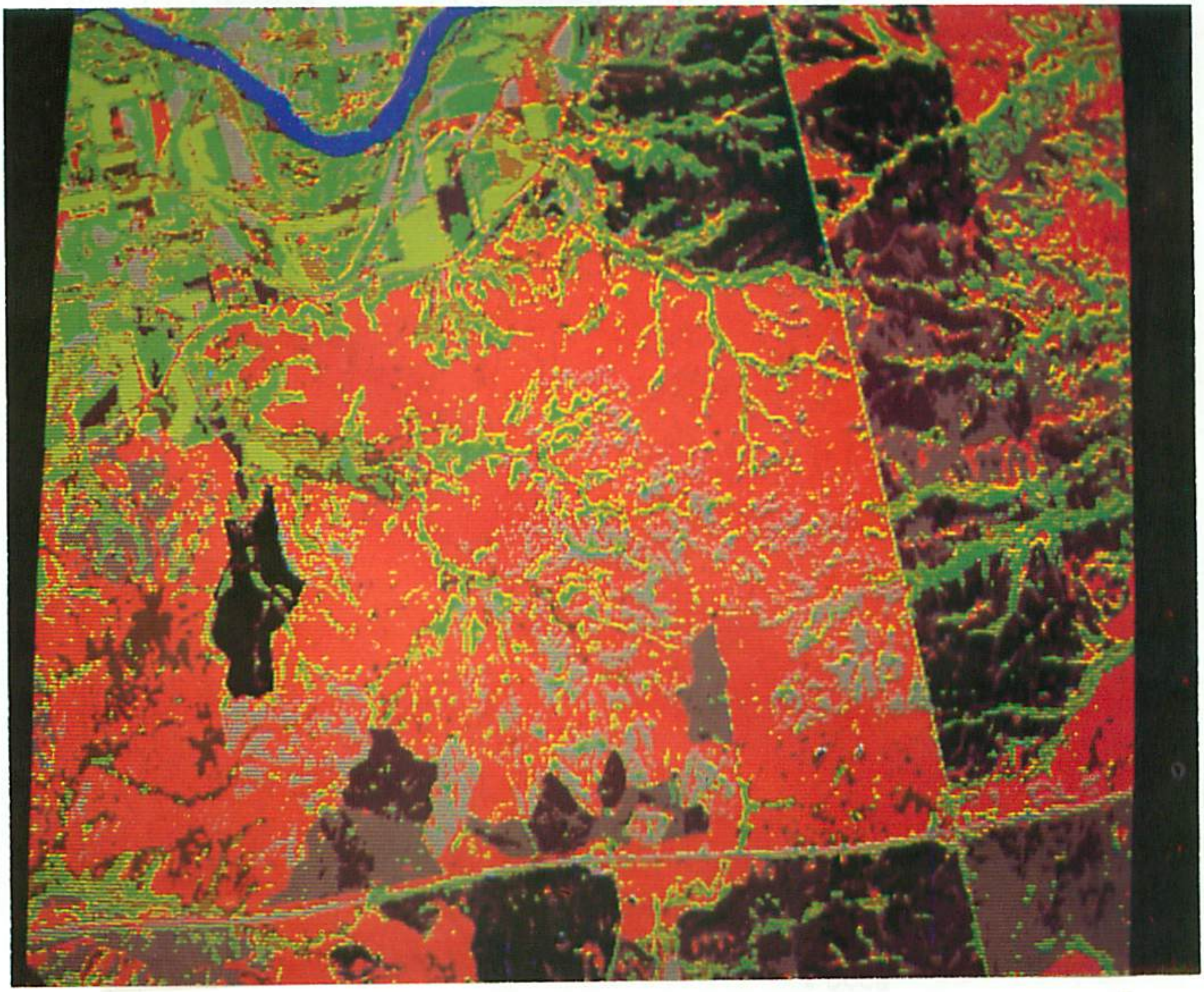
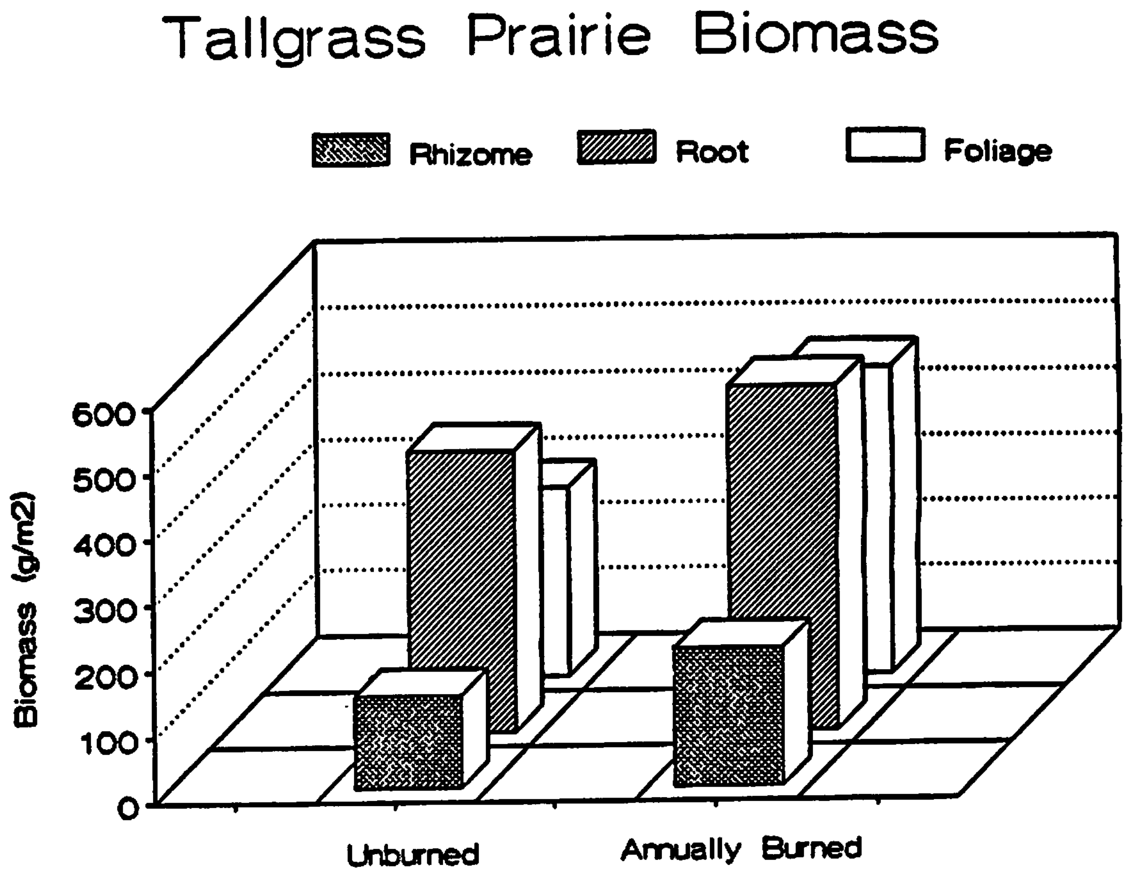


Figure D. Long-term effects of burning in tallgrass prairie have been predicted by the CENTURY model (Ojima 1987, Ojima et al. 1990). Here, the CENTURY models predicts slow deterioration of productivity on annually burned prairie. This deterioration is due to the progressive loss of available nitrogen. The two simulations give different predictions regarding the effect of infrequent burning. The difference in output is caused by the models' treatment of the extent of nitrogen immobilization occurring in the years following fire. Empirical data (data set PAB01) support results from the upper simulation, but also suggest a strong topoedaphic constraint on this effect (e.g. see Figure 12) atmosphere studies of climate. The development of satellite image processing and geographical information system (GIS) procedures became a major thrust of NASA sponsored research on Konza Prairie. These procedures and techniques have some very obvious and useful applications to long-term ecological research, and remote sensing projects of Nellis and Briggs (1987,1988,1989) have begun to demonstrate these possibilities. The entire Konza Prairie site was designed as a fire frequency experiment and these new techniques allow us at long-last to utilize fully this experimental design.

Figures representing specific research findings are included throughout the text. Whenever possible, the specific LTER data-set code(s) from which the figure was constructed and research article(s) in which the results were presented are cited.



A GIS image of Konza Prairie that was generated using an unsupervised classification cluster routine on digital data collected by the SPOT satellite on May 1, 1987 (Nellis and Briggs 1989; Data set code = SAT01).



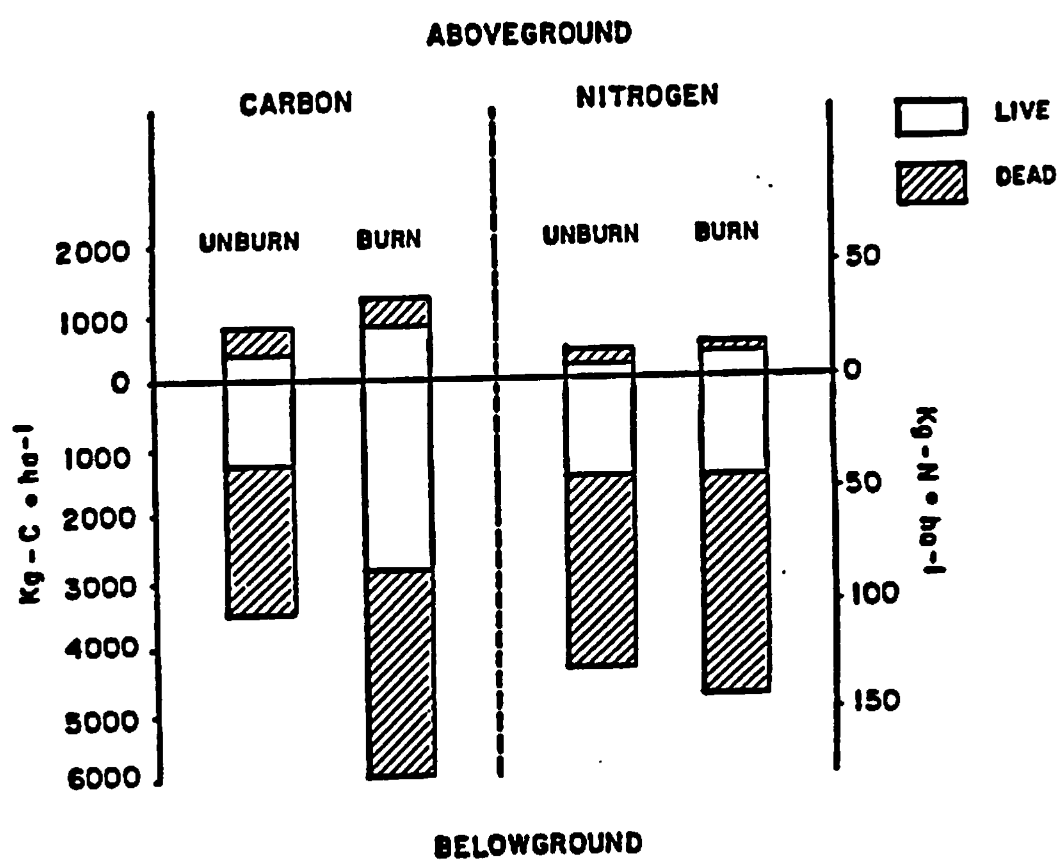


Figure E. Substantial emphasis has been placed on the dynamics of belowground plant productivity. Here, data from Seastedt (1988, top figure) and Ojima (1987, bottom figure) illustrate the dominance of living and dead belowground plant mass to the total standing crop of coarse organic matter. Root windows (data set PRW01) provide a way to link standing crops to seasonal growth and decay patterns.

Section 1. Project Description and Proposed Research

Introduction

The tallgrass prairie was North America's major humid grassland. Once the second largest biome in the contiguous U.S., only small remnants of this "inland sea of grass" remain. The environmental conditions that created the tallgrass prairie also created very fertile soils. As a result, most of the tallgrass prairie has been converted to agroecosystems. The largest surviving tract of prairie is represented by the Flint Hills of Kansas, with about 50,000 km^2 of unplowed native tallgrass vegetation. Konza Prairie Research Natural Area (KPRNA), a 3400 ha tract 10 km south of Manhattan, Kansas, is the largest parcel of tallgrass prairie in North America set aside for ecological research (Figure 1). Konza's development as a research site began in modest fashion in 1970 following purchase by The Nature Conservancy (Hulbert 1973). Now, **Konza Prairie is the most intensively studied grassland on earth.** No other area has experienced the magnitude of research supported by NSF, NASA, USGS and other agencies during the 1986-1990 interval. Our LTER program benefited from the intensive NASA-FIFE research effort operating at Konza Prairie from 1987 through 1989 (Sellers et al. 1988, Strebel et al. 1989). FIFE (First ISLSCP Field Experiment, ISLSCP = International Land Satellite Surface Climatology Project) has given us an appreciation for spatial scales and spatial patterns that, we believe, are relevant and appropriate for LTER questions.

Our tallgrass prairie site has much to offer as a biosphere observatory within the framework of a national or global network (Seastedt and Briggs 1990). Konza Prairie serves as a benchmark for studies of agricultural or grazing land management-water quality relationships (McArthur et al. 1985, Tate in press). The area is a refugium for native tallgrass flora and fauna, and at the same time has become a research site for studying the consequences of exotic species introductions (e.g., James and Seastedt 1986). The combination of NASA and NSF sponsored research has provided new insights into methods for studying vegetation-climate interactions (Sellers et al. 1988, Schimel et al. submitted; Figure 2). These interactions are hypothesized to be the causal links between traditional ecological and climatological interests, and form a logical research emphasis for a national or international network of biosphere preserves (Seastedt and Briggs 1990). Facilitating this interaction is an objective of the 1991-1996 LTER effort.

Figure 1. Photos of Konza Prairie in June (A), April (B) August (C), showing some of complex topography.

Figure B illustrates an interaction of burning and grazing. A fence separates grazed (right) from ungrazed (left) burned prairie. Note that grazers selectively reduce the standing crop of grass such that certain areas do not burn cleanly. Also note the early green-up on the cattle grazed areas, a result of a shift in the abundance of C_3 and C_4 grasses.

Bison were added to a portion of the prairie in late 1987. In photo C, the animals can be seen grazing adjacent to a small permanent exclosure installed to evaluate plant species growth and reproductive responses to grazers. The bison are scheduled to go into LTER experimental areas in 1991.

Research conducted as part of the International Biological Program at other tallgrass sites emphasized effects of cattle on ecosystem dynamics (Risser et al. 1981). While we are interested in effects of large grazers, bison were not established on Konza Prairie until autumn of 1987 and, to date, these animals have not been allowed on LTER intensive study sites. As discussed in the Results of Prior Research section, research during the first ten years of the Konza Prairie LTER program concentrated on fire, the major variable influencing tallgrass prairie. This background research on fire effects, in conjunction with previous research done on grazing and the new, spatially explicit analytical techniques developed as part of the NASA-FIFE program, now allows us to study complex aspects of fire, grazing and climatic interactions.

Development of a Landscape-Level Conceptual Model of Tallgrass Prairie

Our conceptual model of the structure and coupling of tallgrass prairie components is shown in Figure 3. Ecologists tend to filter out or treat as constants those variables not believed to be important to specific questions under study. This filtering exercise involves scaling, an activity implicit in all scientific enquiries (Tansley 1935, Allen and Starr 1982, O'Neill et al. 1986). Our research encompasses a variety of questions within the realms of population, community and ecosystem ecology and attempts to integrate them (e.g., explain community dynamics in terms of population processes; explain system productivity in terms of ecophysiological processes; and explain landscape scale phenomena in terms of spatially explicit patterns of abiotic influences and population responses). This diversity of approaches and interests is one of our strengths. Some of our questions or variables do not directly scale up to units necessary to provide a higher synthesis or integrate ecological information from diverse sites (Seastedt and Briggs 1990). Nonetheless, such comparisons do provide insights into basic ecological processes (Magnuson et al. in press). Moreover, explicit comparisons of population, community and ecosystem phenomena often contribute to a better appreciation of ecological concepts. For example, the evaluation of disturbance effects led us (Evans et al. 1989b) to the conclusion that the disturbance concept is useful only when applied to a specific level of the biological hierarchy (Pickett et al. 1989), i.e., a disturbance to an organism or population is not necessarily measurable at higher levels. Moreover, the same "disturbance" produces potentially very different responses depending upon initial conditions of the system, and other forcing functions such as climatic variables (Figure 4).

Figure 2. An August, 1987, Landsat satellite thermal image (Thematic Mapper, channel 6) of Konza Prairie. Watershed boundaries have been overlayed on the image using an ERDAS software procedure. The influence of watershed treatments on the canopy brightness of this image is evident. Canopies of burned watersheds can be 4 °C cooler than unburned watersheds during this time interval, and grazing can also have both negative and positive effects on canopy temperatures. These results demonstrate that the ecological constraints (here, grazing and fire frequency) can have a large effect on surface climatological variables. These data are part of the LTER image library (SAT01) and are being used to scale up findings from small plot studies (Seastedt and Briggs, 1990).

Ecologists are only now developing methodologies and procedures to study the consequences of spatial patterns on organismic and ecosystem processes. Evidence is accumulating that spatially explicit interactions are the appropriate level for mechanistic interpretations of many ecological phenomena (Urban et al. 1987, Huston et al. 1988). Aggregation of this information using different formulae and approaches produces unique perspectives, all of which are potentially important for specific ecological questions. We therefore advocate this approach to the long-term study of fire and grazing effects on tallgrass prairie, and our proposed studies involve landscape-level, spatially explicit analyses of population, community and ecosystem responses to fire, grazers and climate interactions.

Identification of Important Long-Term Questions

In spite of a rich history of ecological inquiry (c.f. Aldous 1934, McIntosh 1985), important concepts basic to the functioning of tallgrass prairie have been overlooked or unappreciated. For example, John Weaver was the premier prairie ecologist during the period of 1920-1960; his work on belowground aspects of plant ecology will likely never be equalled. Nonetheless, Weaver viewed fire as a destructive force (Weaver 1954, pg 271), and the role of fire as an ecological factor required for the maintenance of tallgrass prairie was not recognized by ecologists until the mid to late 1960s. Why, after 40 years of study, did Weaver not see the importance of fire for arresting forest invasion of prairie? Possible answers include: 1) decades of fire suppression were required for woody species to attain densities to provide an adequate seed source, 2) the droughts of the '30s and '50s suppressed woody expansion even in the absence of fire (Anderson 1982), and/or 3) Weaver's emphasis was on grazed prairie. Fire under moderate to heavily grazed conditions may be a neutral factor. Tests of these hypotheses require a long-term, site specific data base on plant population and community dynamics such as that accumulating on Konza Prairie.

Previous land-use practices (Hamburg and Sanford 1986) and biological legacies of previous communities (Franklin et al. 1987) affect current ecological phenomena. Our site exhibits large-scale patterns in plant species composition not attributable to current management treatments (Gibson 1988, Collins and Glenn 1990). Changes in the physical and chemical properties of soils occur as a result of cumulative changes in the vegetation. The years 1981-1987 (the first 7 years of the Konza LTER program) all had annual precipitation values above the long-term average (Figure 5), and our results from this period were affected by this unusual

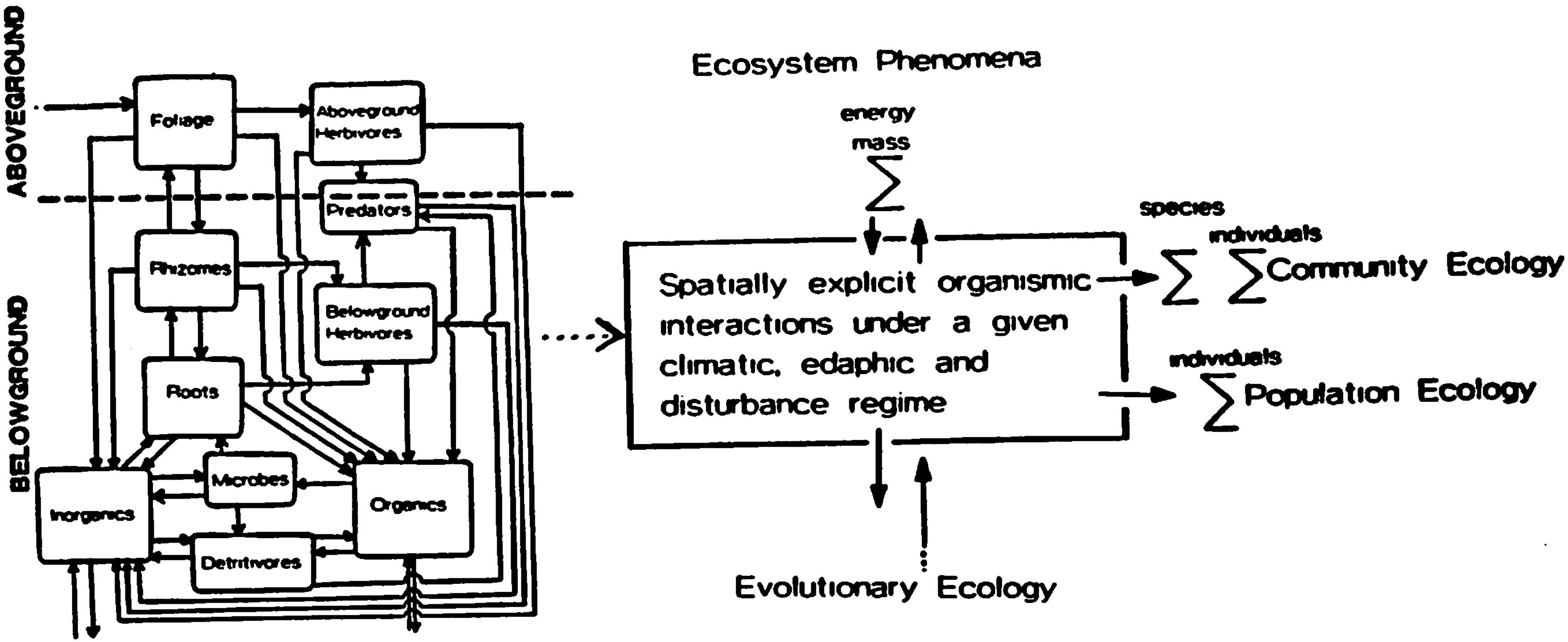


Figure 3. An ecosystem model of tallgrass prairie. The use of different spatial or temporal scales in our LTER studies produces a different perspective. All perspectives, however, begin with spatially explicit biotic-biotic or biotic-abiotic interactions. Aggregation upward provides a holistic perspective of the functioning of the system, while lower-level interactions provide a mechanistic interpretation of higher-level phenomena. Ecologists must remain active at all levels if ecological theory is to concurrently be used in biodiversity and climate-change initiatives.

climatic pattern. Only in 1988 and 1989 were data representative of responses to below-average rainfall. Ironically, our own LTER group initially failed to recognize this potential "wet bias" in our results. Wet years favored plant production in general (and certain species in particular) which in turn increased the C:N ratio of the soil and therefore increased the soil nitrogen immobilization potential. As a result, stream chemistry exhibited directional changes (Tate in press) and the production of the gallery forests (located "downhill" from the prairie) may have been similarly affected by a reduction in available nitrogen (Briggs et al. 1989). The extent to which demographic responses of individual plant and consumer species were influenced by this suite of wet years is not yet known. Only a long-term data base will demonstrate these patterns and relationships. This work becomes particularly relevant given anticipated directional changes in climate. Historical effects or biological legacies will be important in understanding the biotic response to climatic change, and while some effects of drought on tallgrass flora are known (e.g., Weaver et al. 1935, Albertson et al. 1957), we are just beginning to develop predictive models for other system components.

Grazing impacts of cattle on the tallgrass prairie are well documented (Risser et al. 1981), but only now are we proposing to study the fire-native grazer-catena interaction as the central mechanism for maintaining the structural and functional attributes of the tallgrass prairie. Specific hypotheses are presented in subsequent sections. These questions are exciting and relevant to us, and all qualify as legitimate LTER questions using the criteria of Franklin (1989). However, some of these questions are focused at a particular hierarchical level and involve units or processes that do not directly produce quantitative information at higher or lower levels of resolution. Because of the different scales, the list of questions does not (and should not) integrate into a single, unified whole (Seastedt and Briggs 1990). Collectively, however, our research addresses the following areas that we feel are critical to the advancement of ecology as a predictive science:

STUDIES RELATED TO GLOBAL QUESTIONS

1. **ECOSYSTEM-CLIMATE RELATIONSHIPS.** How do fire, grazing and fire-grazing interactions influence processes and patterns in tallgrass prairie and the response of the prairie to climate forcing functions? What will be the ecological response (biophysical, ecosystem, community, population) to climate change given current land use? How will modification of experimental treatments (representing Flint Hills land use patterns) influence the persistence and characteristics of the system? How much control

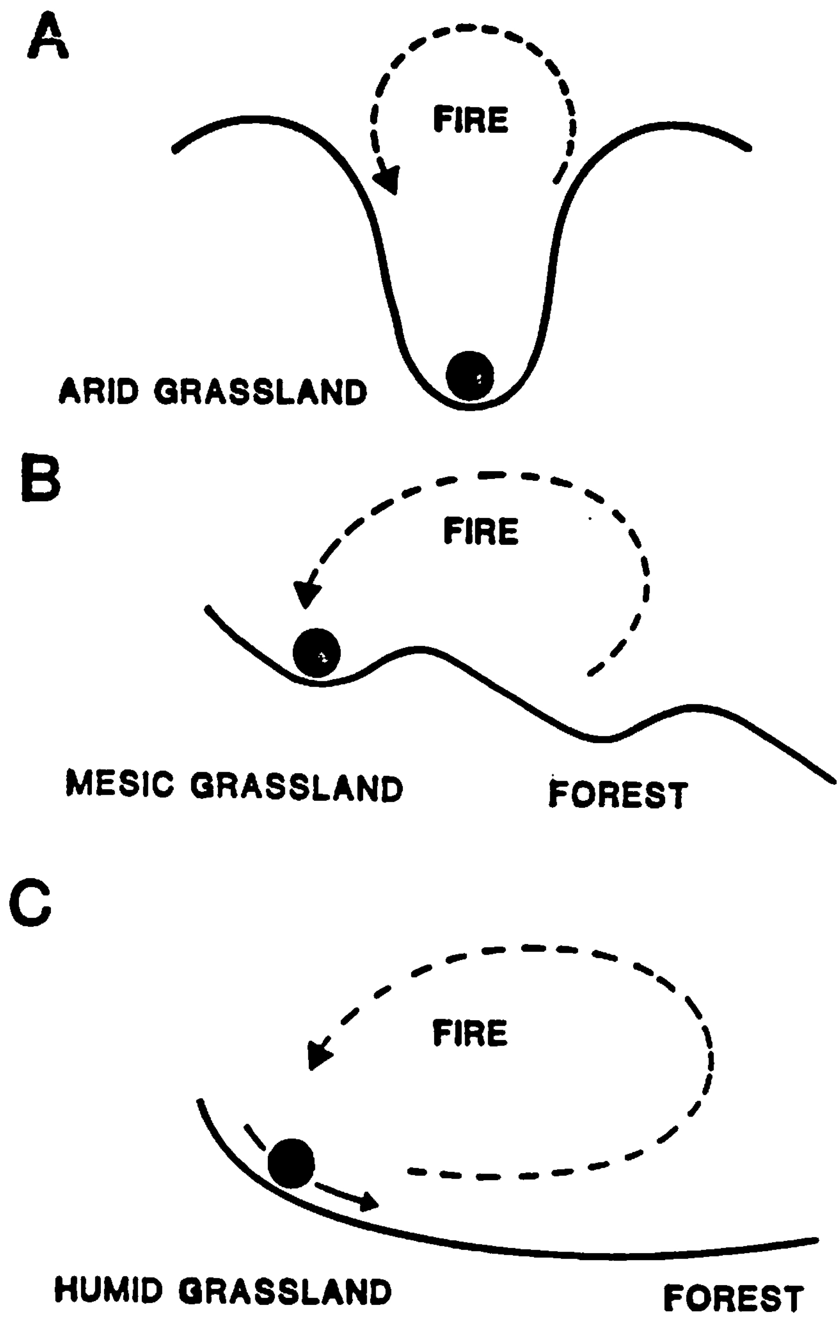


Figure 4. Fire produces different responses depending upon the initial conditions and climatic regime of the system. A system with one strong equilibrium state (A) remains in that state regardless of fire. Under multi-steady state conditions, such as might occur in a mixed grassland (B), fire will return the system to a single state. Under moist conditions (C) fire is required to maintain the system as a grassland. Note that climatic variation may alter the system such that the consequences of the absence of fire could vary (i.e., the system represented by C could be shifted to the one shown in B).

does the biota have on microsite and local climate, and how might these controls be modified by fire and grazing intensities or frequencies? Can patterns observed for the tallgrass prairie be extrapolated to other LTER sites?

Ecology has traditionally focused at the organism to ecosystem hierarchies, but efforts are now underway to predict ecosystem, landscape and regional relationships. We therefore believe that ecologists must be able to scale research questions to the landscape level in order to integrate the importance of their research to the regional scale and to alternative scales where implications for climate change are meaningful (Figure 6). Understanding the landscape controls or constraints on ecological phenomena therefore become a critical LTER question.

2. **THE ECOLOGICAL SIGNIFICANCE OF SPATIAL PATTERNS.** How do position in the landscape and landscape interactions affect ecological phenomena in tallgrass prairie, and what is the importance of the interaction of edaphic and climatic variables on biotic processes? How applicable are the four classes of landform effects (Swanson et al. 1988) in tallgrass prairie? The null hypothesis (spatial patterns do not affect the variable of interest) has been implicitly negated by all Konza researchers (Figure 7). Analysis of the importance of geomorphic patterns and landscape position on ecological processes are underway at scales ranging from plant leaf to watershed levels using remote sensing, GIS and modeling.

Testable hypotheses and corollaries developed from these questions are presented in subsequent sections. We emphasize that we have a synthetic research project that involves all LTER investigators, and combines both of the areas of critical concern listed above. This project is an assessment of how energy, water availability and nutrients control the ecosystem from both bottom-up (parent material, topography) and top-down (effects of herbivores, plant competition) interactions. The focus is multidimensional and covers all core areas of the LTER and all levels of ecological organization illustrated in Figure 3.

Long-Term Climate Patterns In Tallgrass Prairie.

Over the last 98 years, annual precipitation and average maximum temperatures for the Manhattan, KS area (Figure 5) are negatively correlated. This relationship becomes stronger if only growing season precipitation

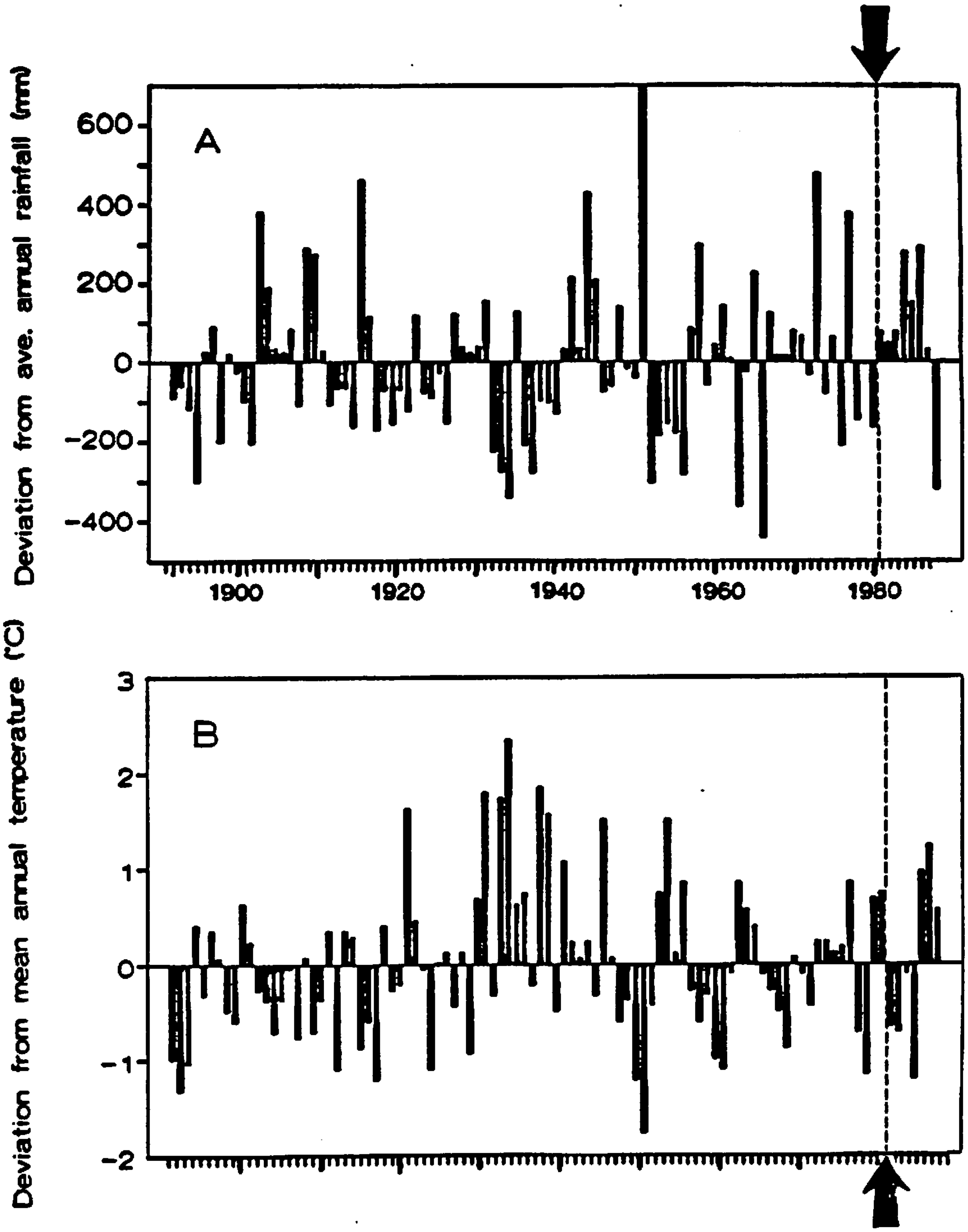


Figure 5. Long-term (1891-1988) deviation from mean precipitation (A) and mean temperatures (B). Note that the deviation in mean temperatures associated with the dust bowl of the '30s was about equal to the differences observed in canopy temperatures of burned and unburned watersheds. These results (data set APT02) show that the first seven years of the LTER study were all wetter than average. We believe this pattern imparted certain characteristics to the biota that affected biogeochemical cycles, particularly nitrogen immobilization/mineralization characteristics.

and temperatures (April through September) are used (Figure 8). The greatest precipitation in our region normally occurs in spring and early summer (Bark 1987). Much of this precipitation is used in evapotranspiration and functions to cool the site. Thus, wetter years, which may also have reduced solar input due to increased cloud cover, tend to be cooler. Figure 8 illustrates the range of temperature-moisture relationships that the vegetation experiences. This analysis suggests why elements of the Southwestern U.S. flora and fauna can be found in tallgrass prairie, but species from dry, cool zones (e.g., the biota of central Wyoming) are absent. Figure 8 can also represent a state-space plot, with year-to-year shifts in the composition of the biota tracking specific temperature-moisture conditions. Weaver (1954 and references therein) documented the expansion of shortgrass species into the tallgrass region during the drought of the 1930s, and we have observed similar changes in abundance during an extended drought in 1988-89.

Although plant populations have exhibited considerable temporal dynamics (Figure 9), it is too early to determine if local extinctions or colonizations are related to fluctuating climatic patterns. It is clear, however, that species "immigrations" into a watershed are unrelated to species richness (Figure 9). In contrast, local "extinctions" are positively correlated with richness. That is, the more species present in a watershed, the more likely some will go extinct. Which species will disappear and whether or not extinction is related to climatic events is an important focus of our proposed research.

Unlike other sites in North America, our climate is at most weakly influenced by the El Nino phenomenon; instead, the Westerlies Modulation is a major influence (B.P. Hayden, U.Va., unpubl. report). Runs of randomness of the climatic data in Figure 5 (Pimentel and Smith 1986) showed no statistically significant trends in precipitation and temperatures. Using a binomial approach, the probability of seven years of continuous, above-average precipitation as occurred in 1981-1987 is 0.008, clearly an unusual event if rainfall is, in fact, independent of previous year's precipitation. The "sine wave" in the long-term temperature record also suggests a non-random pattern (Figure 10). An apparent decline in average annual temperatures occurred from the 1950s to mid 1980s. That trend has now reversed, but, because high year-to-year variability is characteristic of the Kansas continental climate, a warming pattern will have to continue for some time before we can identify warming as a directional trend.

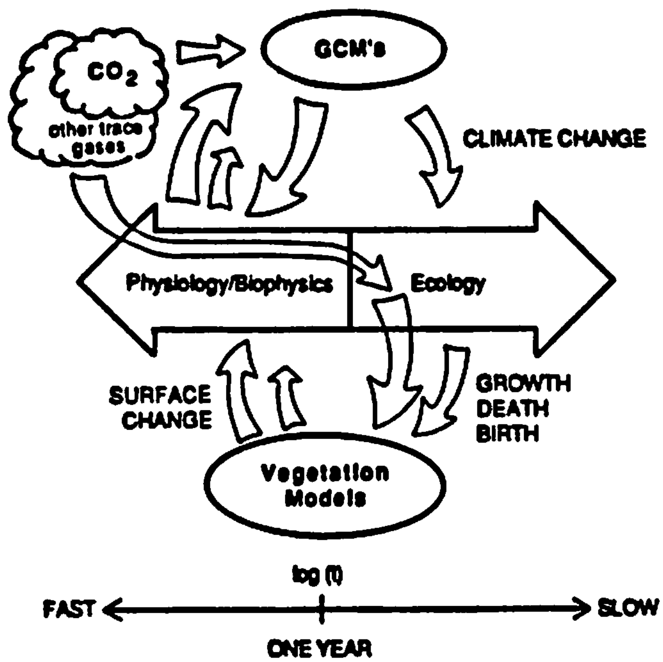


Figure 6. The relationship between ecological studies and atmospheric climate change models (Shugart 1986). Slow processes, the subject of LTER studies, provide the ecological constraints for fine-scaled temporal processes such as biogenic gas flux. The ecological constraints control the short-term response of the system, but are under the long-term effects of atmospheric phenomena. Providing suitable models that adequately depict cause and effect relationships is a major goal of Konza Prairie collaborative efforts. LTER data will be essential in the construction and validation of these models.

LTER Hypotheses and Questions (specific hypotheses are underlined)

I. Controls of Net Primary Productivity (specific hypotheses are underlined)

A. Controls on Ungrazed Prairie

<u>Ungrazed tallgrass prairie exhibits energy, water and nitrogen limitations, with the intensity of the limitation determined by the specific combination of climate, topography and fire frequency</u> (Seastedt et al. submitted; Figures 11,12). The absence of fire results in a reduction in the photosynthetic capacity of litter-shaded foliage (Knapp 1985). However, the absence of fire also results in a build-up of soil nitrate and reduces evaporative losses of rainfall from the upper soil horizons (Seastedt and Hayes 1988). In years or sites where water limitation is unimportant, the combination of greater N availability and improved microclimate of infrequently burned sites results in increased productivity during the year that these sites are burned, as compared to annually burned sites.

<u>Climate can amplify or attenuate the light-nitrogen limitation effect of fire frequency</u>. The prairie will, in general, be much more productive in a wet year following a dry year due to available nitrogen accumulation (Figure 12). Wet years following wet years will have relatively less productivity due to nitrogen immobilization on previous year's root litter. These hypotheses can be evaluated with both whole watershed (remotely sensed canopy brightness measurements; Figure 13), and plot-transect measurements.

B. Net Primary Productivity-Grazing Interactions

Grazing reduces leaf area, which reduces evapotranspiration losses. Thus, grazed areas will have higher subsurface soil moisture levels later in the growing season in years of average rainfall. However, grazing also reduces root biomass and root colonization by mycorrhizal fungi. Once available water has been depleted (as in droughts extending beyond one year), <u>grazed vegetation becomes more sensitive to water stress</u>. Thus, production will be diminished in the second year of drought, and <u>recovery from drought effects will be slower on grazed sites</u> (Albertson et al. 1957).

<u>Soil nutrient availability will improve during drought in grazed sites</u>. First, the lack of normal detritus inputs from roots and rhizomes will reduce the C:N ratio of soil. Reduced microbial immobilization potentials, in conjunction with microbial decomposition processes occurring without concurrent plant uptake of end

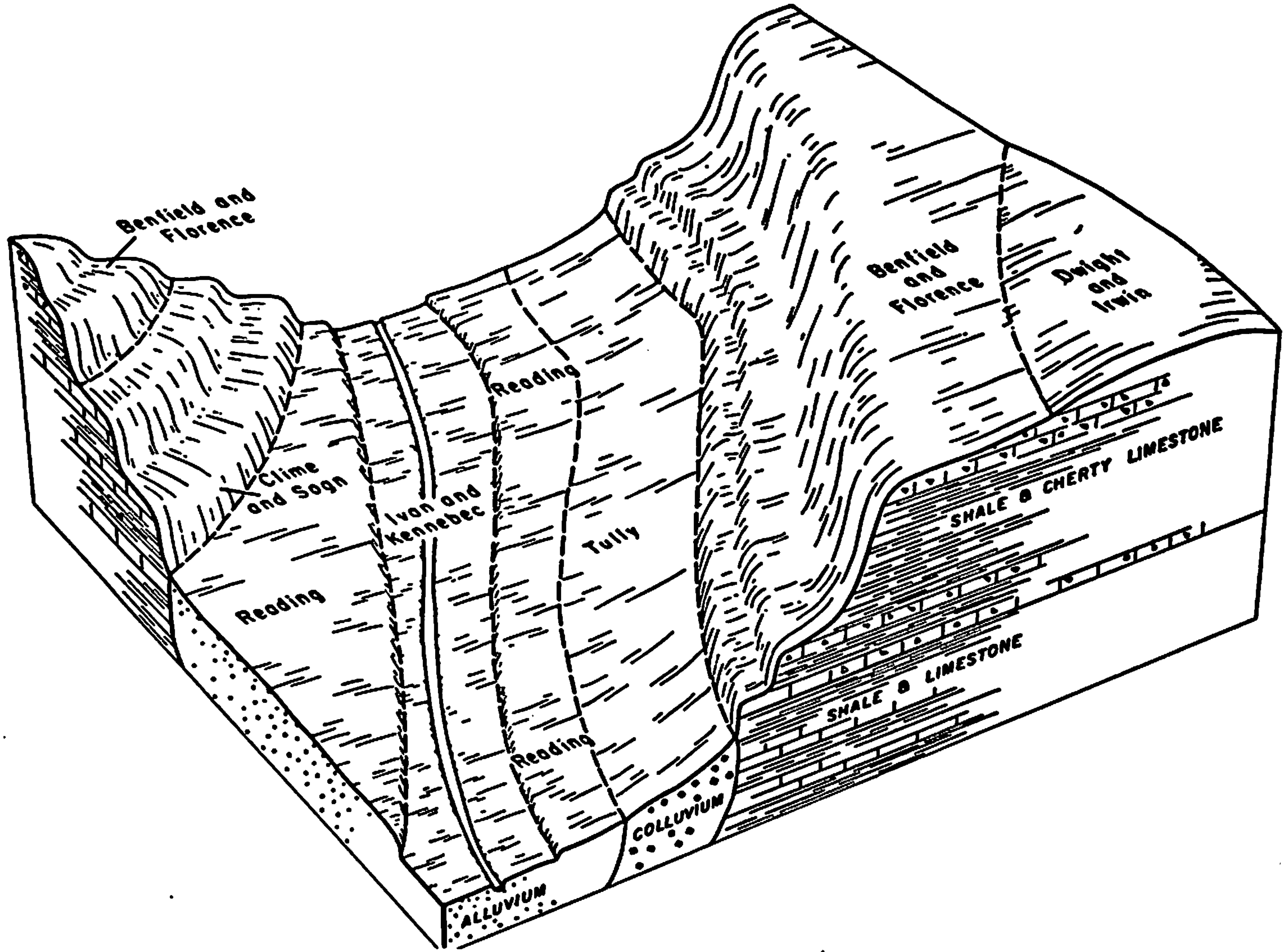


Figure 7. Soils and topoedaphic patterns on Konza Prairie watersheds (Jantz et al. 1975). Watershed units may vary in elevation by about 80 meters and cut through as many as 10 distinct layers of limestone and shale. Limestone layers tend to be permeable to water; shales are not. Water therefore tends to move laterally at limestone-shale interfaces, resulting in seeps and springs where these zones surface. The layers may be tilted, resulting in seeps on only one side of the watershed and possible transport of water across traditional watershed boundaries.

products, will result in an accumulation of inorganic nutrients. Because grazed vegetation will lack the root surface area to exploit higher levels of available nutrients in soils once water is no longer limiting, the production response on grazed prairie will be less than that observed on ungrazed sites.

Grazing negates the effects of fire as an ecological variable, but often substitutes a similar effect. The effects of grazing and burning are scale dependent. For example, analysis of the species composition data from the FIFE sites indicated that sites that were grazed by cattle only or grazed + burned were less similar on a regional scale than burned only or undisturbed treatments. At the local scale, however, the most homogeneous treatments were those that were included in the most heterogeneous groups at the regional scale (Glenn et al. submitted).

The trampling of litter and removal of foliage by grazers mimics some positive aspects of spring burning. Thus, grazed sites tend to experience a late spring environment similar to burned watersheds. However, cattle and bison prefer the warm-season (C_4) grasses, so that heavily grazed sites do not have similar relative abundances of plant species. Light and moderate grazing, like fire, will stimulate foliage productivity in most years. Heavy grazing will negate the potential of a site to carry subsequent fires, and directly affect plant species composition. Heavily grazed sites will most resemble floras from the shortgrass prairie and/or contain elements of the flora of the Southwest.

II. Organic Matter Dynamics

Microbial immobilization of nutrients requires inputs of fixed carbon. Continued annual burning removes aboveground carbon inputs and will eventually result in a decline in soil organic matter (Ojima 1987). However, annual detritus inputs from roots on frequently burned sites exceeds that of unburned sites (Seastedt and Ramundo 1990). Thus, the reduction in soil carbon is slow and significant only on annually burned, ungrazed sites.

Soil organic matter dynamics are an important mediator of net primary production and nutrient availability. Microbial biomass and composition and the active fraction of soil organic matter are dependent upon the inputs of fixed C and N from NPP. Thus the controls on NPP (climate, fire, grazing and topography) will directly and indirectly affect organic matter dynamics. The availability of plant nutrients is controlled by soil

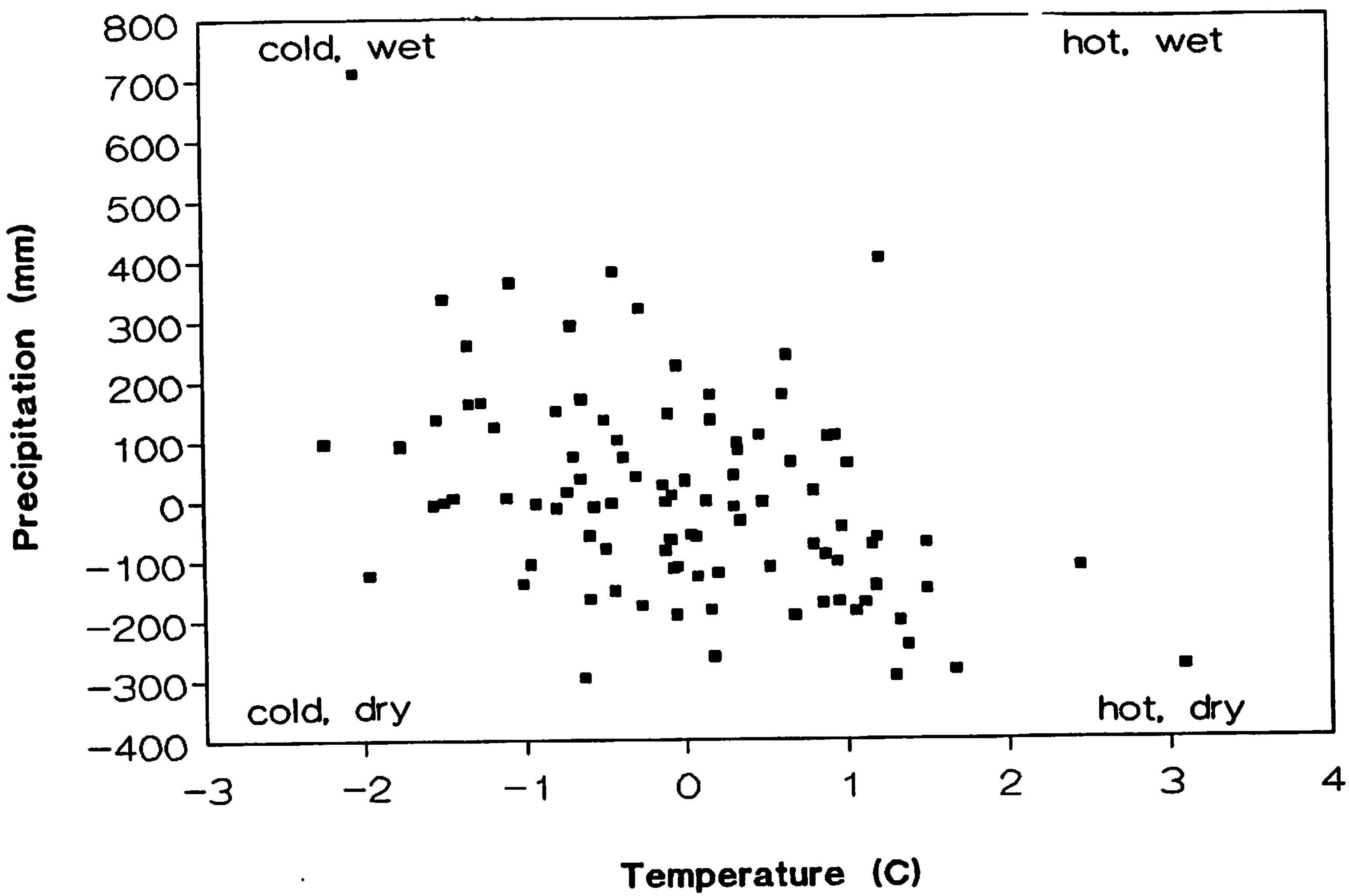


Figure 8. Deviation in growing season (April - Sept.) precipitation plotted against the respective deviation in growing season temperatures, 1891-1988. This pattern represents the 98 year state space growing season environment of the Manhattan, Kansas area, and shows the noisy but significant negative relationship between temperatures and rainfall.

organic matter dynamics. Thus plant nutrient availability is dependent upon decomposition, microbial immobilization of nutrients and turnover of the active fraction of soil organic matter.

Ungrazed tallgrass prairie is limited by some combination of energy, water and nutrients (N and P). These limitations are moderated or intensified by climate, landscape and fire. In the absence of fire in years of adequate rainfall, NPP is limited primarily by energy, although landscape position and climate also control NPP. Fire, however, minimizes the energy limitation. Fire increases the photosynthetic capacity which results in increased C inputs into the ecosystem (Knapp and Seastedt 1986) with little or no change in N input. The increase C input with a greater C:N ratio reduces N availability through N immobilization by plants and microbes (Seastedt and Hayes 1988, Ojima et al. 1990). Thus fire will result in tighter coupling of plant and microbial N dynamics. Long-term annual fires eventually decrease aboveground C input as a result of decreased N availability and soil organic matter levels. Ojima (1987) also measured a decrease in net N mineralization; however, he did not determine if the cause of the decrease was due to increased immobilization or reduced gross mineralization. The increase in C inputs without a concomitant increase in N led to reduced microbial biomass C and N and a change in the composition of the microbial biomass (Ojima 1987). The nature of the change in the microbial community was not studied. We predict that the input of higher C:N ratio plant material will result in an increase in the proportion of fungi compared to bacteria. An increased proportion of fungi would result in slower cycling of N and greater conservation of C.

Grazing in tallgrass prairie reduces the C input and the C:N ratio of the above- and belowground plant biomass, and grazers may negate the fire effect. The decrease in C quantity and quality (C:N ratio) as a result of grazing reduces the immobilization potential of nutrients (Holland and Detling in press). Microbial biomass C and N is also reduced with grazing regardless of fire (Rice unpubl.).

III. Nutrient Dynamics

A. Climate constraints on nutrient availability

Atmospheric nutrient inputs are a function of bulk precipitation (wetfall + dryfall) but contain an anthropogenic component from domestic, industrial and agricultural sources (Figure 14). Outputs are controlled by the interaction of climatic inputs with current and previous states of the system so that a series of wet years results in immobilization of nitrogen within the system. Relatively high export amounts of nitrogen are possible

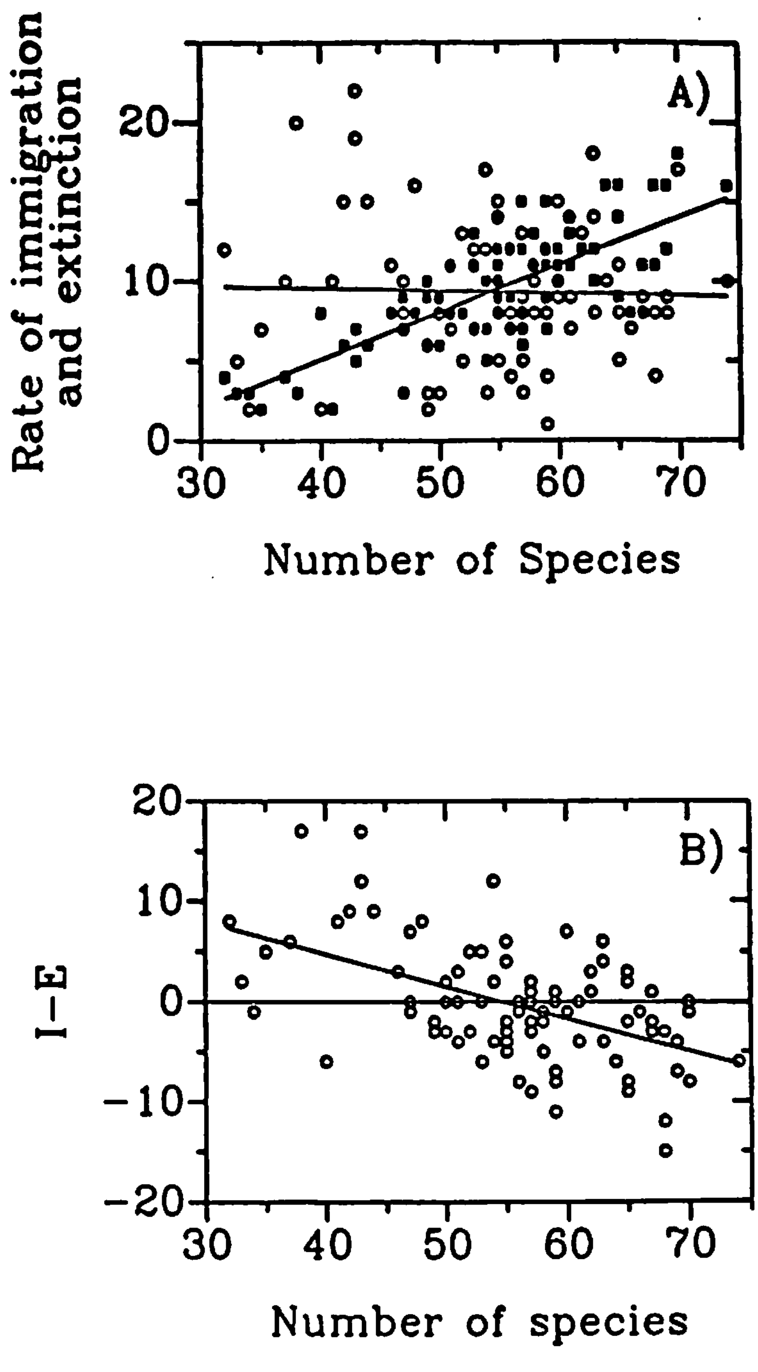


Figure 9. A. Rate of immigration (open circles) and extinction (closed squares) in relation to species richness (R) for each of the 19 species composition sample sites on Konza Prairie over a six year period (1983-1988). The correlation between richness and immigration is nonsignificant, while a strong ($p<.0001$) positive relationship exists between richness and extinctions. B. Relationship between immigration minus extinction (I-E) to species richness across all sample sites ($p<.0001$; from Collins and Glenn submitted).

in a wet year following a dry year. In all cases outputs are less than inputs except during years marked by high-intensity, low-frequency runoff events (floods). Long-term drought will result in an increase in nitrogen concentrations of groundwater and (if present) streamwater.

B. Nutrient dynamics of ungrazed tallgrass prairie.

Nitrogen limitation is a key factor in understanding patterns of net primary productivity with respect to fire frequency in tallgrass prairie. Microbial immobilization of nitrogen on high C:N root detritus results in a reduction in N availability in the first several years following burning. Subsequent reduction in productivity as a consequence of cooler soil temperatures and reduced photosynthetic activity of foliage results in inorganic nitrogen accumulation on unburned prairie.

Nitrogen fixation by free-living microbes such as *Nostoc* and *Azotobacter* is controlled primarily by phosphorus availability. Other sites have reported relatively large populations and large activities of *Nostoc* (DuBois and Kapustka 1983), yet we seldom observe such crusts at Konza. We predict that continued phosphorus enrichment on LTER experimental plots will eventually stimulate the appearance of these N-fixers.

C. Nutrient dynamics of grazed prairie.

Grazing affects nutrient availability in both direct and indirect ways. Central to the plant production response is the change in carbon allocation from roots to shoots. This change in root:shoot ratios reduces the soil N immobilization potential by reducing the inputs of high C:N root and rhizome detritus (Holland and Detling in press). Net mineralization of N is therefore larger, and N uptake by roots may also be increased in years of normal rainfall uptake by plants. Soil and stream water nitrate concentrations will therefore increase in response to grazing intensity due to the reduction in soil N immobilization potential. Moreover, aboveground NPP will be maximized by an intermediate intensity of grazing because of the increase in soil inorganic N availability.

IV. Population Studies

Consumer studies will continue to focus on understanding the successional relationships of plants and animals as affected by fire, climate and grazing. Because we can manipulate both fire and grazing, we are particularly able to study these effects. Fire is generally portrayed as inhibiting plant and animal succession (e.g., Gleason 1913, Sauer 1950), and our research confirms the presence of fire-frequency induced patterns in the

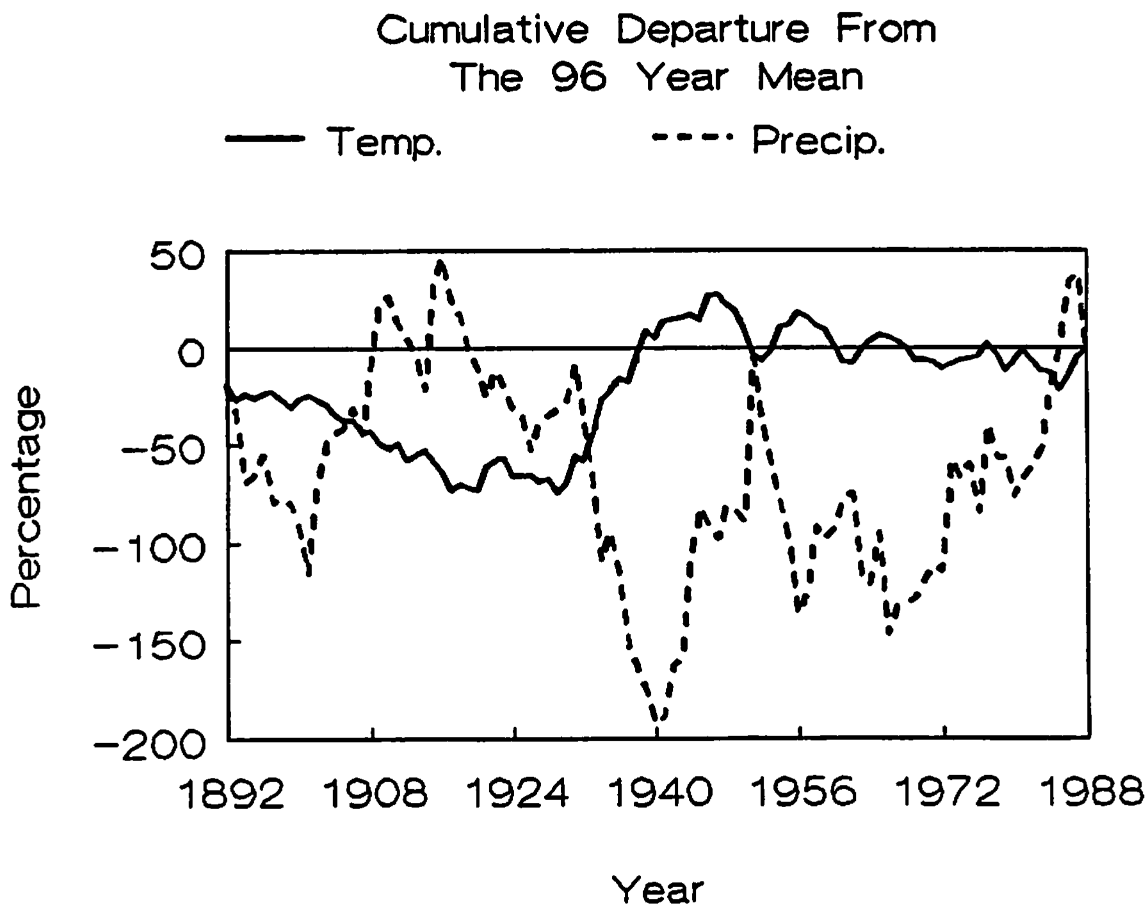


Figure 10. Long-term trends in temperature and precipitation. The most dramatic deviations in temperature and precipitation occurred in the '30s. A statistically significant decline in temperatures occurred from the early '50s to the mid '80s. The drought of 1988-89 ('89 data not shown, but, due to late season rains, will score as a 'normal' year), was obviously minor compared to the '30s.

abundance of various taxa (Zimmerman 1983, Evans 1988a,b, Kaufman et al. 1990). Evidence suggests that grazing will at least interact with if not override the effects of fire on consumers (e.g., Clark et al. 1989). Hence, in the terminology and conceptual framework of Margalef (1969), Connell and Slatyer (1977) and Connell and Sousa (1983), we are concerned with the resistance and adjustment stability of the various floristic and faunal communities in response to fire and grazing pressures. Questions for the proposed research interval therefore will evaluate the magnitude of the responses of bird, small mammal and grasshopper populations, and the extent to which these responses can be linked to common variables. Our initial interests of relating diversity to fire frequencies now are expanded to the more complex relationships between patterns of diversity and abundance of these groups and the complex Konza Prairie landscape. Inclusion of the impacts of landscape features on consumers is becoming increasingly important as evidence now suggests strong geomorphic/topoedaphic effects on spatial distribution and interspecific partitioning of space on tallgrass prairie (Figure 25).

Certain forbs appear to respond more strongly to nutrient additions than do the dominant grasses (Figure 15). Grass to forb ratios may be more nutrient controlled than previously thought. The forb rooting strategy (deep tap roots with relatively few fine roots in the upper zone of maximum nutrient availability; Weaver 1954) would also imply this response. We hypothesize that forbs exhibiting these patterns should benefit by short term drought, which may improve soil nutrient status via reduced immobilization and/or reduced plant competition for nutrients while deep soil water remains available. Thus, although frequent burning may result in declines in many forb populations relative to C_4 grasses, this may be offset by an enhancement of forbs in drought years due to enhanced nutrient availability.

Factors affecting plant species composition of the tallgrass prairie are not only a function of fire frequencies and grazing intensities, but also of interactions of topoedaphic factors (soil fertility and water availability) with these variables. Species composition measurements (and diversity indices) are scale dependent measurements and ecological treatments such as fire and grazing may influence the scaling relationships (i.e. distributions) more than they do the actual abundance of these species. There is a significant positive relationship between distribution and abundance of plant species at Konza (Collins and Glenn 1990). That is, species with high average cover values are more widely distributed than species with smaller average cover

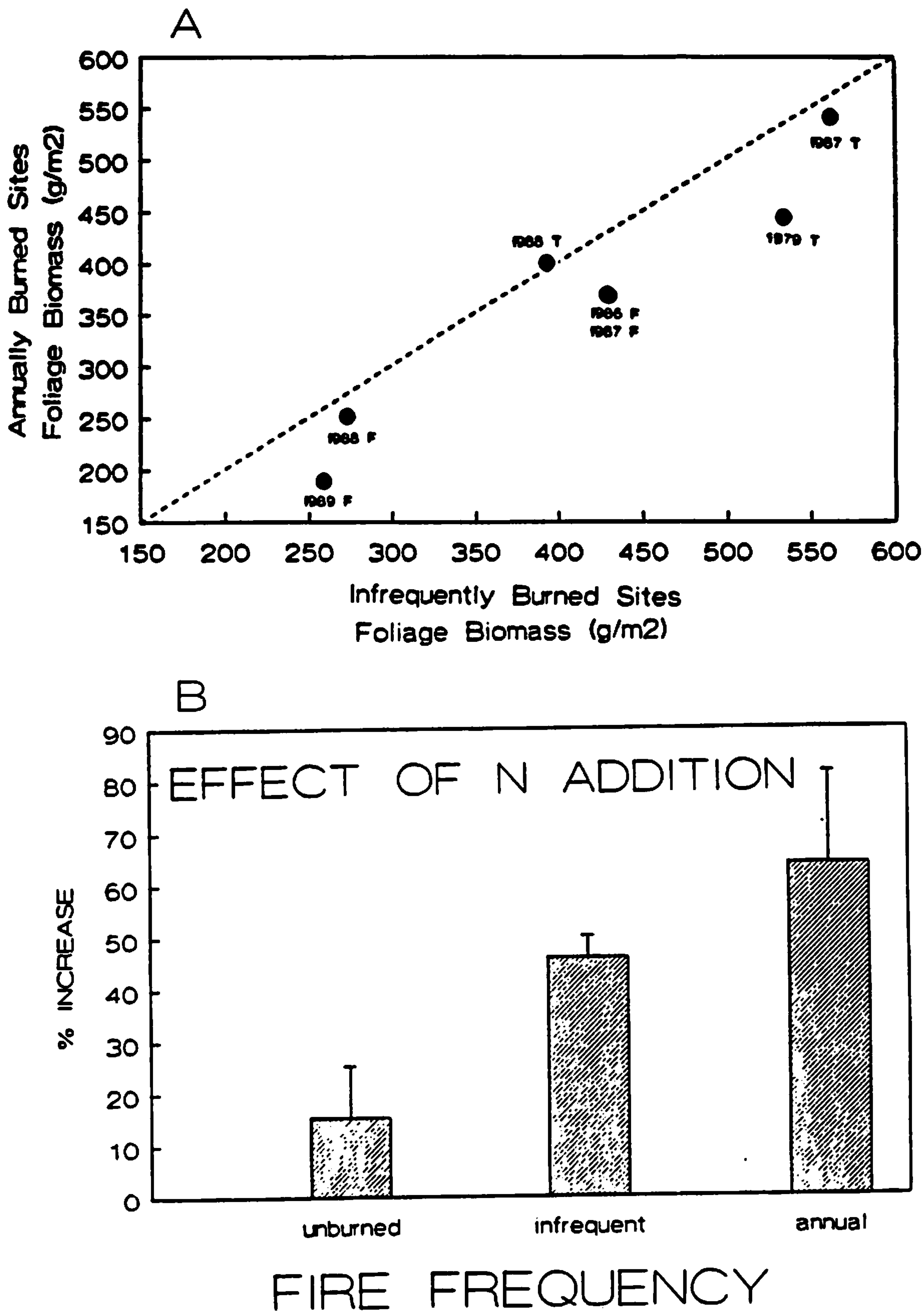


Figure 11. A. Production on infrequently burned sites generally exceeds that of annually burned sites when both sites are simultaneously burned (T = lowland (Tully) soils, F = upland (Florence) soils). B. The sensitivity of plots to nitrogen additions suggests that the observed production patterns are due to fire-induced variation in nitrogen limitation (Seastedt et al. In review, data set PBB02 and additional studies).

(Figure 16). The degree of scatter in this relationship would suggest, however, that numerous scale-related variables, such as fire, nutrients, grazing and productivity, also affect species composition and dynamics.

Multivariate statistical analyses will be used to assess the influence of fire regime, grazing and topoedaphic effects on vegetation patterns. Plant species richness, relative abundance distributions and diversity indices will be calculated to assess the combined influence of these processes on plant species diversity at both the alpha (within local habitat) and beta (variation across environmental gradient) scales. The effects of fire/grazer interactions on species diversity will be a central focus of the analysis and the influence of bison grazing on plant species diversity will be examined in relation to current model predictions (e.g., Milchunas et al. 1988). Current ideas on the role of grazers in grassland community structure suggest that grazers can increase diversity by either increasing habitat heterogeneity or by reducing the competitive dominance of the dominant perennial grasses. These alternative mechanisms should be reflected in effects on different diversity components, the former mechanism should primarily influence species richness, whereas the latter is predicted to strongly influence the evenness component. In addition, species composition data are being used (Collins and Glenn 1990, submitted; Figure 17) to test theoretical predictions concerning spatial and temporal changes in species abundance and distribution as a test of predictions from landscape-level species distribution models (e.g., Levins 1969, Brown 1984) and the core-satellite hypothesis (Hanski 1982).

We hypothesize that the interacting influences of native ungulate grazers and fire over the topographic gradient will result in unique patterns in species relative abundances, distributions and diversity at different spatial scales. We further predict that local abundances and within population diversity of plant species can be explained by predictable effects of fire, grazers and their interactions on plant growth dynamics, sexual and vegetative reproduction, and demography. Differential responses of grass and forb populations to fire and grazing are strongly influenced by effects of these interacting processes on plant species competitive relationships and outcomes, and secondarily by direct effects on plant growth, reproduction and mortality. Due to the relative importance of vegetative reproduction relative to seed production in the maintenance of local tallgrass prairie plant populations, we predict that patterns in plant population abundances will be more closely related to variation in vegetative than seed reproduction. Local soil disturbing activities of bison, however, may

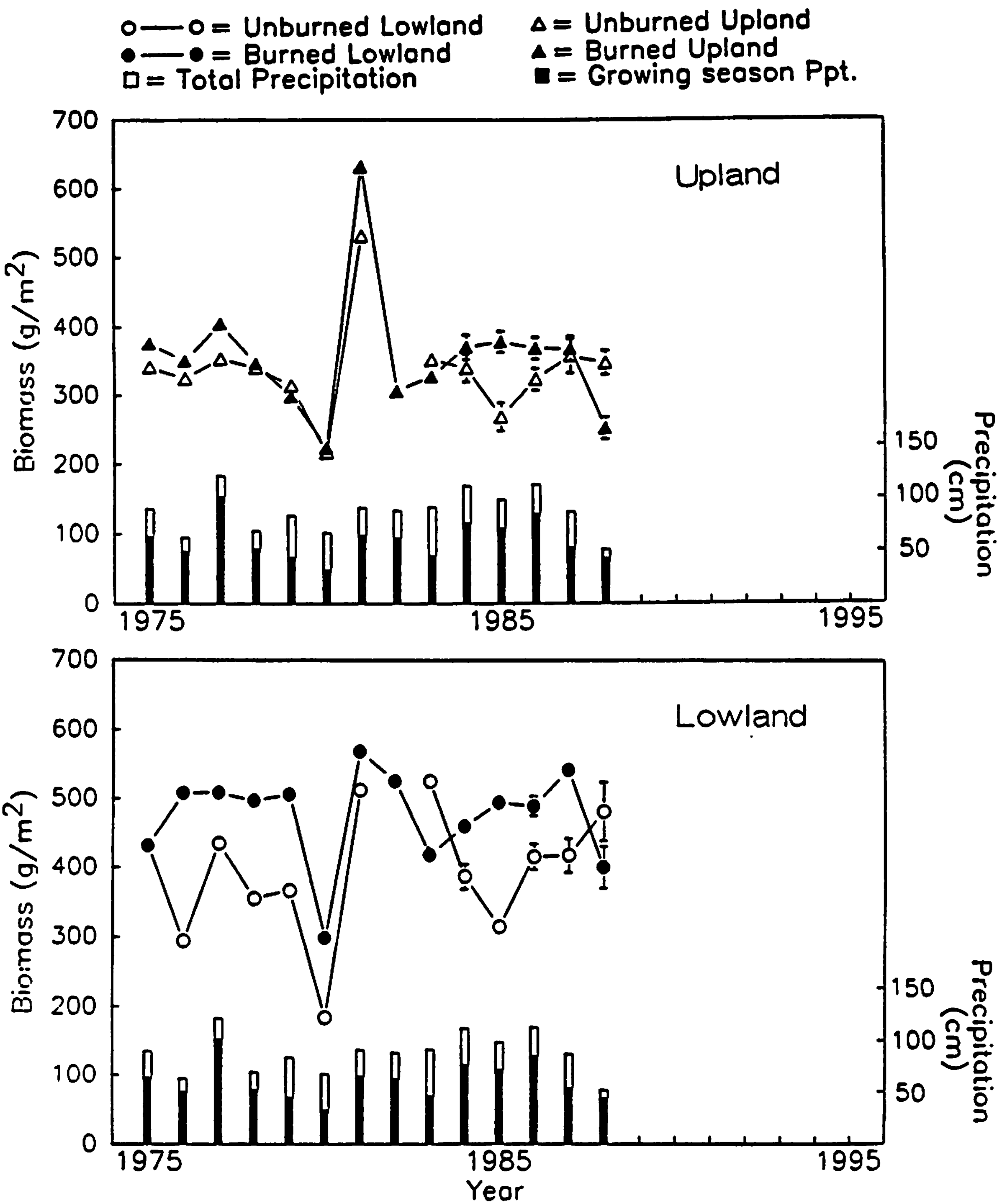


Figure 12. Upland and lowland foliage biomass from annually burned and unburned watersheds (data set PAB01). These results illustrate that the plant response to fire is mediated by topographic position. In general, burning tends to favor biomass production in lowlands, but not in uplands, and the extent to which the system responds to climate (i.e. 1980 drought year followed by 1981 'normal' year) is mediated by landscape position.

shift the balance between these two modes of plant recruitment in local patches and may thereby influence genetic diversity within local populations.

There has been much recent debate concerning the potential interacting roles of grazing and mycorrhizal symbiosis on grassland community structure (Grime et al. 1987, 1988; Bergelson and Crawley 1988) but necessary long-term field studies are lacking. Mycorrhizae have been hypothesized to influence plant community structure by suppression of mycorrhiza-inhibited dominants or enhancing evenness of species abundance through translocation of resources to subordinate species via hyphal conditions. Our preliminary studies on tallgrass prairie plant species, indicate that mycorrhizal abundance influences relative competitive abilities of co-occurring plant species (Hetrick et al. 1989) and that intensive grazing inhibits mycorrhizal symbosis (Hetrick et al. 1990). <u>Grazing by bison will result in different responses among co-occurring plant species and shifts in plant community structure, and these grazing effects may be a result of both *direct* effects on plants and *indirect* effects on mycorrhizal abundances and resulting shifts in competitive relationships between C_3 and C_4 species</u>. Thus, we predict that grazing, fire and topography will all interact to influence plant population and community responses and many of these interactions may be strongly mediated by effects on mycorrhizae and plant competitive relationships.

V. Disturbance Studies.

All of the above questions involve variables that could be considered disturbances. Beyond these, we recognize that rare but intensive events (tornados, hail, floods) can have a strong influence on the long-term dynamics of the system. The measurements we have in place to study questions concerning the other four core areas are mostly sufficient to address the consequences of these rare events. However, we are prepared to mobilize our efforts or resources into the study of the effects of an extreme weather event, a large accidental fire, or a major insect outbreak if the situation warrants such a response.

KONZA PRAIRIE LTER EXPERIMENTAL DESIGN

Konza Prairie is a complex landscape consisting of grazed and ungrazed watersheds burned at various intervals (Figure B). Konza Prairie's founder, the late Dr. L.C. Hulbert, created this design for the specific purpose of studying fire and grazing effects on community and ecosystem processes. The design has many strengths and several weaknesses. If fire frequency (1, 2, 4, 10 and 20 year burns) exhibits strong interactions

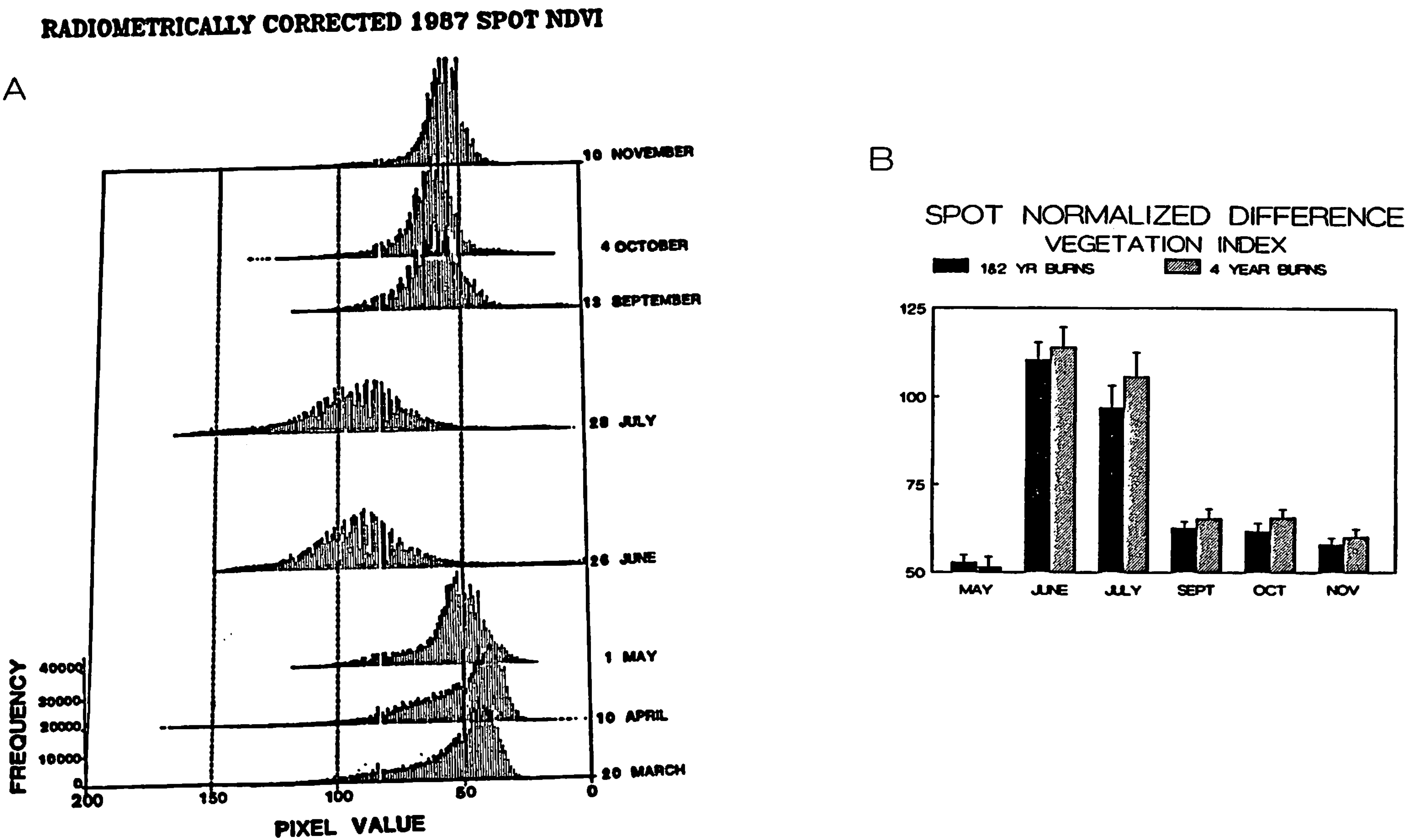
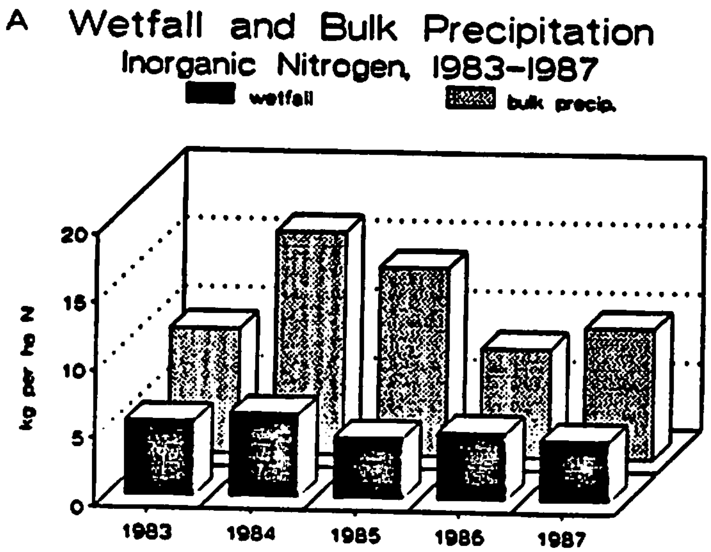


Figure 13. A. SPOT digital data (data set SAT01) provide a 'normalized difference vegetation index' by ratioing several wavelengths of reflected light. This analysis provides an index of productivity (at least on burned watersheds); note that NDVI values are highest and most variable in midsummer. B. Extraction of mean watershed values using ERDAS procedures demonstrates that the NDVI for infrequently burned sites is higher in July than that of more frequently burned sites. These differences appear to correspond directly to production values. This analysis is currently a dissertation project by Benning.

with the time of year of fire (winter, spring, summer, autumn), we would need a 5 x 4 factorial design. Add three levels of grazing (none, moderate, heavy), and we would need 60 specific treatments prior to replication. This design ignores the complex topoedaphic effects created by the limestone and shale layering of the Flint Hills landscape.

Previously, we have let the specific questions select the appropriate experimental design. Our initial LTER questions focused primarily on the effects of late spring burns of varying frequencies on upland and lowland communities, or on the characteristics of 1, 2, 4, or 20 year burns. Not all treatments were replicated for LTER measurements, but replicated short-term intensive studies were used to statistically validate LTER findings (c.f. Kaufman et al. 1990, Seastedt and Ramundo 1990). Our interest in grazing-fire-soil fertility interactions resulted in the establishment of the LTER Belowground Plots in 1986, which do provide long-term, statistically valid comparisons among treatments. Ironically, while such information may be statistically valid, the generality of the results from small plot studies may be questioned because of the potential for "founder effects" on the system response.

Given our central questions involving fire-grazing-landscape interactions, the watershed (catena) remains the best "experimental unit" for most of our research. We believe that grazing intensities (none, moderate, heavy) and topoedaphic effects can be nested within a watershed unit. In the past, we tended to study the extremes of annually burned versus long-term unburned prairie. We will continue certain measurements and observations on those treatments, but substantial information suggests that annual burning or extended periods of fire suppression on any particular site were low probability events, unlikely to persist for extended periods. Thus, expansion of the experimental design to include native grazer treatments and detailed analysis of fire-bison-topoedaphic interactions will focus only on sites burned at 4-year intervals because this regime is most similar to estimated natural or pre-European settlement fire frequencies (Pyne 1982, 1986) and because expansion of sampling to include grazing and topoedaphic effects on *all* burn frequencies is not feasible. Measurements on a watershed burned every four years means that data are actually gathered on sites burned in the year of study, or that have been left unburned for up to three years. By using four watersheds in this effort, at least one watershed will be burned each year; thus, major patterns of fire-grazing-climate interactions will be detected. As before, we will have to use short-term experimentation on replicated



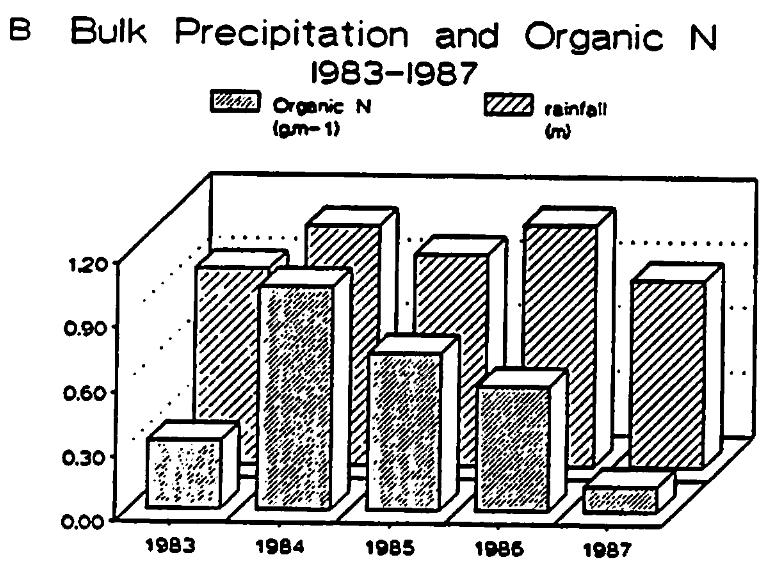


Figure 14. A. Inorganic nitrogen content of wetfall and bulk precipitation. B. Organic nitrogen content of bulk precipitation graphed with precipitation amounts (from data set NPL01 compared with NADP records). Measurements of local and regional contributions to nutrient deposition in precipitation is an ongoing LTER project (Seastedt 1985, Gilliam et al. 1987, Ramundo and Seastedt, submitted).

watersheds or plots to provide statistically robust interpretations of our observations. We also plan to use remote sensing and geographic information systems (GIS) to offer spatial pattern measurements at various scales for the treated watersheds.

Bison are scheduled for introduction to the new intensive study sites in autumn of 1991. All LTER plots are permanently marked, and a cessation of measurements on certain sites does not preclude that measurements can be resumed, either intermittently or more intensively, at a future date. Fire treatments as shown in Figure 8 will be continued on all Konza Prairie watersheds.

NEW AND CONTINUING RESEARCH

In addition to continuation of long-term study of tallgrass prairie patterns in relation to fire/climate, we propose to expand the LTER study significantly to 1) assess the role of fire/bison grazing interactions on populations, community structure, net primary production (NPP), organic matter and nutrient dynamics, 2) conduct a more spatially explicit analysis to patterns of variation across topographical gradients, and 3) analyze patterns at larger spatial scales by linking analysis of population, communities and ecosystem properties with patterns detected at the landscape level using remote sensing and GIS. **Thus, the central question and goal of the proposed research is to understand how grazing influences biotic and ecosystem processes and patterns imposed by fire frequency over the landscape mosaic, all of which are subjected to a variable (and possibly directional) climatic regime.**

Plant Communities (Collins, Hartnett, Gibson)

Plant communities will be studied by obtaining estimates of % cover of all vascular plant species. Vegetation will be sampled in a series of 10 m^2 circular plots on upland and lowland soils in watersheds representing varying fire frequency as done previously. Sample plots within 4-year grazed and ungrazed watersheds will be arranged along an elevational transect rather than the simple upland/lowland stratification employed in past and current Konza LTER studies (Figures 18, 20; see "Konza Prairie Experimental Design" section).

Four permanent transects will be established representing each of four treatment combinations (grazed and burned at 4-y intervals, ungrazed and burned at 4-y intervals, grazed and long-term unburned, and ungrazed and long-term unburned). Transects extending along an elevational gradient will be distributed

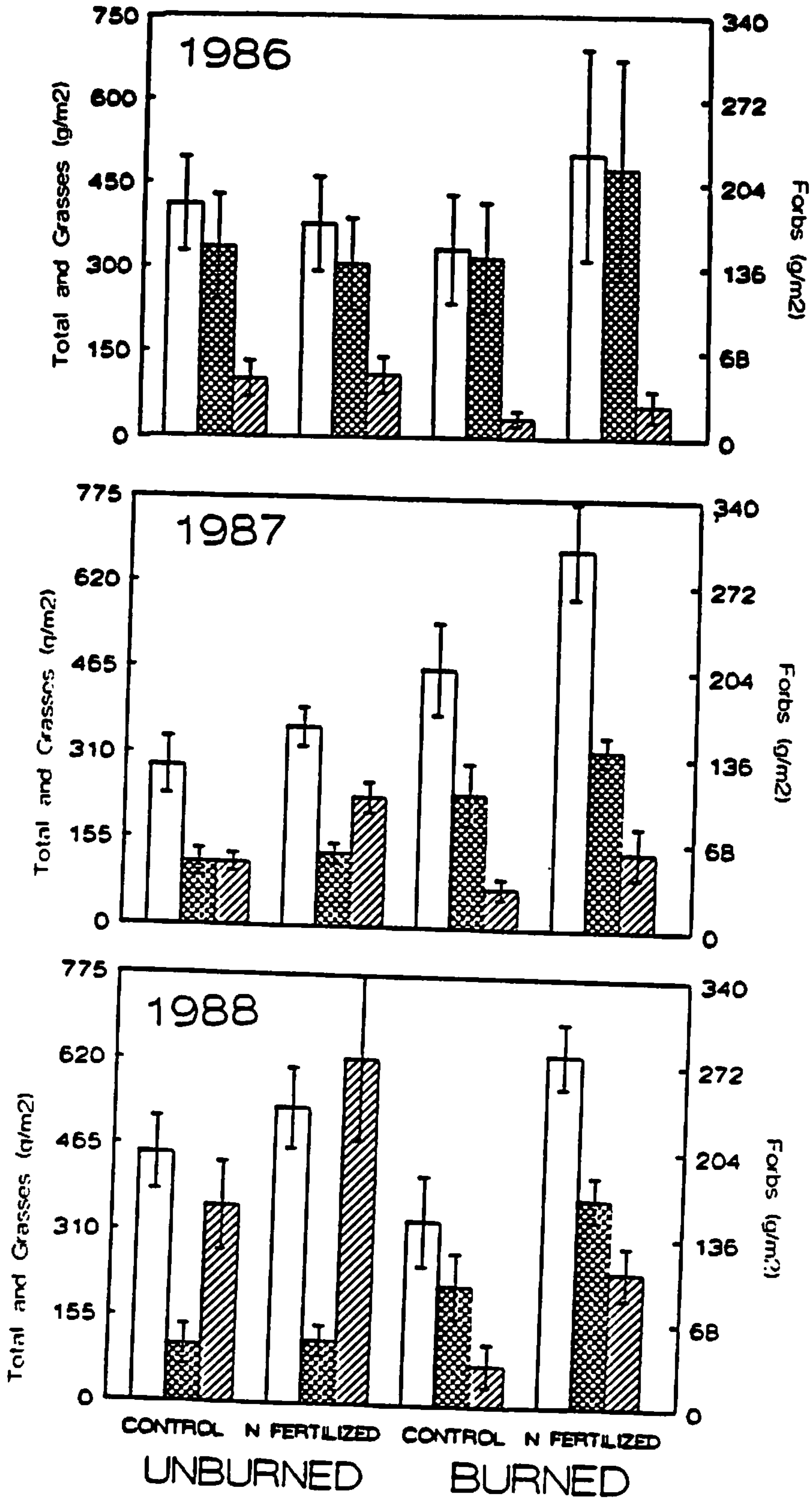


Figure 15. Foliage production response on the Belowground Plots (see Figure 26). Open bars = total biomass, checked bars = grass, lined bars = forbs. Note the biomass scale for forbs has been enhanced relative to grasses and total biomass (data set PBB02).

among replicate watersheds representing each of these 4 treatment combinations (Table 1). Sampling points at a minimum of six positions along the topographical gradient will be established and permanently marked along each transect (Figure 18). Points 1 and 2 will be located on the level uplands (corresponding to the topographical positions of current upland Florence soil sites), 3 and 4 will be located at intermediate slope positions, and 5 and 6 will be located in the lowland areas (corresponding to the topographical position of current lowland Tully soil sites). Sample points will be selected such that the elevation, slope, aspect, soil type and hydrological features (e.g., position relative to a seepage zone) of each of the 6 transect positions will be similar among transects. Mapping of geomorphic, hydrologic and surface/ground water characteristics across topographic gradients in the 4-year burn watersheds (see "Geomorphic Studies" & "Landform Effects on Hydrology and Surface/Ground Water Chemistry" below) will aid in the establishment of comparable transects among watershed. Ten 10 m^2 circular plots will be established and permanently marked at each of the six topographical positions. The percent cover of all vascular plant species in each circular plot will be measured three times during the growing season as done currently. For each species, the maximum cover value attained during the growing season will be retained for analysis.

This proposed experimental design expands our current studies of tallgrass prairie plant communities by assessing the role of native ungulate grazers (bison) and fire-grazer interactions on long-term patterns in plant community structure and by utilizing a landscape approach. This approach encompasses much more of the spatial variation present than existing LTER methods, will allow more spatially explicit analyses of plant community characteristics, and will provide a more complete understanding of the interacting roles of fire, grazing, topography and annual climatic variation in determining long-term patterns of tallgrass prairie community structure. It will also facilitate integration with studies assessing patterns at the landscape level using remote sensing, and GIS allowing the simultaneous study of vegetation patterns at multiple spatial scales.

Several ecological models predict a relationship between productivity and species richness in plant communities (Grime 1973, Connell 1978, Huston 1979, Tilman 1982). Recent research indicates that this relationship holds across but not within plant communities. We recently analyzed productivity-richness relationships at three spatial scales at Konza (Collins and Briggs unpubl.). At the transect level, total standing crop was significantly negatively correlated with richness in all years from 1984-1988 (Figure 19). At the soil

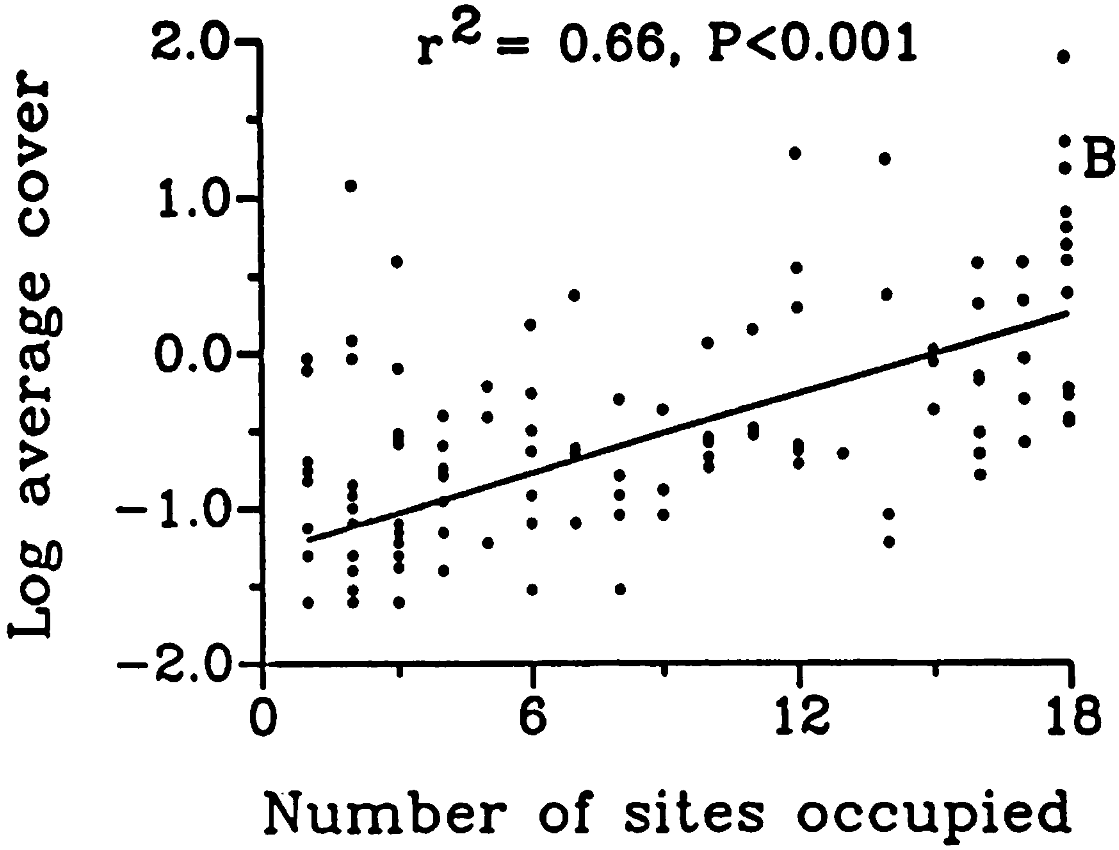


Figure 16. Cover values for a species regressed against occurrence of that species in the census. Although there is a wide scatter around the line, a significant positive relationship indicates that common species have higher average cover values than sparse species (data set PVC02, Collins and Glenn 1990a).

type and watershed levels, richness was again negatively related to productivity in all years except the severe drought of 1988. Implicit within this model is the notion that as production on a site changes from year to year, there will be a corresponding change in richness. A clear temporal relationship would provide strong support for the model. There were significant relationships between richness and productivity in 3 of 7 watersheds and 6 of 14 soil type comparisons over time. The short duration of this analysis (5 years) reduces the statistical power for the temporal analysis. These results indicate that a relationship between productivity and richness does exist within communities at Konza. The inconsistent temporal results may imply that other factors such as site history or disturbance also contribute to temporal variation in species richness.

Net Primary Production (Knapp, Hartnett, Seastedt)

Our documented record of aboveground biomass and NPP at upland and lowland sites now covers a 15 year period (Figure 12). We have previously analyzed these patterns relative to precipitation inputs and other meteorological phenomena (Abrams et al. 1986). Long term patterns of greater NPP in burned versus unburned and in lowland vs upland are consistent throughout this time period. However, in dry years, NPP is not increased by fire. Moreover, at the more xeric upland sites, burning only infrequently increased aboveground biomass. This response is similar to that of mixed-grass prairies to fire (Redmann 1978), perhaps reflecting both the decrease in water availability at upland sites as well as different species composition. The maintenance of this long term record will provide a sensitive ecological index of regional/global climate change, especially when coupled with trends in plant population data.

We estimate NPP by harvesting all aboveground biomass in 20 0.1 m^2 quadrats per treatment/soil type in late August/September (peak season biomass). These quadrats are located adjacent to the circular plots used for plant community sampling (see above). We separate live and dead graminoids from forbs/woody species as well as previous year's dead biomass. Losses in biomass due to decomposition are minor within the initial 3-4 months of the growing season (prairie litterfall has a turnover time of 3-4 years) and the current season senescent foliage can be readily distinguished and separated from the older detritus of previous years. Thus, NPP is estimated as the sum of green and current year's senescent foliage at peak season biomass. Over the last 5 years, we have sampled an annually burned and an unburned site at 2-wk intervals throughout the growing

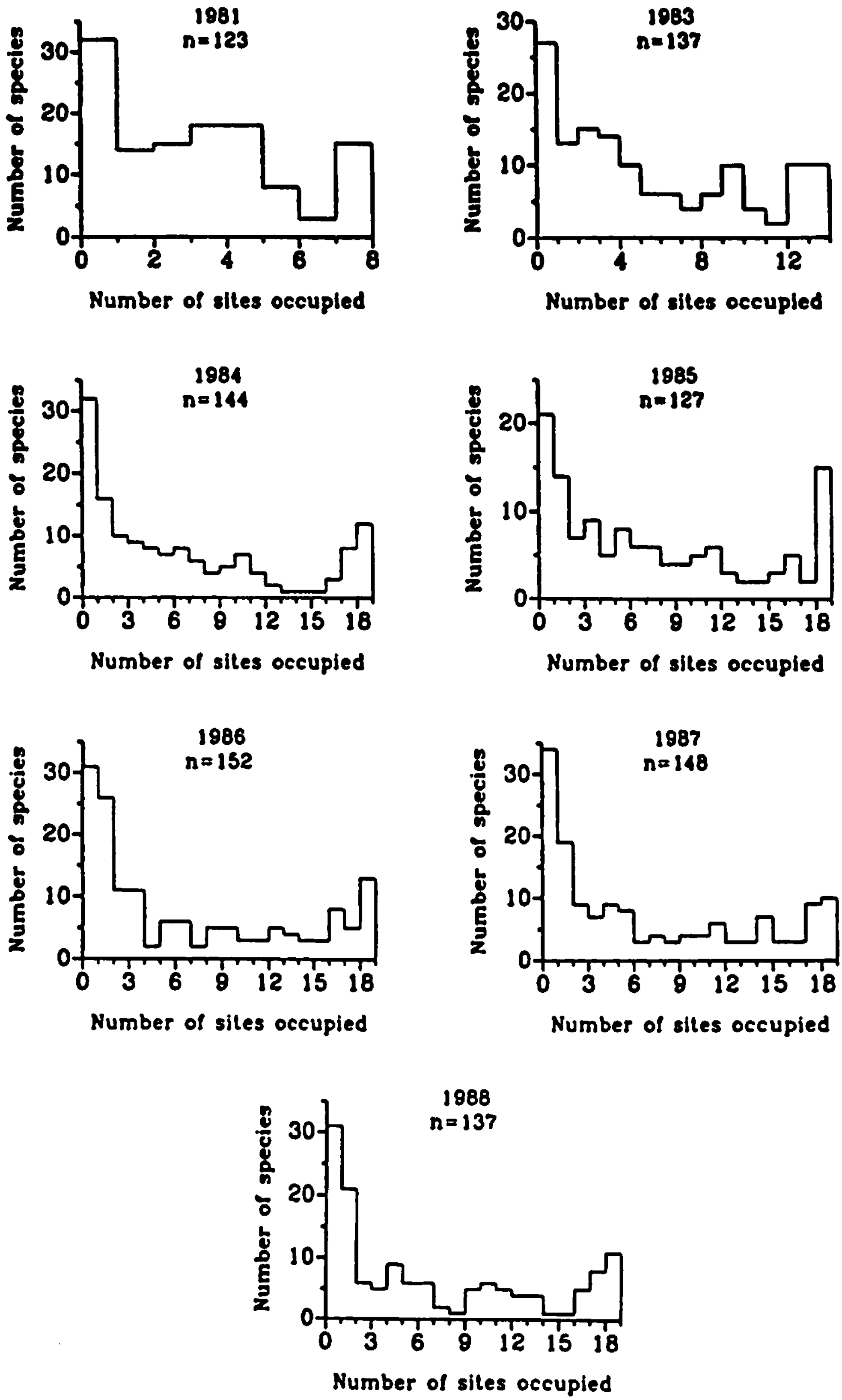


Figure 17. Species distribution patterns among sample sites at Konza Prairie, 1981-1988. N = total number of species among all sites. The results provide clear support for the core-satellite model of Hanski (1982) which predicts a bimodal distribution of species regional abundance. That is, most species tend to be either regionally common or regionally rare (Collins and Glenn submitted).

season and compared NPP estimated by summing positive biomass increments to the single harvest method described above. We have found no significant differences in NPP estimates from these two methods.

Recently, we reassessed our biomass sampling scheme (20 0.1 m^2 quadrats sampled per site) to determine if our sampling was adequate or if we could reduce the number of quadrats harvested. Using several statistical procedures (monte carlo and jack-knifing techniques) we concluded that a sample size of 20 was adequate for detecting treatment effects for all biomass components except forb production. Moreover, we can not decrease our sampling effort without a marked reduction in our ability to detect treatment effects in all categories (Figure 20; Briggs and Knapp submitted).

Measurements of aboveground NPP will also be expanded to include variation in topography. Our past sampling of upland/lowland sites has produced a valuable 15 y record which we plan to continue (Figure 12), and additional sampling for topography/production relationships will be confined to areas adjacent to the plant species composition transects described above. A preliminary study of the relationship between topography and biomass showed that productivity on hillsides is usually more similar to uplands than lowlands (Figure 1.a), but that significant variability along topographic gradients occurs probably due to small-scale differences in water availability (Figure 21.b; Knapp et al. unpubl. data).

The addition of bison adds another level of complexity and their consumption of biomass must be accounted for in production estimates. Watersheds scheduled for grazing were sampled prior to bison introductions and seldom were there significant differences in NPP between replicate ungrazed and (soon-to-be) grazed watersheds. Thus, the relative impact bison have on aboveground biomass can be quantified by comparison with ungrazed replicates. Estimating the effect that bison have on NPP would require frequent sampling of movable exclosures to determine yield consumed by the herbivores. Remote sensing procedures also offer some new approaches to this problem. We have already conducted preliminary studies (Turner unpubl.), and we plan to sample such exclosures in the short term as part of a related research project on bison grazing and topography by Hartnett, but due to the labor intensive nature of this approach, we do not propose that foliage consumption be a LTER core measurement.

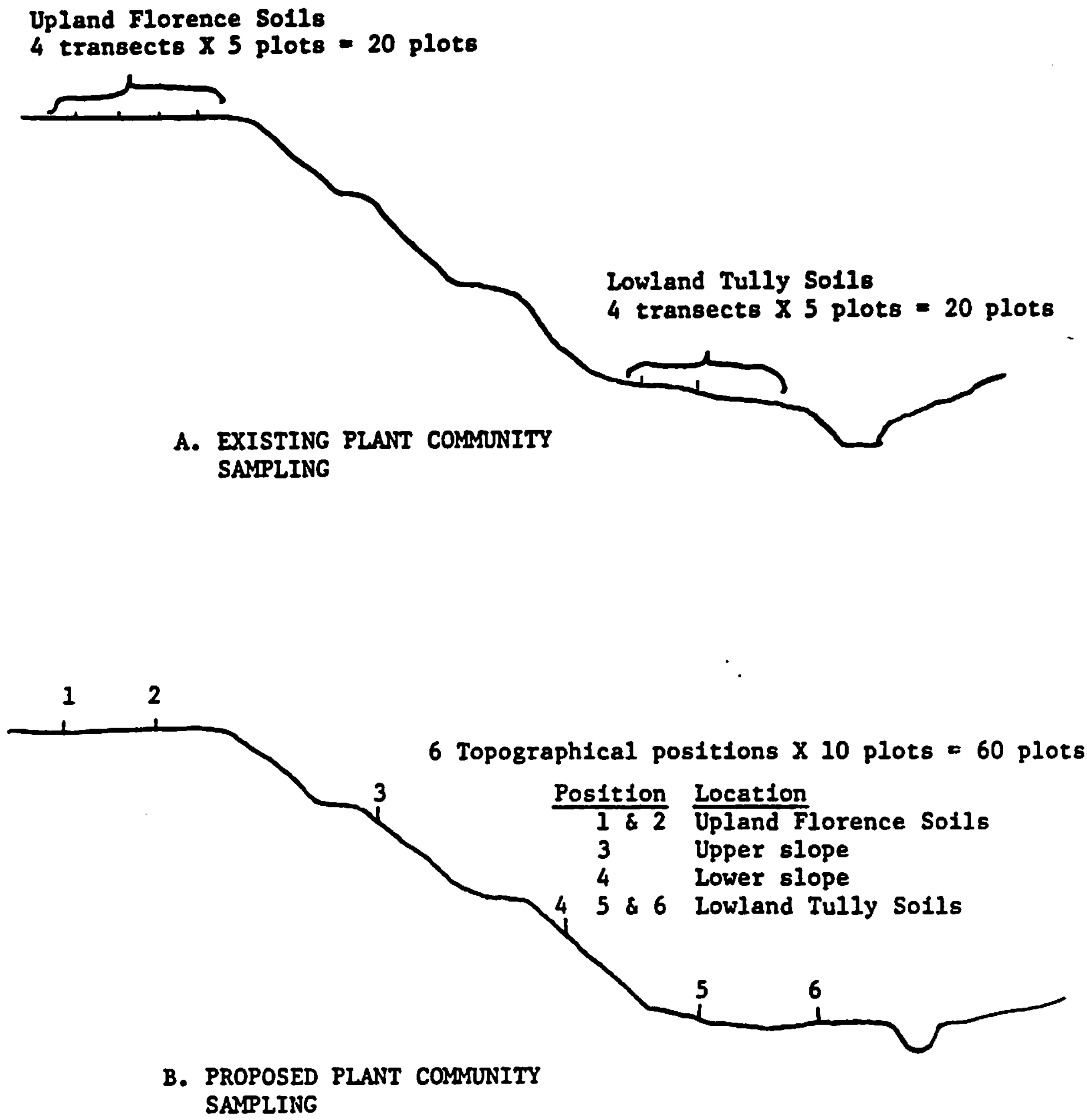


Figure 18. Existing and proposed sample design for plant species composition, foliage productivity, and selected belowground measurements. The number and positioning of hillslope plots will be located based on known geomorphic properties of the watershed (see Figures 32 and 42).

Plant Populations (Hartnett)

Long-term study of characteristics of tallgrass prairie plant populations are important in that 1) they provide an understanding of the plant demographic and life history responses that cause observed community patterns, 2) demographic and life history responses (such as the balance between sexual and vegetative reproduction) may strongly influence patterns of genetic variation within populations and hence overall patterns of biodiversity in tallgrass prairie, and 3) characteristics such as seed and rhizome production patterns are important in understanding both above- and below-ground consumer population dynamics (see "Consumer Population Studies" below). Thus, there are important linkages between plant population features and tallgrass prairie community structure, diversity and consumer populations.

Preliminary studies on perennial forbs such as goldenrod (*Solidago canadensis*), prairie coneflower (*Ratibida columnifera*) and ironweed (*Vernonia baldwinii*) on Konza indicate that plant biomass, stem numbers, flower head production and seed production increase with years since fire, and that fire alters the balance between sexual and vegetative reproduction (Knapp 1984, Hartnett submitted b). Preliminary studies also suggest that changes in forb species abundances with fire are not closely correlated with changes in their seed production (Hartnett submitted a.). Thus, the underlying demographic processes causing observed changes in plant species' abundances with fire in concert with stochastic variation at small spatial scales (Glenn and Collins 1990) require further study (Rabinowitz et al. 1989).

Recent studies on the responses of two dominant grasses (big bluestem and switchgrass) to grazing by bison showed that plant growth and reproductive responses to bison differed under burned vs unburned conditions in a given year (Vinton and Hartnett unpubl.) and that effects of grazing varied with plant density and growth stage (Hartnett 1989). In addition, carryover effects were evident in that heavy grazing in one year significantly reduced tiller emergence and growth rates in the following year. Bison grazing on Konza is highly patchy and the spatial patterns of grazing differ between burned and unburned sites. This additional spatial component associated with bison will influence our proposed vegetation sampling methods (see above).

Our proposed long-term study of plant population characteristics include measurements of patterns of abundance, flower, seed and rhizome production of dominant grasses and forbs, and the mapping of woody

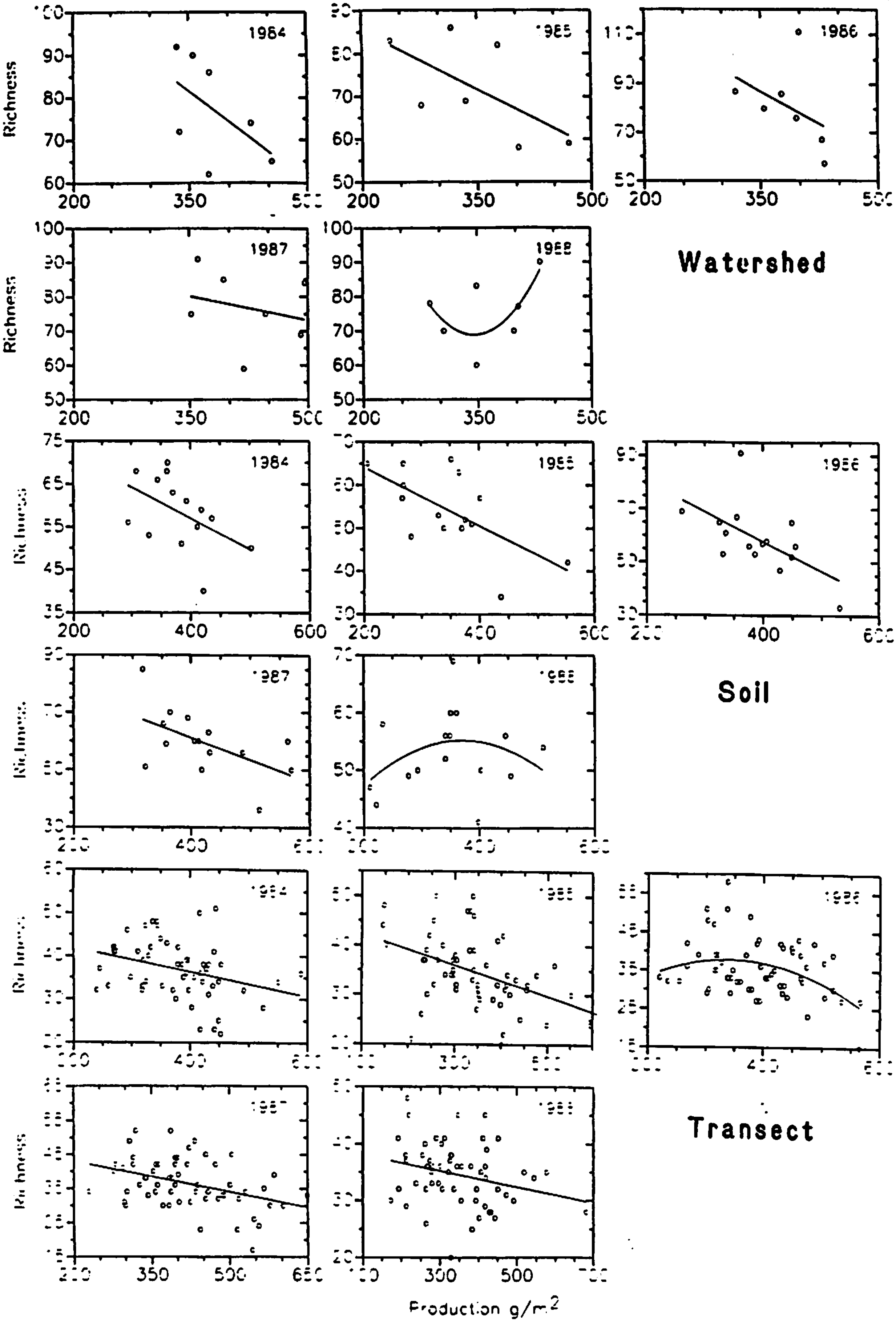


Figure 19. Species richness plotted against foliage production at three spatial scales (transects within soil types, soils within watersheds and whole watersheds; data sets PVC02 and PAB01). All regressions at the transect level and all but 1988 at the soils level are significant. Trends are similar at the watershed level, but the small number of data points reduces statistical power.

vegetation. Data discussed above as plant species composition will be used to track plant population responses to fire, grazing and annual climatic variation. Although most previous studies on tallgrass prairie community structure have focused on only the suite of the most abundant species (e.g., Collins 1987, Gibson 1988), processes such as grazing, fire or climatic stress may have large effects on populations of sparse species, and, understanding the influence of fire-grazer-climate interactions on biodiversity requires assessment of responses of species at the tail end of the relative abundance distribution as well (Rabinowitz et al. 1989). Thus we will examine the relationships between grazing-fire-climate patterns and the frequencies of sparse plant species as well as the dominants that contribute disproportionately to total productivity and other system processes.

In 1981, we initiated long-term records for density, height and seed production of three dominant tall grasses, big bluestem, little bluestem and indiangrass (see "Results From Prior NSF Support"). We propose in 1991 to initiate additional long-term studies of six numerically important forb species as well. Forb species that differ in seasonal phenology may differ considerably in response to treatments. For example, growth and reproduction of late spring forbs may be affected directly by fire, whereas later blooming species may be affected by fire indirectly through altered competitive relationships (Hartnett submitted a). Thus, the forbs studied will include a mixture of early, mid and late season species. Sampling will be similar to existing methods for sampling the three grasses and data on individual plant height, aboveground biomass and inflorescence biomass will be collected.

These data on grass and forb populations will be collected each season in each treatment area sampled for plant community composition (Table 1). In addition, representative grass and forb species that propagate both sexually and vegetatively (e.g., big bluestem, indiangrass, prairie goldenrod, aster) will be sampled each season for number of new rhizomes per plant, rhizome length and total new rhizome biomass, as well as sexual reproductive effort. These data on relative magnitudes of sexual and vegetative reproduction, along with data from concurrent long-term mapping and monitoring of the numbers and sizes of genets (clones) of dominant rhizomatous forbs (a related project initiated by Hartnett in 1990) will provide insight into the potential effects of varying fire/grazing regimes on both spatial pattern and genetic diversity within tallgrass prairie plant populations. Data on patterns of seed production among a variety of grasses and forbs, along with intensive

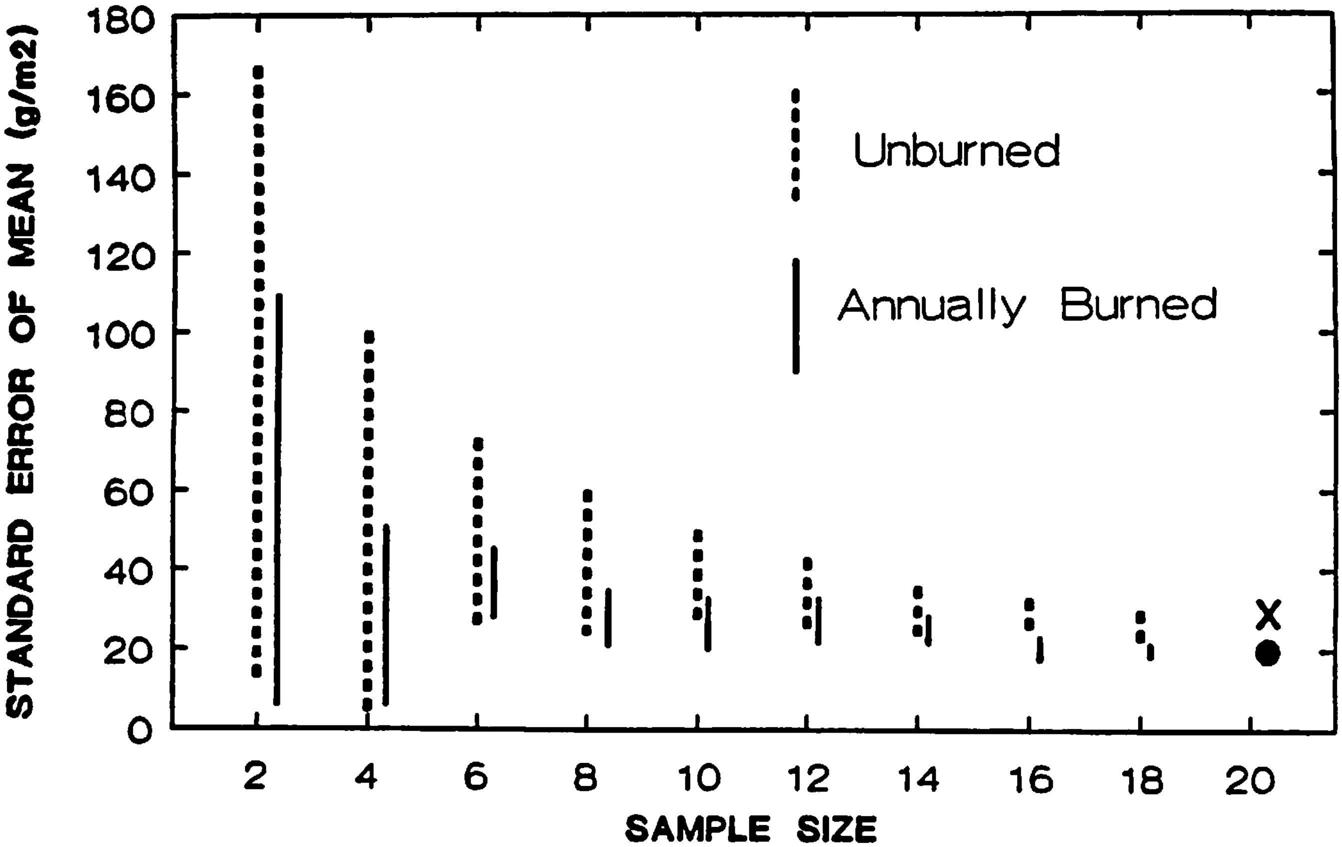


Figure 20. Effect of sample size on estimates of standard errors associated with mean foliage biomass on burned and unburned sites (PAB01; Briggs and Knapp submitted). Note the intrinsically higher variance associated with unburned watersheds.

short-term manipulative studies (see "Consumer Population Studies" below) will increase our understanding of the effects of fire and bison on plant-small mammal interactions.

Mapping of Woody Vegetation (Briggs)

The location of each individual tree, shrub and patch of shrubs have been determined on 12 watersheds every five years since 1981. Each watershed is surveyed in parallel lines approximately 15-20 m apart. The location of all individuals are marked with a unique symbol for each species on a large scale aerial photograph. Height is recorded to the nearest meter for trees, while for shrubs the approximate diameter and shape of the patch is drawn on the overlay. Individual tree locations and heights and shrub diameters and shapes have been digitized into the ERDAS geographical information system.

The number of trees increased by over 60% on an unburned watershed over the 1981-1986 period, while in an annually burned watershed the number of trees decreased (Figure 22). The spatial patterns of woody tree species invading tallgrass prairie appear to be a function of dispersal vectors, habitat availability and reproductive mode as well as burning regime. Under a variety of burning regimes red cedar (*Juniperus virginiana*) and hackberry (*Celtis occidentalis*) were significantly more uniform in their distribution pattern than American elm (*Ulmus americana*), eastern cottonwood (*Populus deltoides*) and honey locust (*Gleditsia trichanthus*). Trees with wind dispersed seeds had contagious distribution while most trees with bird-dispersed seeds were regular to random in their dispersion patterns (Briggs and Gibson submitted).

We propose to continue sampling at five year intervals to study the related effects of burning, soil, and now, grazing on the establishment and growth of woody plants in prairie communities. We will also study how these factors affect the prairie-forest boundary. These questions will be more rigorously examined with the increased spatial resolution of the Konza GIS data base that is in its early stages of development.

Consumer Population Studies (Kaufman, Zimmerman, Evans)

Since 1981, long-term data sets have been obtained on small mammals, birds and grasshoppers (Figure 23). Comparisons of spatial-temporal variation in population patterns and responses to fire indicate that different groups and species are controlled by different factors (Mushinsky and Gibson in press, Kaufman et al. 1990). These data have been collected to establish links between temporal variation in abundance and diversity and patterns of climatic variation, to describe more fully the manner in which periodic fire forced

Table 1. Konza LTER proposed experimental design for plant community sampling.

TREATMENT	WATERSHEDS	SAMPLE DISTRIBUTION	SAMPLE SIZE+
Annually burned	1C, 1D	Upland & Lowland	80
2-year burn	2C, 2D	Upland only	40
4-year burn/Ungrazed	4B, 4A N4d	Topographical gradient	120
4-year burn/Grazed	N487, N484 N4A	Topographical gradient	120
•Unburned/Ungrazed	UB, UD	Topographical gradient	120
•Unburned/Grazed	NUB, NUA	Topographical gradient	120

•Burned at 20 year intervals + Number of 10 m^2 circular plots.

fluctuating patterns of density and diversity of consumers, and to verify uni-directional changes associated with fire frequencies.

Small mammals have been censused in 28 permanent prairie plots to establish patterns of spatial-temporal variation in density and diversity, and effects of fire (Figures 24,25) and topoedaphic conditions on these characteristics. Data were collected during spring, summer, and autumn using live-trap census lines (20 stations at 15 m intervals with 2 live-traps per station) that started in upland, crossed through the slope, and ended in lowland. Manuscripts summarizing eight years of data are now being prepared. We will continue to census small mammals in 14 study plots in four ungrazed watersheds with experimental fires at frequencies of 1,4 (two sites out of phase by two years), and 20 years and three watersheds to be grazed by bison with experimental fires every 1, 4, and 20 years. Continuation of these censuses will enable us to incorporate the effects of bison grazing into our analysis of temporal variation of density and diversity. Intensive short-term manipulative studies will be used to study plant-small mammal interactions.

Methods for estimating bird and grasshopper densities will continue largely unchanged from previous LTER studies, as described in the Konza Methods Manual (see Data Mgmt. section). These procedures involve censuses (sweeps or visual counts) along permanent transects. Hence, unlike other LTER studies, these collections already employ an approach conducive to landscape interpretations. Some reduction in the intensity of these efforts is anticipated. In previous years these activities were conducted and directed by LTER supported postdoctoral students. Now they will be conducted by faculty and student assistants. Nonetheless, continuation of these data is important, particularly since other sites have similar data suggesting directional trends and/or strong responses to climate variables (e.g., Holmes at Hubbard Brook and Joern at Arapahoe Prairie in the sandhills of Nebraska). A related research project has begun to explore long-term patterns in infestations of gall-forming insects, another guild of insect consumers, in relation to fire regime. Hartnett and Fay have thus far documented strong effects of fire regime on insect infestation levels during the 1988-89 dry years.

Belowground Studies (Hetrick, Todd, Rice, Schwab, Seastedt)

Belowground plant biomass has been studied on the "Belowground Plots", a set of 64, 100 m^2 plots created to study the belowground response to fire, mowing and nutrient additions (Figure 26). Live and dead

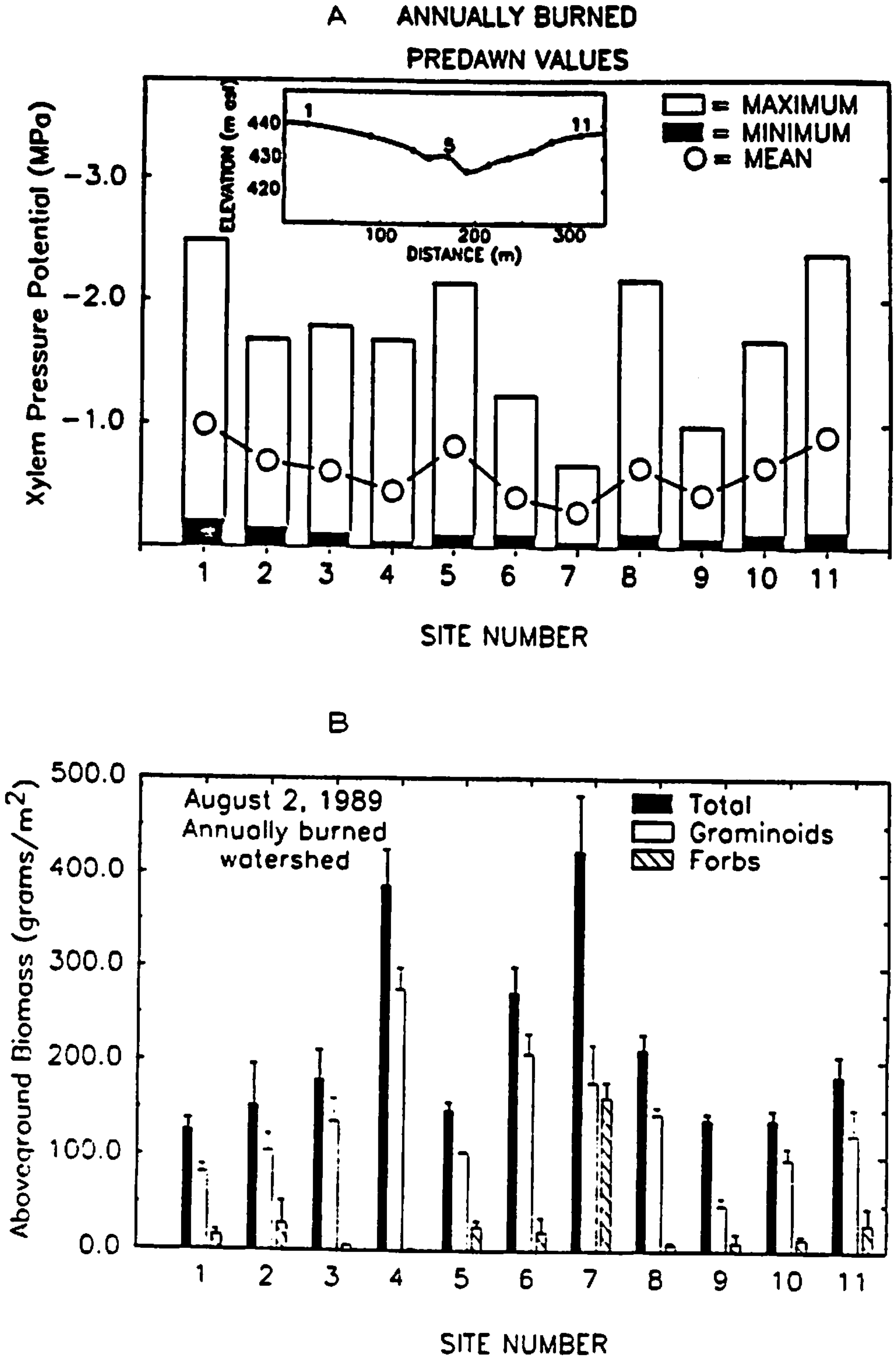


Figure 21. A. Seasonal maximum, minimum and mean leaf xylem pressure potential (more negative values indicate greater water stress) measured at predawn in big bluestem, the dominant grass on Konza Prairie. Measurements were made at two week intervals throughout the growing season of 1989, across a topographic gradient in an annually burned watershed. Site numbers refer to topographic locations identified in the figure insert. B. Patterns of aboveground biomass partitioned into grasses, forbs and total foliage. Site numbers refer to the topographic locations identified above. Error bars indicate 1 std. error of mean. Note that upland and hillside locations tend to have similar levels of production and are distinct from lowlands. As expected, water stress correlates well with topographic location and production, but note the influence that a small deviation in the topographic gradient (site 5) has on water availability and biomass.

roots and rhizomes are harvested in autumn of odd-numbered years. These are washed, sorted, dried and ground for nitrogen and phosphorus analyses following procedures described in Hayes and Seastedt (1987) and Seastedt (1988). Samples taken to harvest rhizomes are also used to sample macroarthropods and earthworms, while separate samples are taken for nematodes, microarthropods, soil chemistry and mycorrhizal spore density counts (e.g., Figure 27). Fire, mowing and nutrient treatments to these plots will continue as shown on Figure 26. Shifts in plant species composition as a result of the respective treatments have already occurred, and we now believe this experimental design is useful in evaluating some of the mechanisms causing negative effects of fire on certain forb species. Nitrogen limitation as a consequence of annual burning appears to explain some of the competitive advantage obtained by C_4 grasses. When annually burned plots are fertilized, forb densities increase. These data on forb responses in the Belowground Plots, when integrated with measurements of forb life history and demographic responses to fire-grazer treatment effects in the experimental watersheds (see "Plant Population Studies" above), will provide a more complete understanding of how fire-grazer-topoedaphic interactions influence plant species competitive relationships and community structure and diversity.

Another important reason for continuation of this experiment is to test predictions of Aber et al. (1989) regarding chronic nitrogen enrichment (Figure 28). Unlike forest systems, we predict no decline in plant productivity and continued accumulation of organic nitrogen. We do, however, expect to see other similar patterns and document the fate of added nitrogen and phosphorus (see below). We will continue fire and mowing experiments in conjunction with nitrogen enrichment. These treatments will inhibit invasion by woody species, and maintain the experiment as a grassland study.

Foliage biomass harvests on Belowground Plots will be continued on an annual basis. Porous cup lysimeters (Hayes and Seastedt 1989) will be installed so that soil water nitrogen content can be measured. We will discontinue other LTER lysimeter measurements except those in conjunction with the USGS study (see below). Belowground measurements of roots, rhizomes, nematodes, mycorrhizal spore densities and soil chemistry will be continued on an infrequent (five year) interval.

Plant root biomass data are supplemented by measurements obtained at eight, 40 cm x 40 cm plexiglass root windows (e.g., Hayes and Seastedt 1987, Seastedt and Ramundo 1990). Initial treatments consisted only of burned and unburned plots. Since 1987, treatments have consisted of a two-factor design

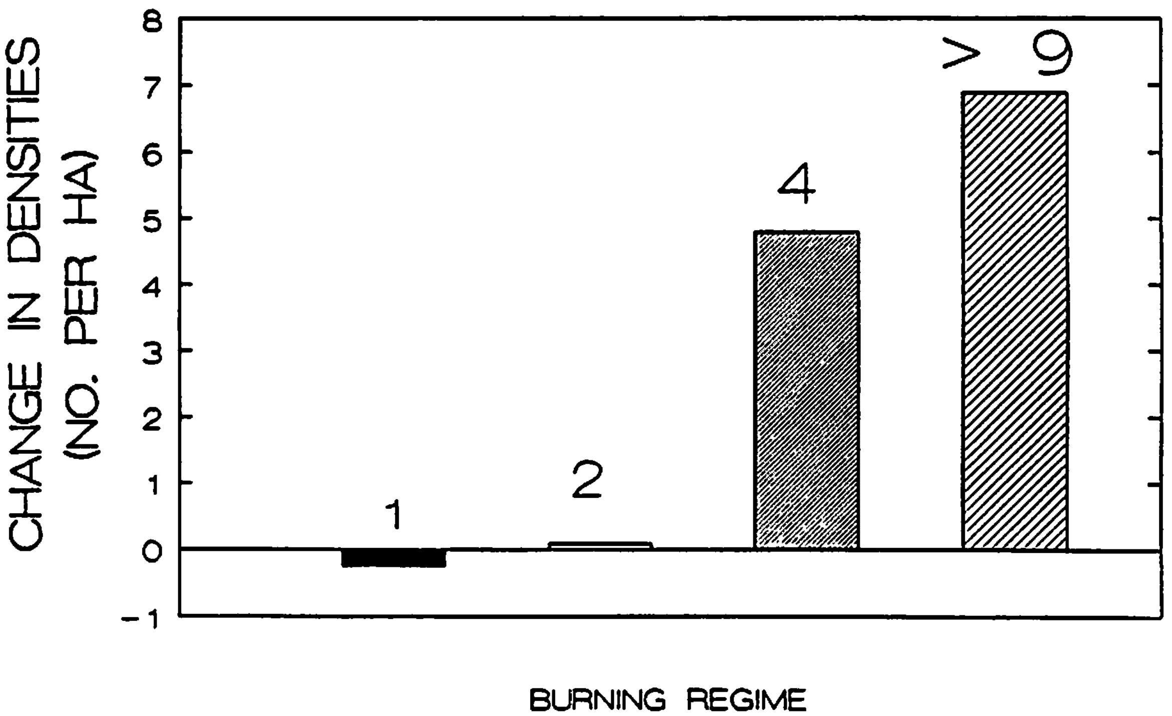


Figure 22. Change in tree densities on annually burned (1), 2-year burns (2), 4-year burns (4) and long-term unburned (>9) watersheds. These results (data code PWV01) were obtained over the 1981-1986 interval, a consistently wet period. The next census (1991) should suggest how climate patterns may influence these results.

involving burning and clipping. Roots have been traced every two weeks during the growing season. Length, appearance of new roots and decay of old roots (the latter two measurements obtained by comparison with previous tracings) are obtained for 10 cm x 10 cm increments. All tracings are archived. These data provide useful time-series indices of root response to climatic and treatment effects and are needed to correctly interpret the root biomass data. The root window measurements will continue until we can install a mini-rhizotron system on the Belowground Plots.

Organic Matter Studies (Rice, Schwab, Seastedt)

Standard litterbag studies of foliage and root decomposition and mineralization have been conducted on Konza Prairie in conjunction with forest and prairie litterfall measurements (Seastedt 1988, Briggs et al. 1989, Seastedt and Ramundo 1990). Organic matter amounts at 5 cm and (where possible) 25 cm depths have been obtained at 5 year intervals on upland and lowland soils of LTER watersheds.

The long-term dynamics of soil organic matter at the landscape level (transects) will be evaluated by several techniques. To detect a shift in the composition of the microbial community, the population of bacteria, actinomycetes and fungi will be determined annually. Population size will be assessed by plating on differential media (Wollum 1982). We are aware of the deficiencies of this approach; however, it is an accepted technique and can be compared to existing data bases. Population counts may be supplemented at a later date by direct microscopy or new techniques derived from studies at the Kellogg Biological Station, LTER and the NSF Microbial Ecology Center. The stable, active and mineralizable fractions of soil organic matter will be determined on a four year cycle prior to the burn year. Total soil organic C and N levels will be measured. The size of the active fraction of the soil organic matter will be estimated as described by Paul and Juma (1981). Mineralization of C and N will be determined by a modification of the Stanford and Smith (1972) technique to include an estimate of C mineralization by CO_2 production. The ratio of C to N mineralized can also be used to estimate of the quality of the soil organic matter.

Microbial biomass C and N and inorganic N will be measured four times per year on the Belowground Plots to establish a good data base on the dynamic nature of these pools on the tallgrass prairie. In addition to the annual determination of the microbial composition by plate counts, substrate induced respiration (SIR) will be used to estimate the relative contribution of fungi and bacteria to the overall microbial activity (Anderson and

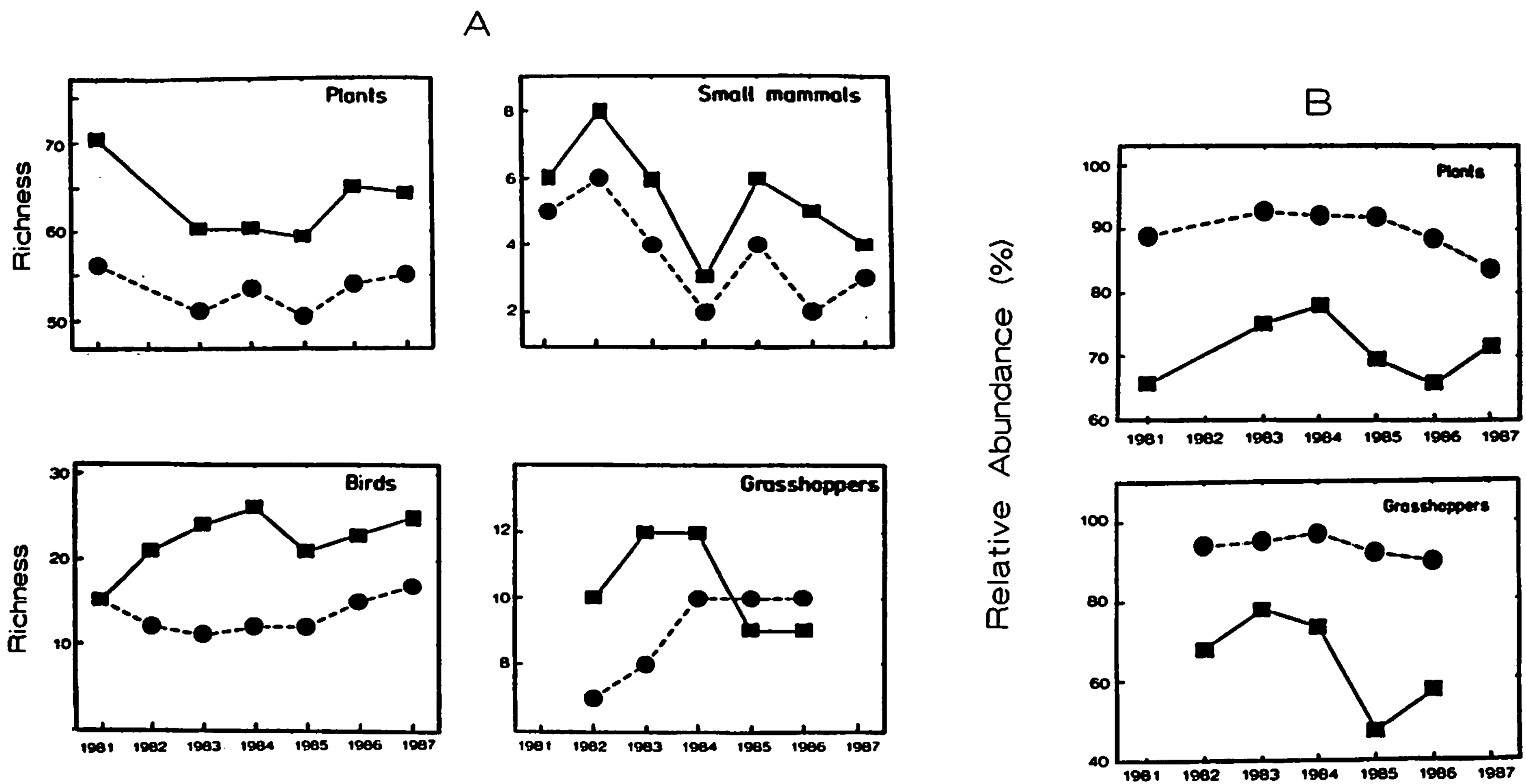


Figure 23. A. Average richness (number of species) in annually burned (circles) and unburned prairie (squares) demonstrates that annual fires generally reduce species numbers on tallgrass prairie. Grasshopper diversity, however, exhibits a different pattern. B. The relative abundance (percentage cover) of grasses appears to strongly control the percentage composition (% of numbers) of grass-feeding grasshoppers. These data (CBP01, CGR01, CGR02, CSM04, and PVC02), were initially obtained to address questions specific to a given taxon. Now, however, comparisons of patterns among the groups provides an index of generality regarding the underlying controls.

Domsch 1975). SIR will be assessed several times per year until we establish the optimal time and frequency for adequate assessment. Total soil organic C and N, the active and mineralizable fractions of soil organic matter, will be assessed on a four year cycle as with the transect data. Since fire and grazing result in a change in N immobilization-mineralization, net and gross N mineralization will be estimated to determine which process is dominant. Estimates of net and gross N mineralization will be derived from isotopic dilution experiments with ^{15}N under laboratory conditions as described by Myrold and Tiedje (1986). Supplemental funding will be sought to permit labelling of the active fraction of soil organic matter and plant fractions with ^{15}N and $^{13}C/^{14}C$ to trace the N and C dynamics through the prairie soil ecosystem.

Nutrient Dynamics (Schwab, Hetrick, Rice, Seastedt)

The consequences of nutrient limitation in tallgrass prairie are being studied at several levels of resolution within the ecological hierarchy. At the organism level, we are studying how plant characteristics associated with nutrient limitation (Chapin et al. 1986) and mycorrhizae affect specific species growth responses. Another focus is how nutrient and water interactions along a topographical gradient affect the response of specific species. At the community level, we are using the Belowground Plot experiments to determine how nutrient availability affects the relative abundance and distribution of the prairie species. At the ecosystem and landscape level, we are evaluating the effects of nutrient availability on patterns of NPP and on energy and water exchange with the atmosphere. Hence the topic, "Effects of Nutrient Limitation" becomes an integrating focus on much of our LTER effort.

Phosphorus studies have emphasized plant-mycorrhizal interactions. The biomass of native grasses and forbs growing on the prairie soils seldom increases in response to P applications despite the low concentrations of "plant available" P as determined by agricultural soil tests. One of the means by which the native species acquire P is through symbiosis with mycorrhizae. It is possible that the mycorrhizae obtain P by enhancing mineralization of organic matter (Gerdemann 1968) or by dissolving inorganic P sources (Bolan et al. 1987). Recent research (Jayachandaran et al. 1989) demonstrated that mycorrhizae can access the minute concentrations of P which are released during the chelation of Fe by natural complexing agents. It is not clear whether or not mycorrhizae can produce these complexing agents, but they can take advantage of them. Current research is focusing on the rates of mineralization of P as affected by mycorrhizae. We have modified

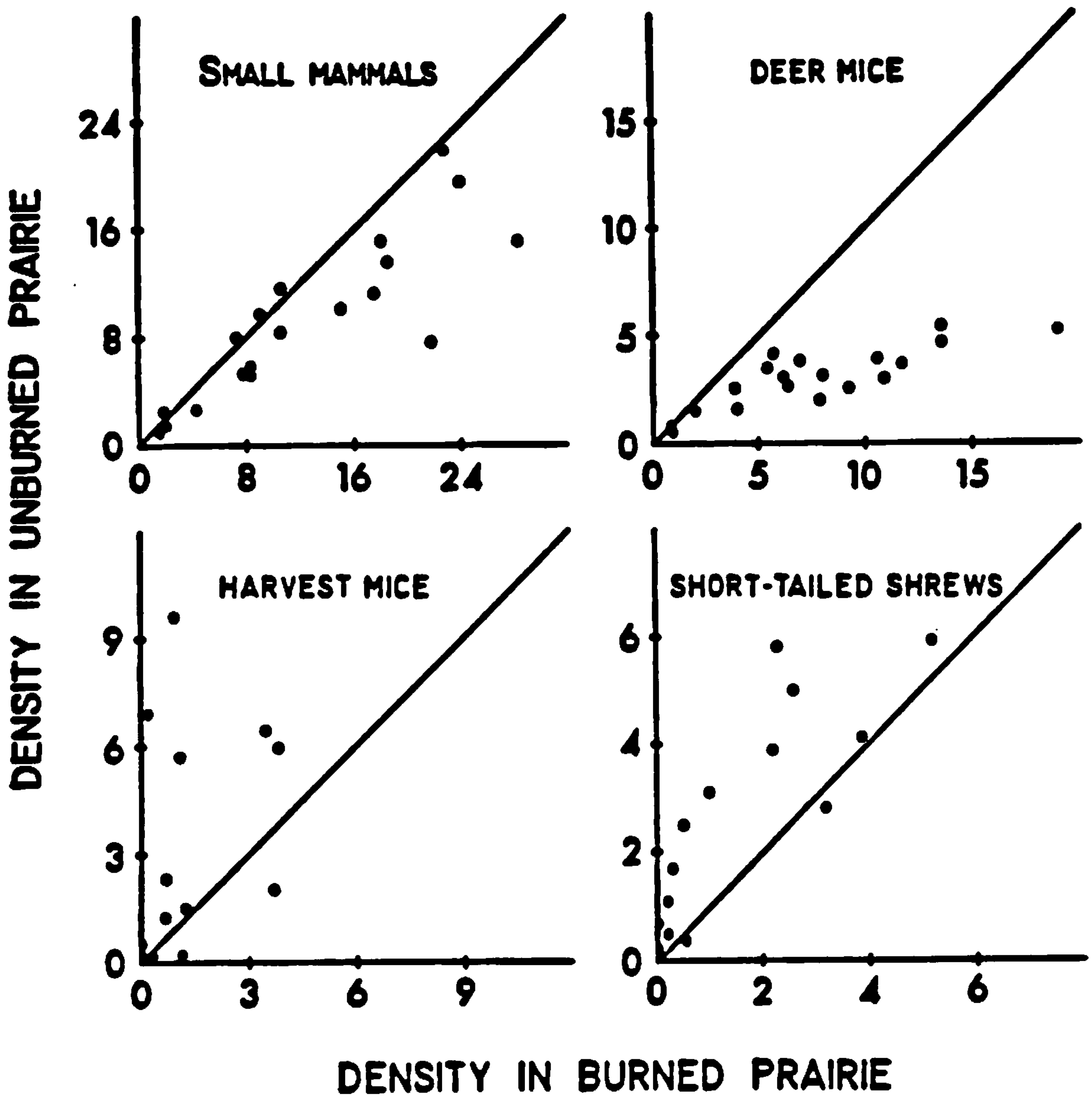


Figure 24. Fire alters the density of small mammals in tallgrass prairie as can be seen when relative densities from periodic censuses in burned and unburned prairie are plotted against each other. The positive effect of fire on total small mammals and deer mice and the negative effect of fire on western harvest mice and short-tailed shrews are illustrated. Fire-negative responses also can be illustrated for prairie voles and southern bog lemmings. Data are from Konza LTER Data Set CSM04.

the method of Pons and Guthrie (1946) to physically separate soluble organic and inorganic P. Using ^{32}P labelling and established kinetic analysis, the rates of mineralization of organic P can be quantified.

Estimates of within-watershed patterns of soil nitrogen availability were made by Klittich (1988) and J. Hetrick (1989). Those results indicated that autocorrelation patterns often seen for agronomic systems and oldfields using kriging and co-kriging procedures (e.g., Robertson et al. 1988; Figure 29), are not evident in native prairie. Our hypothesis for this phenomena is that microsite (e.g., a few centimeters to meter) variation generated in the native prairie is homogenized by plowing. This variability therefore disappears from the semi-variograms allowing the somewhat larger scaled sources of variation to be observed. In a more detailed analysis, estimates of the mineralization of soil organic nitrogen across several Konza Prairie transects using the 6 month incubation procedure of Stanford and Smith (1972) were completed. These data have yet to be analyzed, but they should provide definitive patterns of nitrogen availability across the catena.

J. Hetrick was partially supported by LTER during the present grant to study the consequences of long-term nitrogen and phosphorus fertilization to inorganic and organic soil phosphorus dynamics. This work was conducted on an experimental grassland site maintained by the KSU Agronomy Department that had been fertilized annually for over 40 years. This site was selected over Konza Prairie because of the long history of nutrient additions, and because results would be useful in making predictions about long-term nutrient effects on both native and agricultural systems. Current theory of phosphorus cycling suggests that Mollisols maintain an active organic phosphorus cycle (Cole et al. 1977), but that the inorganic phosphorus cycle may be relatively more important (Tiessen et al. 1984). Results from this study (J. Hetrick 1989) indicate that fertilizer additions increase the inorganic phosphorus fraction, while addition of nitrogen results in an increase in the organic phosphorus fraction as a result of biological immobilization and chemical stabilization mechanisms. Overall, nitrogen availability exhibited strong controls on phosphorus dynamics, a finding consistent with observations from vegetation studies (Seastedt 1988, Ramundo et al. 1989). Verification of these findings will be conducted using both transect and Belowground Plot studies.

Wetfall (NADP measurements), bulk precipitation, throughfall, soil water, stream, groundwater, plant and soil nitrogen measurements have been routinely obtained on Konza Prairie during the current project interval. Emphasis is primarily on N and P content. Short-term measurements of net mineralization (Ojima

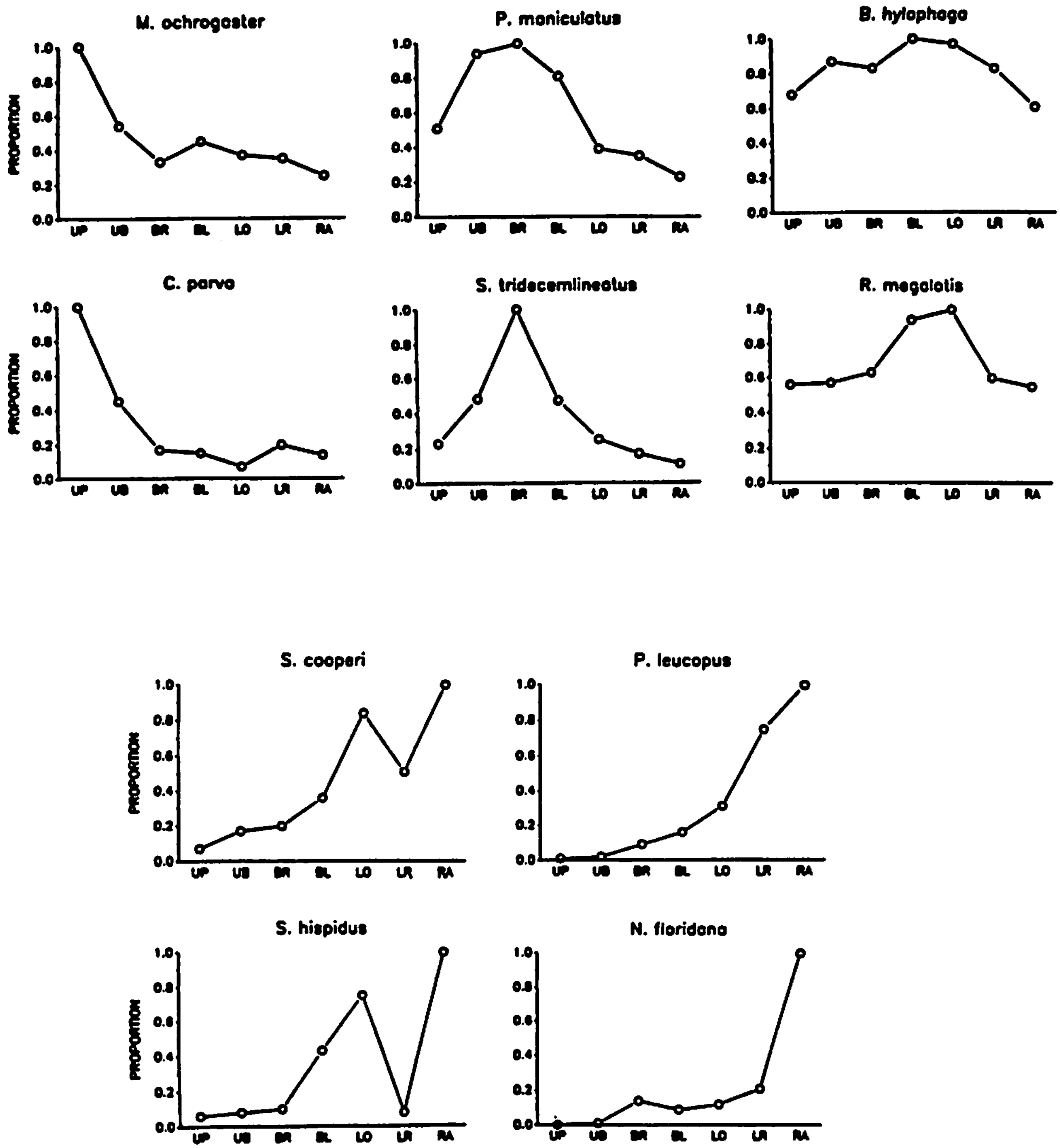


Figure 25. Small mammals are non-randomly distributed across landscape features on Konza Prairie. This figure illustrates five general patterns of relative distribution of captures (for each species, the site with the greatest captures = 1.0) across a toposequence from upland prairie (UP) to prairie (UB) immediately above rocky limestone breaks (BR) to moderately deep soil region below the breaks (BL) to relatively flat, deep soil lowland prairie (LO) to lowland prairie next to ravines (LR) to ravines with a mixture of grass, shrubs, and trees (RA). Landscape distributions for microtine rodents (Microtus ochrogaster and Synaptomys cooperi), shrews (Cryptotis parva and Blarina hylophaga), and Peromsycus species argue for some form of interspecific partitioning. Data from a short-term non-LTER study by B. Clark and others.

1987, Schwab unpubl.), N-fixation (Eisele et al. 1989), and denitrification (Groffman unpubl.), and a plant-microbial interaction study on N dynamics (Firestone unpulb.) is underway. Nitrogen availability to plants remains a central focus as this factor explains a large amount of the variance of the system response to fire and grazing, and also acts as a constraint on vegetation-climate biogenic gas flux (Schimel et al. submitted). The availability of the element, as mediated by fire-grazing-climate interactions, may also explain much about outcomes of plant competition interactions, and plant-mycorrhizal relationships (see "LTER Hypotheses and Questons" above).

Our largest commitment to nutrient measurements in terms of number of samples routinely analyzed involves dissolved forms (bulk precipitation, throughfall, soil water, groundwater, storm-event stream samples and baseflow stream samples), which are obtained on a weekly basis, given availability of samples. We propose to continue these, with emphasis placed on accurate measurements of bulk precipitation inputs and stream and groundwater outputs. Quality control procedures for our analytical measurements have been evaluated by routinely checking our numbers with those obtained by other laboratories (e.g., Ramundo and Seastedt submitted; Figure 30).

Landform Effects on Hydrology and Surface/Ground Water Chemistry (The Wet Group)

To understand landscape controls and constraints on ecological phenomena, the Wet Group proposes to expand current LTER stream research (i.e. nutrient transport and water yield modeling) to include studies of geomorphology, hydrogeology, and surface/ground water chemistry. The complexity of the Konza landscape (Figure 7) requires our research effort to be focussed initially on the most intensively studied LTER watershed, N04D, with later expansion to all of Konza Prairie.

Concurrent with the expansion of data collection, we shall develop a spatially explicit model of surface/ground water dynamics and nutrient/sediment transport within the watershed. This physico-chemical modeling effort will progress in conjunction with the soil-vegetation modeling (see "Modeling" below), as our goal is an integrated soil-water-vegetation model.

Spatially-distributed process models require a network through which space is apportioned into relevant modeling units. The proposed model will capture the effects of physical terrain on plant-soil-water dynamics; accordingly, space will be apportioned into relevant polyhedra using the Link-Node approach

KONZA PRAIRIE LTER BELOWGROUND STUDIES PLOTS

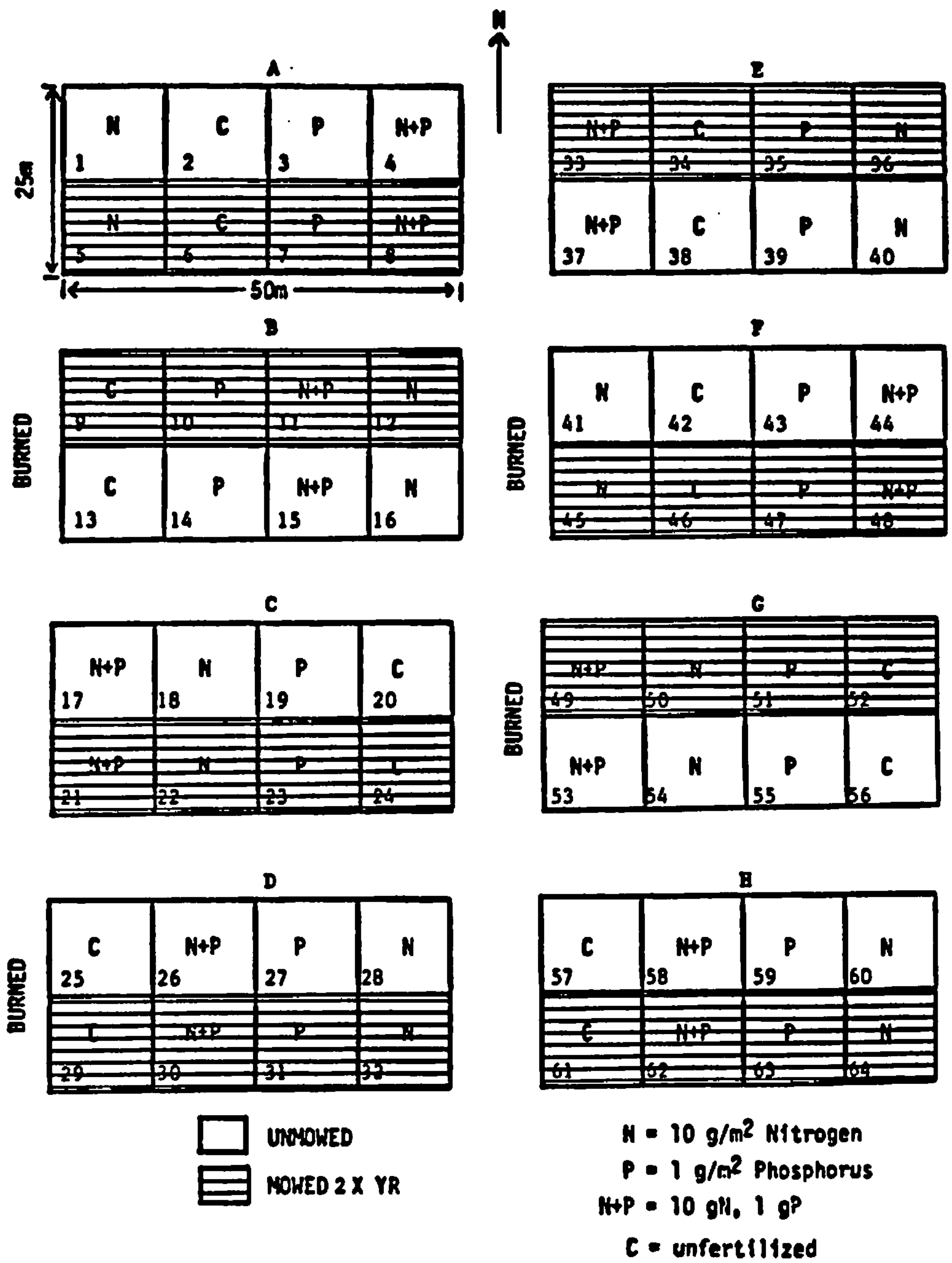


Figure 26. Experimental design of the Belowground Plots, installed on Konza Prairie in 1986. Fertilization is done annually in the spring. Foliage, roots, rhizomes, soil chemistry, nitrogen mineralization, soil microbial biomass, mycorrhizae, nematodes and arthropod abundance have been measured on these plots (Data sets PBB02, PFS01, XMS01, XNS01, NBC01, CSA01, CSA02 and undocumented results).

outlined by Chen and Orlob (1972), rather than into the conventional grid of uniform areas or parallelopipeds. The Link-Node approach was originally developed in conjunction with a model of the complex estuarine ecology in the San Fransico Bay-Delta system. It has recently been used to simulate the movement of water and chemicals in a variably saturated porous medium (Tracy and Marino 1987).

The Link-Node technique divides the physical system into a series of discrete volume, area or length units call "Nodes" (Figure 31). The nodes are characterized by the physical properties associated with the storage of mass in the system. For example, in studying the flow of groundwater, a node would be characterized by the surface area, storage coefficient and aquifer thickness at the node. The nodes are then interconnected by flux paths called "Links" (Figure 31). The links are defined by the physical properties associated with mass transfer. For example, a link would be characterized by the hydraulic conductivity and hydraulic gradient between the two nodes connected by the link as well as the representative dimensions of the link. The state of the physical system being simulated from one time period to the next is then computed using the principle of mass balance.

The main advantage of the Link-Node approach over other numerical simulation techniques is that any number of state variables can be computed at each node, each having a variety of different governing equations. The division of the nodes and link connection can remain the same for each of the state variables being considered, with only the parameters defining the mass storage in a node and mass flux between nodes, varying from one state variable to the next. This allows the model to be developed for one of the physical systems that is well understood, such as surface water, and later expanded to include groundwater flow, chemical, nutrient and sediment transport and vegetative growth without having to develop new numerical solution procedures or redefining the simulation network. Moreover, the contingent character of the Link-Node network enables an increase (or decrease) of resolution through the further subdivision (or aggregation) of existing nodes and links as additional data become available.

The first step to apportioning the watershed into an appropriate network of Link-Node polyhedra is to define features of the landscape. A 1:2000-scale topographic (1 m contour) map of the N04D watershed will be used as a base map to which geologic, geomorphic (see below) and soil maps will be overlain using our GIS system. Soils will be mapped by W. Wehmueller (U.S. Soil Conservation Service) at no cost to LTER.

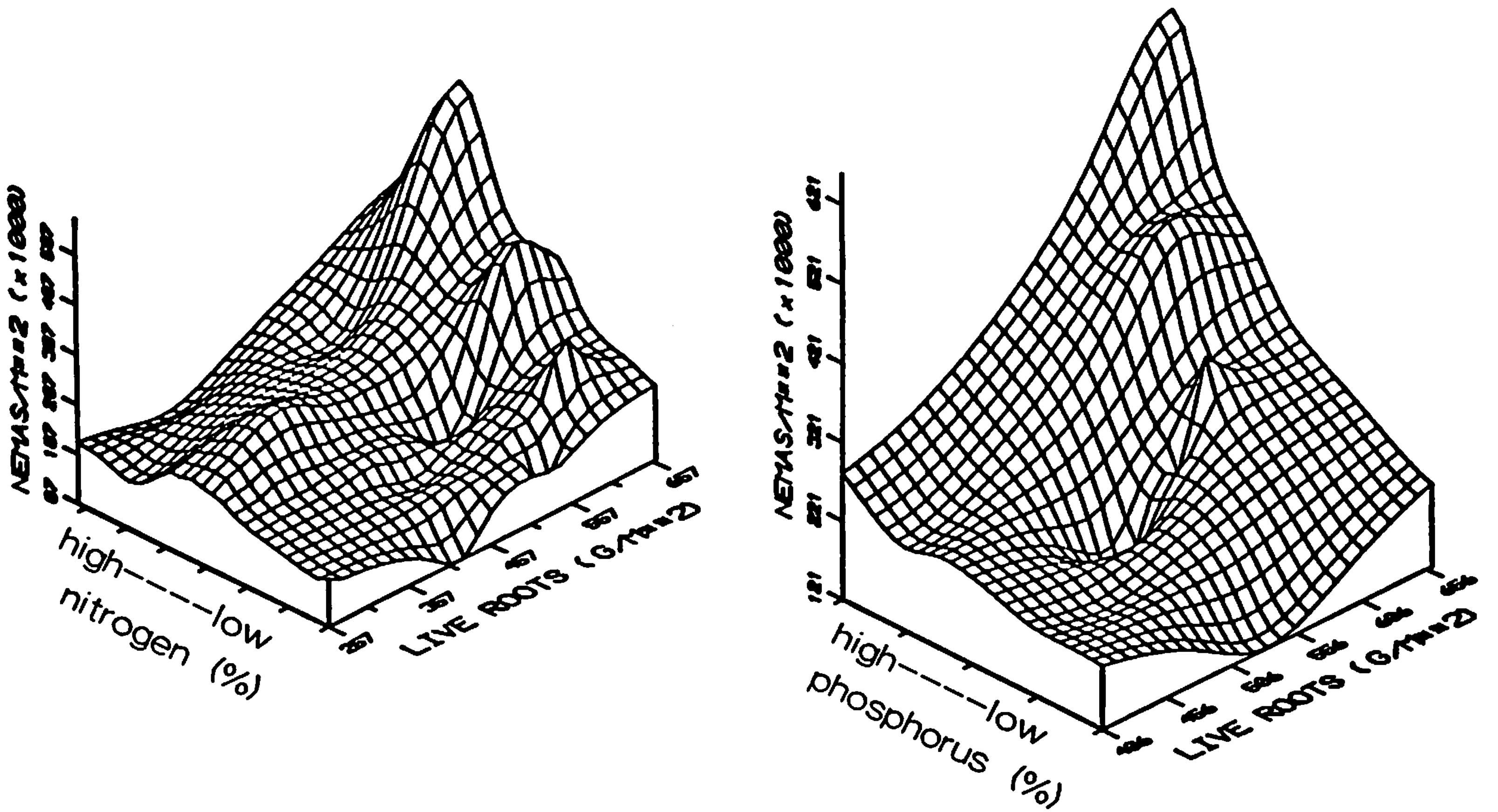


Figure 27. Densities of obligate phytophagous nematodes, Heliotylenchus, from the Belowground Plots as a function of live root biomass and N and P concentrations. These organisms show a strong fixed carbon-nutrient interaction, with densities largely unresponsive to treatments except when both factors concurrently increase (data set XNS01).

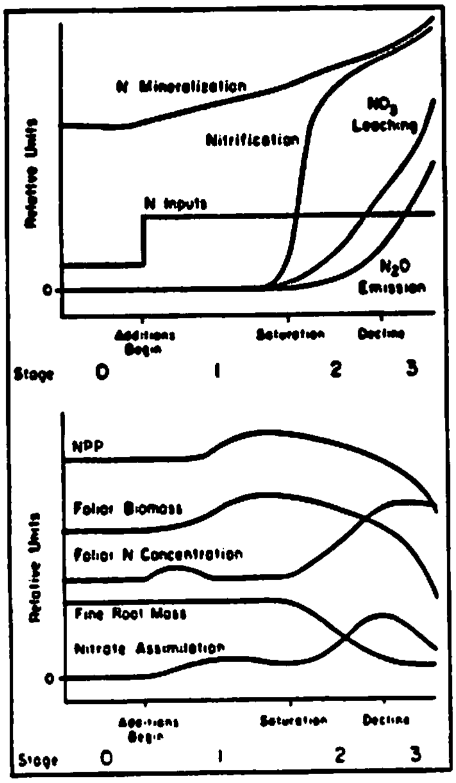
The initial configuration of the Link-Node network will be motivated by extant data on surface water movement collected since 1986 by J. Koelliker and C. Tate for use in a hydrologic model. Data from infiltration studies, groundwater/surface water flow, chemistry and sediment transport studies described below will be added later.

Geomorphic Studies (Oviatt and Martin)

Our long-term goal is to develop a comprehensive model of the geomorphology that can be integrated with the findings of other groups studying surface water, groundwater and biotic systems in the N04D basin with the ultimate goal of determining the role of geomorphic processes and history in the ecosystem as a whole (Figure 32; Swanson et al. 1988). We have three major interrelated objectives: 1) to map the geomorphology and geology of the drainage basin in detail; 2) to determine the geomorphic history of the basin; and 3) to measure and monitor the rates of modern geomorphic processes operating in the basin.

Features to be mapped include: thickness, texture, and composition of surficial deposits (stream deposits, slope deposits, loess); bedrock and alluvial knickpoints in stream channels; bedrock (at the surface, and at shallow depth); gravel bars in stream channels; terraces; cut-bank exposures; and eolian deposits on ridge tops.

Geomorphic history will be documented from the initiation of erosion in the drainage basin (ca. 20 million years ago), to historical (post-European settlement) changes in the landscape. We are restricted by the limited and relatively young sedimentary record of geomorphic history preserved in the drainage basin because the long-term trend in the basin is one of erosion [i.e., sediments are not stored for long periods (Smith 1990)]. Cores of alluvium and colluvium that mantle the valley bottom will be taken at locations where the cross-sections are surveyed (see below), as well as in other areas, and sediments in stream-cut exposures will be described. Coring will provide data on thickness and lateral changes in grain size and composition of deposits stored in the basin, and will also provide an opportunity to collect organic material for radiocarbon dating. By mapping positions of deposits of different age in the valley and by comparing these data with independent paleoclimate records and data on alluvial cycles from other areas, it may be possible to determine whether the Konza alluvial cycles are related to climate changes or to internal geomorphic controls (Womack and Schumm 1977, Patton and Schumm 1981, Hereford 1984). In addition, results from the dendrochronological study (see



The four stages (0–3) correspond to those described by Smith (1974) and Bormann (1982) for ecosystem response to pollution loading. Stage 0 is the pre-treatment condition. In stage 1, increased deposition is occurring, but effects on the ecosystem are not evident. For a limiting nutrient such as nitrogen, a fertilization effect might result in increased ecosystem production and tree vigor. In this stage, retention of nitrogen is most efficient, and that retention does not damage, and may enhance, ecosystem function. In stage 2, negative effects occur, but they are subtle, nonvisual, and/or difficult to measure. Only in stage 3 do visible effects occur, resulting in major environmental impacts. Different species and environmental conditions could alter the timing of effects.

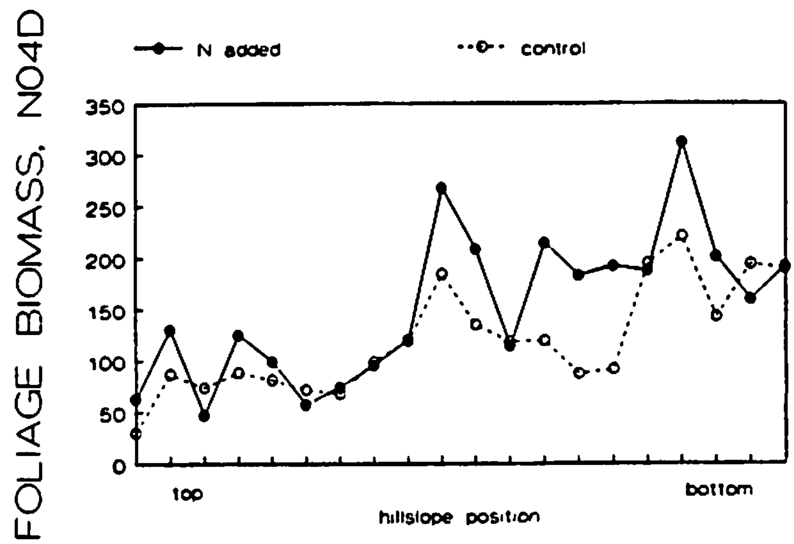


Figure 28. A.Effects of chronic N additions (Aber et al. 1989). The Belowground Plots will be used as a cross site comparison with ongoing studies at the Harvard Forest. Many of the transient effects will be influenced by topographic position. Figure B shows that fertilization response of NPP in 1989 (a dry year) was strongly moderated by hillslope position. Fertilization had no significant effect on upland sites. We expect our Mollisol soils to be much more resistant to change than the more weathered New England soils. We predict much higher nitrogen storage as organic nitrogen. Continued hot, dry weather, however, should result in net mineralization of organic N and patterns suggested by Aber et al.'s models.

"Graduate Projects in Progress") on lowland tree species can potentially be used to estimate a date when alluvial fills stabilized and began to support vegetation (see Sigafoos 1964, Everitt 1968). Sampling trees in sensitive sites on the upland or the margins of valley floors can be used to gauge recent climatic fluctuations. Also, original federal land survey records and historical photographs will be searched to compare pre-European settlement channel and vegetation conditions to present conditions.

Modern geomorphic processes will be measured by: 1) surveying channel cross-sections at various locations along the stream representing a variety of channel configurations (Emmett and Hadley 1968, Emmett 1974, Leopold 1976); 2) studying transport of gravel in stream channels by the use of marked boulders, and scour chains buried vertically in gravel bars (Leopold et al. 1966); 3) placing erosion/deposition pins along hillslope transects to document short-term rates of erosion and deposition (Clayton and Tinker 1971); 4) setting out dust traps to collect samples of wind-blown sediment entering the basin (Smith et al. 1970); 5) studying hillslope hydrology (i.e., infiltration, overland and subsurface flow) and sediment yield using Gerlach troughs (Leopold and Emmett 1967) at sites having different slope, geology, aspect and vegetation; and 6) measuring suspended sediment and dissolved load in runoff samples taken at the flume to show relationships between processes of sediment generation, storage within the basin and output from the basin (Caine and Swanson 1989).

Groundwater–Surface Water Interactions (Tate, Macpherson)

Understanding groundwater-surface water interactions is of critical importance for several reasons: 1) our long-term record of hydrology (Figure 33) and nutrient dynamics; 2) Konza represents the only benchmark for studies of groundwater-surface water contamination by agricultural practices in this region; and 3) we have the opportunity to advance stream ecology by studying the importance of longitudinal (upstream), lateral (riparian, floodplain), vertical (groundwater) and in-stream controls plus storm events on supply and availability of essential elements for biotic productivity (Meyer et al. 1988). Both nitrogen and phosphorus are important controlling factors of algal biomass in Kings Creek and nitrogen varies both spatially and temporally within a watershed with groundwater inputs into the stream channel influencing the spatial variation of nutrients (Figure 34; Tate in press).

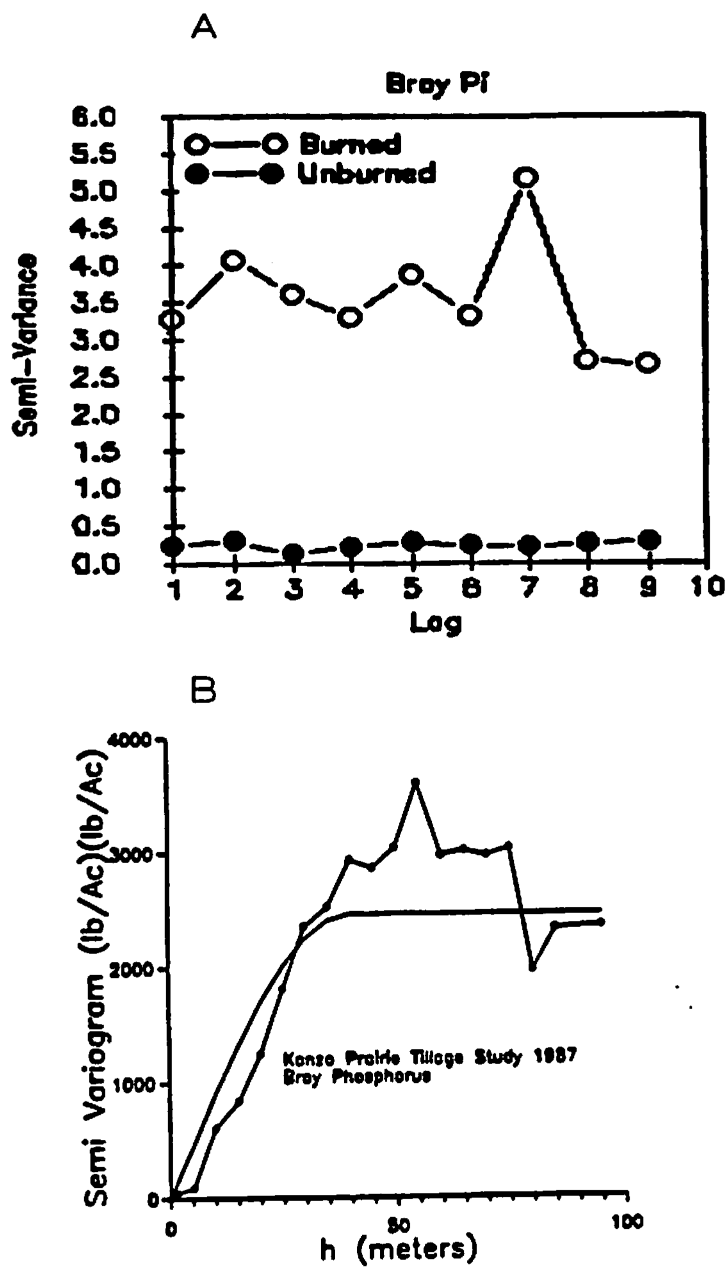


Figure 29. Semi-variograms of soil phosphorus concentrations. The absence of autocorrelation in upland prairie soils (A) is contrasts sharply to the more typical pattern observed for a Konza agroecosystem (B). (Note 1 lag = 5 m in A). Similar results have been observed for nitrogen. These findings are from short-term studies (Sisson and Schwab unpubl., J. Hetrick 1989), that supplement long-term fire-frequency related measurements.

The geology of Konza can be described as a series of thin limestones interbedded with thick shales. Fracture flow probably dominates in both permeable limestone and less permeable shale units (Figures 7,32). Because the units are nearly horizontal in space, the streams dissecting the N04D watershed cut through progressively older strata, and are fed by (during wet periods) or lose water to (during dry periods) several limestone units. The nature of the relationship between groundwater and surface water is important to understanding the overall hydraulic and chemical regime at Konza. The dynamics of groundwater-surface water interaction may be difficult to determine over a short period, but should be discernable (and, eventually, predictable) over a long period of time. To this end, we will continue to monitor surface water flow and chemistry (Tate and Koelliker), and the well casings of the 18+ observation wells installed on N04D will be surveyed to calculate heads and map probable groundwater flow paths (Pomes, USGS).

Our goals in studying the inorganic and organic groundwater chemistry of Konza Prairie are three-fold: 1) to identify variations in the water chemistry within the N04D watershed; 2) to use these variations to evaluate factors controlling the groundwater chemistry and identify probable flow paths; and 3) to attempt to evaluate the extent of groundwater-surface water interactions.

The chemistry of groundwater and surface water depends upon abiotic and biotic processes occurring from precipitation to throughfall to the unsaturated (soil) zone as well as in the saturated zone of an aquifer system. Preliminary analyses confirm that significant variations in specific conductivity, nitrate and dissolved organic carbon (DOC) exist, even in a single stratigraphic horizon. Understanding the causes for these variations will improve our understanding of chemical and biological processes operating at Konza. The sampling program will be designed to characterize groundwater from different stratigraphic horizons by its chemical signature. Water samples will be collected from several stratigraphic horizons in the unsaturated zone (lysimeters), the saturated zone (observation wells), springs, as well as above and below seeps (groundwater discharge points into streams). Current precipitation, throughfall and stream water sampling will be continued. Samples will be analyzed for major elements and dissolved organic carbon; representive samples will be analyzed for isotopic character and trace elements. In addition, with the continuation of our KSU/USGS cooperative agreement, Thurman and Pomes will identifiy the types and amounts of natural organic compounds present in DOC (i.e., fulvic and humic acids, carbohydrates, soluble fatty acids and alcohols) which can be used as natural tracers for

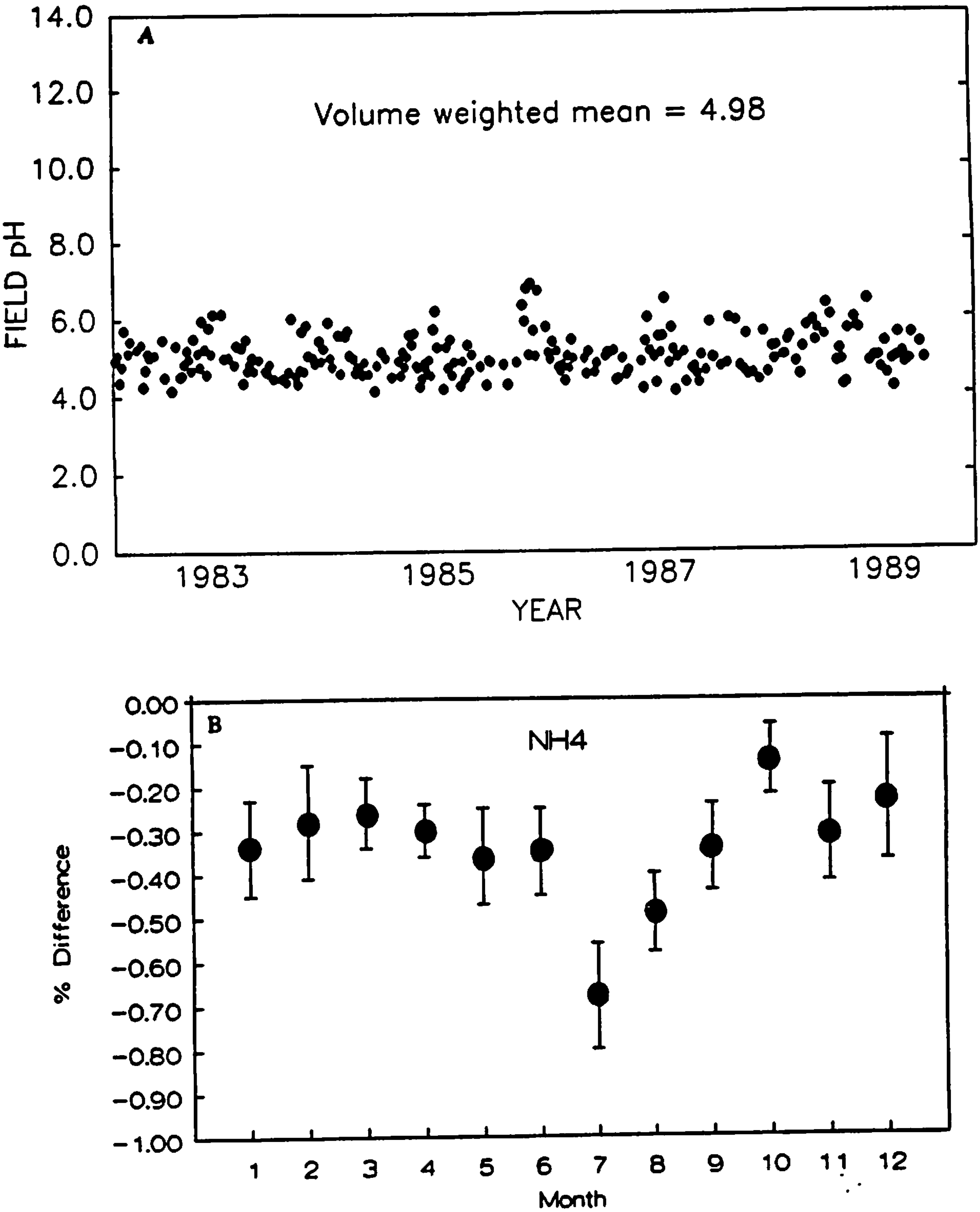


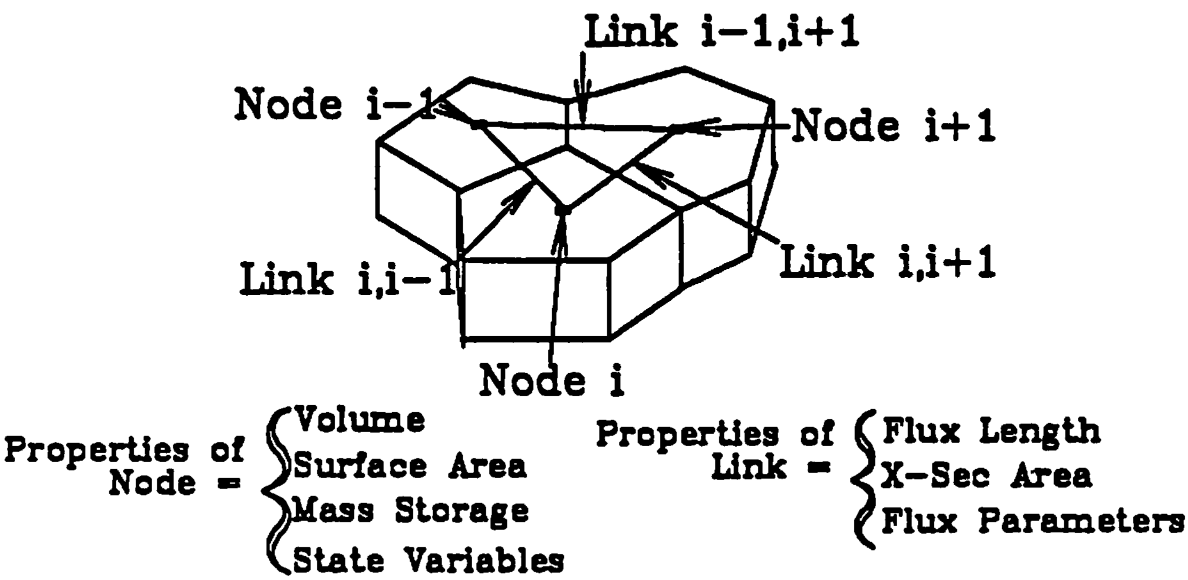
Figure 30. A. Acidity (pH) of individual wetfall events, as measured by our laboratory prior to shipping samples to Illinois for analysis as part of the NADP effort. An analysis of monthly average volume-weighted results indicates that late winter precipitation is more acidic than at other times of the year. The second figure (B) compares ammonium values obtained by our lab compared with samples sent to Illinois for analysis. Our results, which have been verified by an independent laboratory, indicate that a strong seasonal bias exists in NADP estimates of ammonium concentrations (Ramundo and Seastedt, submitted; data sets NTF01, NADP1). While the bias is generally known among researchers, the extent of site biases and the seasonality of these biases have not been documented. These correction factors need to be established if NADP data are to be used in multisite analyses.

water movement and indicate compounds available to the microbial community. Also, if enough inorganic geochemical data are collected and additional funds are found, Macpherson and Sabina Bock (Kansas Geological Survey) will attempt to determine the geochemical reactions affecting the groundwater chemistry, which can then be used to suggest probable groundwater flow paths. The controlling geochemical reactions are best discovered using reaction-path modeling programs such as PHREEQE (Parkhurst et al. 1985). This computer model increases our ability to predict changes in water chemistry along groundwater flow paths, and adds the capability to form and test a hypothesis about the hydrochemical system. The progress of chemical reactions (or the extent of reaction) will help us suggest specific pathways along which groundwater moves at the Konza. These pathways should confirm pathways predicted by hydrologic analysis, but may also reveal complexities, such as mixing of water from different aquifers, which are not obvious from simple analyses of head distribution. After identifying potential groundwater pathways at Konza and confirming that groundwater flow is relatively fast, we will test our hypotheses by using conventional water-tracing techniques (dye or conservative tracer) to determine the time of travel and identify the extent of hydrodynamic dispersion along the flow path.

Landscape-GIS Studies (Nellis, Briggs, Henebry)

The entire research site has served as an experimental unit for a number of landscape-related questions (Nellis and Briggs 1988) and is currently being used in both NASA and NSF-sponsored projects on interfacing biological phenomena with climatological variables. Our ARC/INFO and ERDAS systems allow us to aggregate data from the smallest unit of a GIS (determined by the specific data set) up to a single value for the entire site. While this system has been totally operational only since 1989, Nellis and Briggs (1987,1988, 1989), Briggs and Gibson (submitted) and Seastedt and Briggs (1990) have begun to explore the potential of this technology (Figures 2,35).

The NASA-FIFE project provided us with all TM and SPOT images for the 1987-1989 interval (Table 2). We are currently attempting to obtain additional pre-1987 images. We propose to continue collection of all relatively cloud-free Landsat TM images of the site, and supplement these data, when possible, with SPOT images and aerial photography. These data allow us to select sample area and sample numbers appropriate for



Definition of a Link-Node System

Figure 31. For systems modeling, Konza Prairie will be divided into a network of discrete "Link-Node" compartments using GIS. Variables at the "Nodes" characterize the matter/energy stored at that site. Nodes are interconnected by flux paths or "Links". Any number of state variables can be computed at each node with each state variable following a different system of governing equations. This Link-Node system will serve as the spatial infrastructure for the integrated soil-water-vegetation model we propose to develop.

Table 2. Satellite Image and GIS Inventory

Current Holdings

1) Over 50 AVHRR images of Konza from 1987 and 1988 are available. These images are 256 X 256 subset of the original images.

2) Multispectal Scanner Images

22 April 1986	11 May 1986	15 August 86

3) Thematic Mapper Images

12 August 1983	15 May 1984	22 Jume 1985	09 April 1987
11 May 1987	12 June 1987	14 July 1987	15 August 1987
31 August 1987	18 October 1987	27 April 1988	13 May 1988
06 June 1988	01 August 1988	25 August 1988	26 September 1988

4) SPOT

Multispectral Images

20 March 1987	05 April 1987	10 April 1987	01 May 1987
31 May 1987	01 June 1987	06 June 1987	11 June 1987
26 June 1987	27 June 1987	18 July 1987	23 July 1987
28 July 1987	02 August 1987	07 August 1987	17 August 1987
13 September 1987	23 September 1987	24 September 1987	03 October 1987
04 October 1987	24 October 1987	30 October 1987	04 November 1987
09 November 1987	13 April 1988	09 May 1988	25 May 1988
20 June 1988	05 July 1988	21 July 1988	05 August 1988
31 August 1988	06 September 1988	16 September	18 October 1988
23 October 1988			

Panchromatic Images

06 June 1987	26 June 1987	08 August 1987

Current GIS Coverages

1) Digital Elevation Map (DEM). It has a horizontal resolution of 25 meters and a vertical scale in tenths of feet.
2) Slope derived from the DEM.
3) Aspect derived from the DEM.
4) Roads, Trails, Piplines and Powerlines
5) Boundary Lines
6) Fence Lines
7) Konza Geology
8) Research Treatment Areas
9) Soils (only Riley County)
10) Woody trees and shrubs of selected watersheds. These coverage have locations as well as species and height of all individuals.

Note: The rest of 1988 and all of 1989 Spot and TM images will be provided by NASA-FIFE project. All historical TM and MSS images with low cloud cover of Konza during the growing season are scheduled to be purchased. In 1990 and thereafter at least one low cloud cover SPOT MSS and/or TM image of Konza during the growing season will be purchased.

specific questions as well as test the importance of spatial scales in measurements of various ecological phenomena (Seastedt and Briggs 1990). We have expanded our GIS capability beyond the LTER minimum standard installation with the addition of PC ARC/INFO University Lab Kit that we are sharing with the Department of Geography.

Modeling (Henebry, Tracy)

We propose to build upon the extensive grassland systems modeling efforts developed over the last two decades. Our goal is an integrated soil-water-vegetation model that explicitly addresses the topoedaphic gradients found at Konza and translates these landscape features into constraints on biotic processes.

Soil moisture is a dominant physical constraint on NPP and soil fertility in most years. As we discussed in "Landform Effects on Hydrology and Surface/Ground Water Chemistry", the initial configuration of the Link-Node network will be motivated by extant data on surface water movement. Model development will focus on the most intensively studied watershed on Konza, N04D.

Concomitant to the development of the model's physico-chemical subsystems by members of the Wet Group, especially J. Tracy, are the development of the vegetation and soil organic matter subsystems by G. Henebry. Soil organic matter dynamics will be simulated using a version of CENTURY (Parton et al. 1987) that has been modified to take advantage of the Link-Node network of physico-chemical subsystems. CENTURY simulates decomposition rates in the multiple soil organic matter compartments as a function of soil temperature and precipitation and includes both carbon and nitrogen flows. The plant growth section of CENTURY will be replaced by links to a version of the high-resolution GRASS model (Coughenour 1984) that has been revamped to reflect Konza conditions.

GRASS operates through a nested temporal hierarchy reflecting a range of environmental influences on graminoid growth. Tillers are divided into three functional classes, each of which has distinct age classes and nitrogen content. The coarse time scale of one day governs growth, translocation, nitrogen uptake and root respiration. Each day is divided into light and dark periods. During the light period, an hourly increment governs canopy light, temperature and cloud cover. The finest time scale of several minutes is reserved for soil heat and water fluxes, stomatal flux, plant water potential and leaf energy balance.

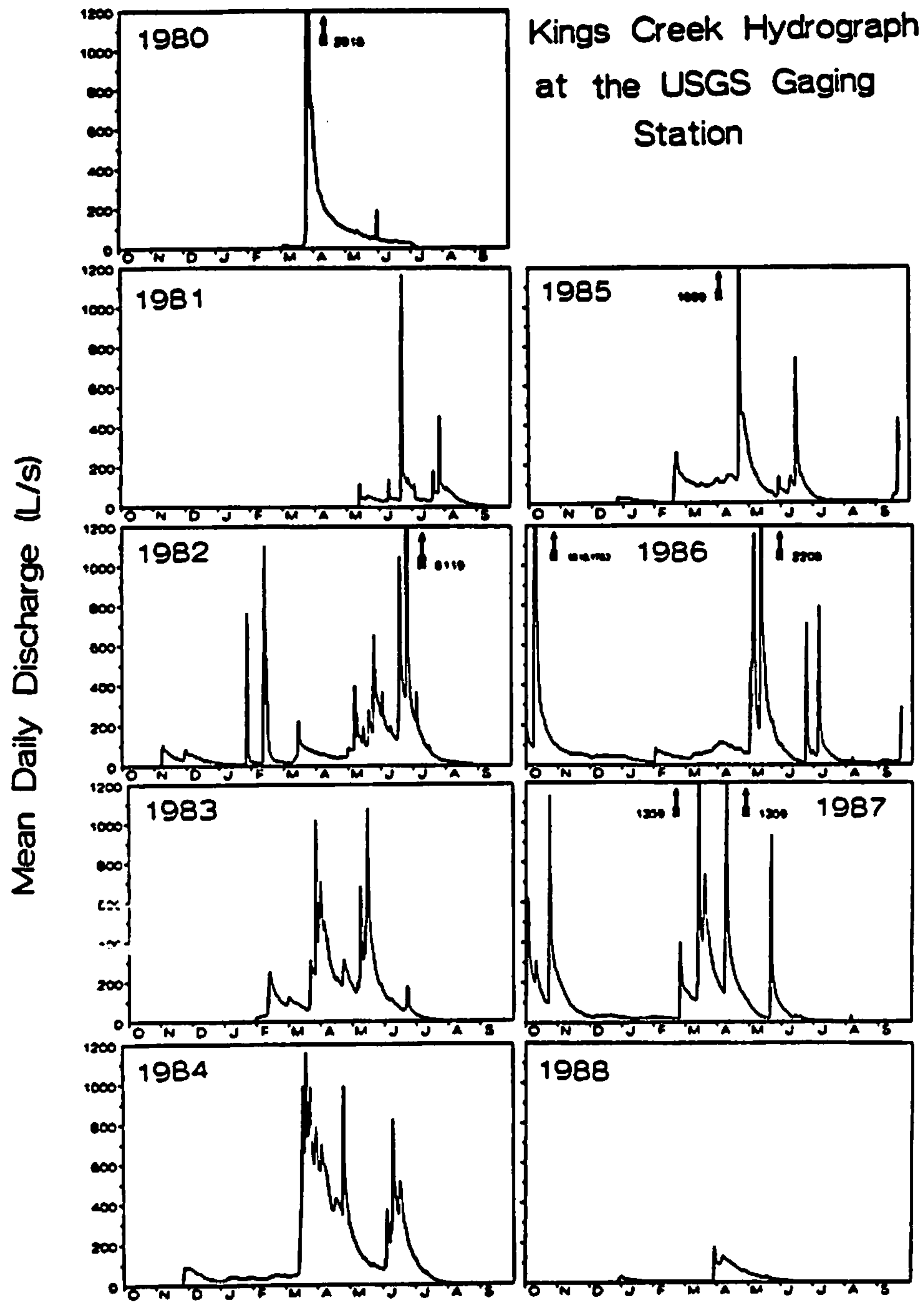


Figure 33. Kings Creek hydrograph showing the unpredictable flow regime of prairie streams in northeastern Kansas. Water year 1982-1987 reflect the above average precipitation during this period. The 1988 water year represents the first year of a drought. No flow occurred from July,1988 until September, 1989. These data are obtained by the USGS and routinely transmitted to KSU.

A version of GRASS is currently being used in our NASA-supported study of grazing-climate interactions. While it does provide the fine temporal resolution required by GCMs, the problem of scale-up currently limits its utility. Our integrated model will initially focus on resolving the fire-grazing-landscape dynamics within the catena. One of our objectives in the latter stages of the funding period is to address the scale-up issue; specifically, how can we best integrate over the landscape (N04D watershed to KPRNA to Flint Hills) to achieve adequate resolution without computational burden. At this stage of model development, the direction to pursue is not clear. Indeed, Neilson et al. (1989) cite it as a "key hurdle" in the simulation of climate-biosphere interactions. However, as our integrated model takes shape, we will be able to identify critical parameters and forcing functions through sensitivity and uncertainty analyses. Moreover, the Link--Node network provides a natural mechanism for exploring the model's spatial scaling effects. With these data in hand, we will be better able to modify and scale-up the integrated model using remote sensing/GIS images of Konza and the Flint Hills. Our proposed model does address other "key hurdles" indicated by Neilson et al. (1989), namely, the nesting of ecological process models and the linkage to physical process models.

Critical to the development of these models, indeed all spatially-explicit models, is an understanding of the covariance structure of observed variables (e.g., soil moisture, biomass) within and across relevant spatio-temporal scales. Such data are necessary for model calibration and validation. For instance, analysis of multivariate transect data can reveal the statistical structure of the field which, in turn, can be used to compute optimal estimates of ensemble mean values of a variable field for a given time and location as well as to estimate missing values. Such techniques are being used in synoptic meteorology (Thiebaux and Pedder 1987) and quantitative geography (Griffith 1988). We do not, however, envision the need for a sampling program beyond those outlined in other sections of this proposal due to the already extensive data sets gathered through LTER and FIFE.

Finally, the integrated model we propose requires substantial computational power. While initial development can occur on local workstations, uncertainty analyses and production runs will demand supercomputer resources. KSU has recently acquired a minisupercomputer (SCS-40) that can accommodate some of this demand. However, we will turn to the National Center for Supercomputing Applications (NCSA) for most of our need for processor power. NCSA is equipped with both serial (CRAY-XMP/48, CRAY-2) and

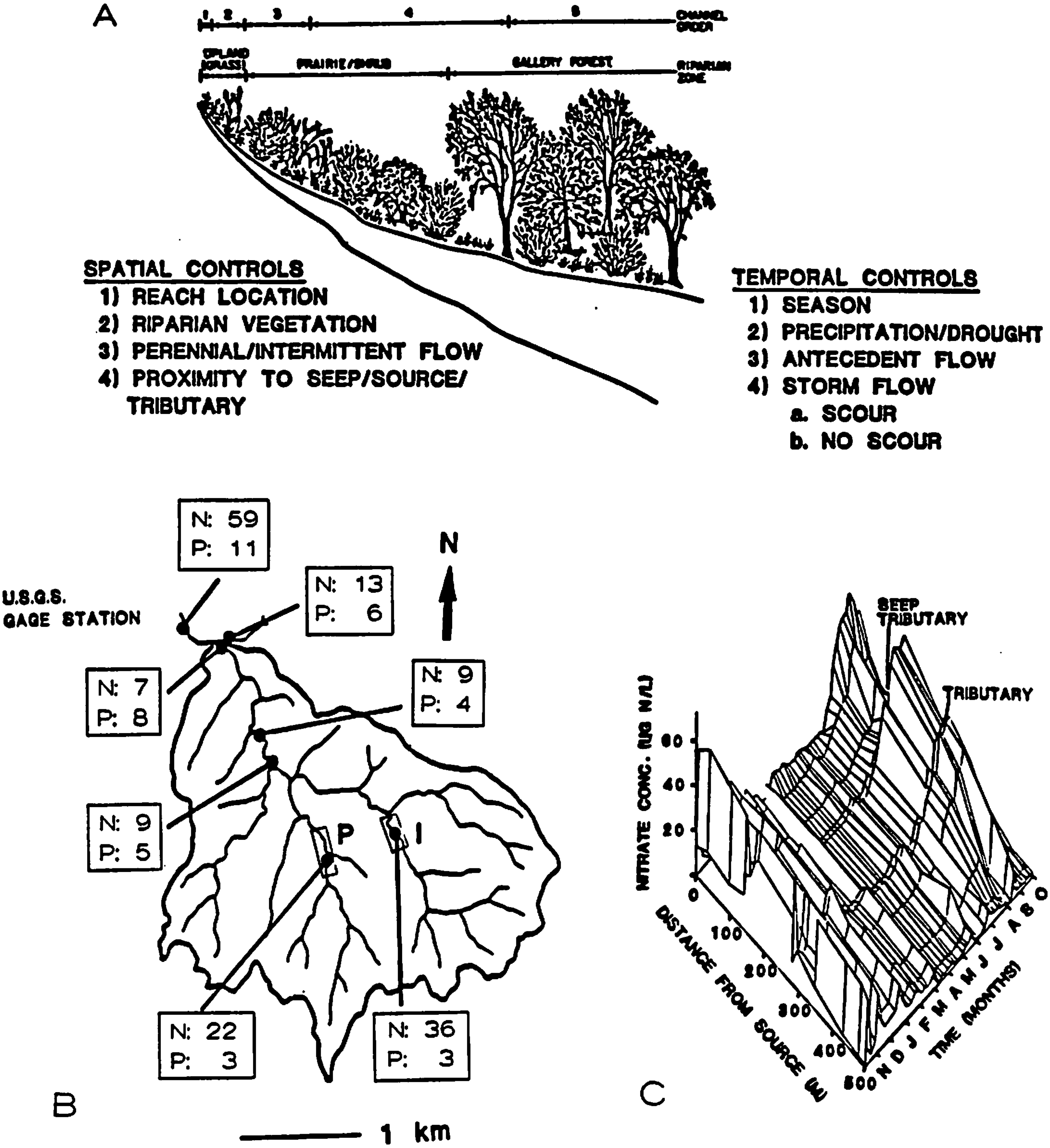


Figure 34. Controls and patterns of nitrogen in Kings Creek. A. Factors controlling nitrogen dynamics.

B. Spatial variation of nitrate and phosphate in Kings Creek drainage (N: means ug NO_3-N/L, P: mean ug PO_4-P/L).

C. Spatial and temporal variation of nitrate in a perennial reach (Box P in B). These data are from Tate (in press) and data set NWC01).

parallel (Connection Machine CM-2) machines. Development of the integrated model for N04D will use the serial machines. Extension of the integrated model to the multiple-watershed and regional scales will require a degree of concurrent processing that is available only on a massively-parallel computer as will be discussed in section 10 (New Projects and Technologies).

Section 2: LTER Specific Topics

1. The Core Areas

Research at our site is question driven, and categorizing these topics into the five core areas is a simple task. Individual hypotheses were listed under core area headings. Elsewhere (Evans et al. 1989) we have reported our objections to the use of generic "disturbance questions" to tallgrass phenomena. Our system is fire (and potentially, grazer) maintained. The question becomes: what, if any, is the effect of disturbance at a specified focal level (Pickett et al. 1989)? Because a disturbance is an event (Rykiel 1985), the system response can potentially be measured at any scale. At some scales the response is negligible and thus the disturbance is absorbed by the system perhaps at higher focal levels (Collins 1990). That is, a grasshopper grazing on a tiller of a big bluestem has little impact on watershed productivity but may have dramatic consequences for its seed production. We are fortunate to have an experimental system at Konza in which pre-disturbance conditions and their variance are known, allowing us to measure system response to predictable disturbances such as fire and grazing at any functional level. At the same time, we recognize that high-intensity, infrequent events such as tornados, hail storms and floods can have long-term effects on the system. The measurements proposed for the other core areas are sufficient to detect these impacts.

2. Long-term Experiments

Fire and grazing records are carefully maintained for all management units on Konza Prairie. Ongoing data sets listed below represent output from our specific LTER long-term experiments. In addition to the replicated watershed-level fire and grazing study, the late Dr. L. C. Hulbert established a series of plots for species composition studies (Figure 36). These plots have already proved valuable beyond their original purpose; Hetrick and Gibson (1988) studied fire-topographic effects on mycorrhizal spore abundance. These plots, along with several other plot experiments initiated by Hulbert, will be continued. The Belowground Plots

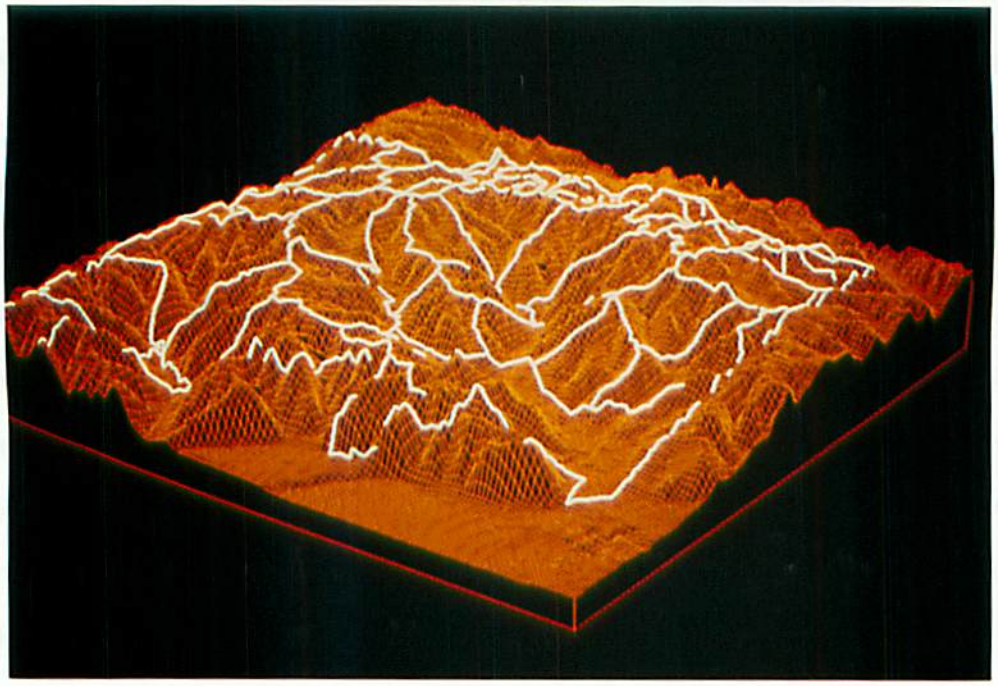


Figure 35. Digital elevation model of Konza (using the TIN module of ARC/INFO) with the watershed boundaries overlaid.

(Figure 26), were added in 1986, and additional, long-term fire frequency/fertilization plot experiments were initiated in 1988 (Seastedt et al. submitted).

3. Long-term Data Sets

The first land acquisitions that led to the organization of Konza Prairie occurred in 1970. Prior to that date, the site was a private cattle ranch. Aerial photographs of the site are available, and these data have been used to study riparian forest dynamics (Abrams 1985). Hulbert obtained both species composition data (Gibson 1989), and plant production data (Abrams et al. 1986) during the '70's prior to the initiation of the LTER in 1980. Other historical data sets that are available on the data network to the LTER investigators include: 1) weather data from Manhattan KS from 1891 to present, 2) mapping of woody trees and shrubs, 3) bird species lists, including dates of observation and nesting records, and 4) NPP and plant species composition data from long term (50 years) fire and cattle grazing experiments conducted on plots within 10 km of Konza (Towne and Owensby 1984). The LTER data sets, showing the length of time of collection and current status, are listed in Appendix C.

4. Data Management

If Konza Prairie is the most intensively studied grassland on earth, it follows that our data management group has an immense responsibility and plays a key role in Konza's continued development. While the State of Kansas provides considerable site management support, we have yet to obtain state support for Konza Prairie data management. This means that the LTER data management personnel function in a larger role and manage non-LTER data as well. For example, we plan to procure a large portion of the NASA-FIFE database.

The overall objectives of the Konza Prairie LTER Data Management (KPLDM) plan are to assure data integrity (correctness, at all times, of all items in the database), improve security (protection against loss of data), and facilitate use of data by the original investigator(s) as well as by future researchers. Our goal is the development of a research database to address scientific questions ranging from local to global scales.

Data management at Konza Prairie LTER has been an important component of the project since 1981 (Gurtz 1986). J. M. Briggs, the current data manager, has been with the project since 1984. He has been involved with the data managers at other LTER sites and is currently working on a manuscript with S. Stafford (Andrews), B. Michenier (North Inlet), and B. Benson (Northern Temperate Lakes) entitled "Computer

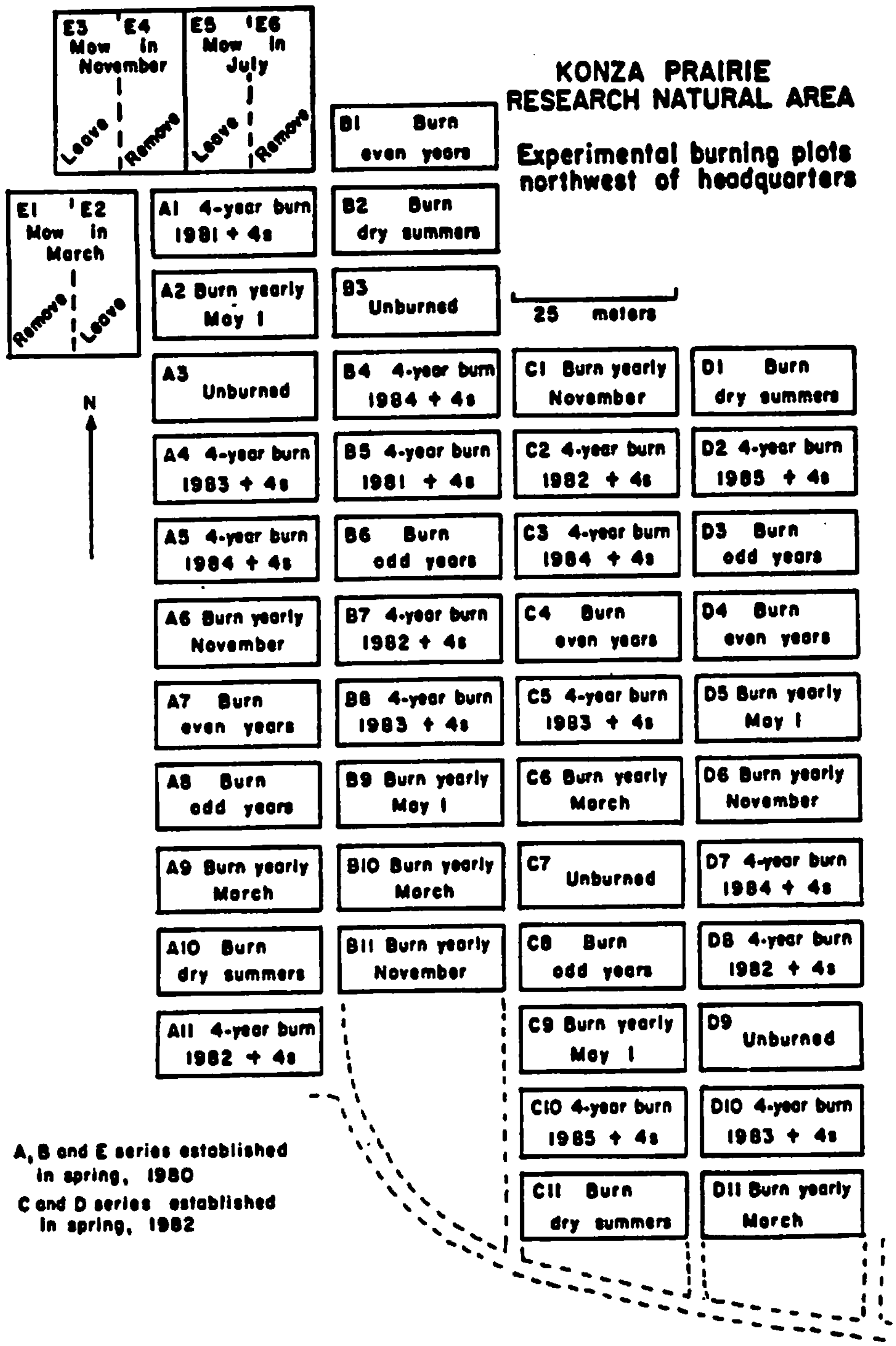


Figure 36. The Hulbert plots, an experiment to study fire effects on plant species composition, initiated in 1980.

Revolution in Ecology". Briggs has a working relationship with all the scientists at Konza and has published/submitted articles with Collins, Evans, Finck, Gibson, Kaufman, Knapp, Nellis and Seastedt. This emphasizes both the importance of data management at the project synthesis level, and the value (at our site at least) of having a trained biologist in this position as data management coordinator.

C. Kinderknecht, network manager and computer programmer, joined KPLDM full time in January 1988. Before that time he worked as a programmer and has written the data entering, data checking, data reformatting, network utilities and the data documentation programs. In addition, he has written many specialized programs for many of the LTER investigators ranging from vegetation species summary, specialized spatial statistics, image processing, and jackknifing programs. His expertise in computer programming has allowed Briggs to assume a more generalist role as an active researcher/synthesizer.

Hardware and Software

KPLDM has acquired various computer hardware and software to accomplish the objectives listed above and to maintain the data base. These are discussed below.

Figure 37 and Table 3 summarize the present extent of hardware and software facilities available to the Konza Prairie LTER research staff. At present, we have linked the personal microcomputers of most LTER researchers directly to each other and the Konza Prairie data bank through the Novell Network (Figure 38). This allows data, reports and manuscripts to be transferred among researchers. Our Konza Prairie data bank includes archived LTER data with an electronic data catalog that allows any connected investigator to browse necessary documentation such as data format, site location, etc. Our administration on campus has supported our need for electronic mail and data transfer on campus and across the network, and is in the process of installing fiber optic cable in our building to allow us to be connected to campus-wide ethernet connection. Such a connection is vital for our campus and off-campus communication in addition to our network activities.

The new image processing and GIS equipment recently purchased will allow us to expand our efforts in both spatial variability and ecosystem modeling. Briggs has received training in the use of both the ERDAS and ARC/INFO software at both company facilities and at the LTER sponsored GIS/Remote Sensing Workshop. Nellis also has been trained on this software. This equipment and training, coupled with the array of remote-sensing data available from the NASA-FIFE experiment on Konza from 1987 to 1989 have allowed us to build

Konza Prairie LTER PC Network

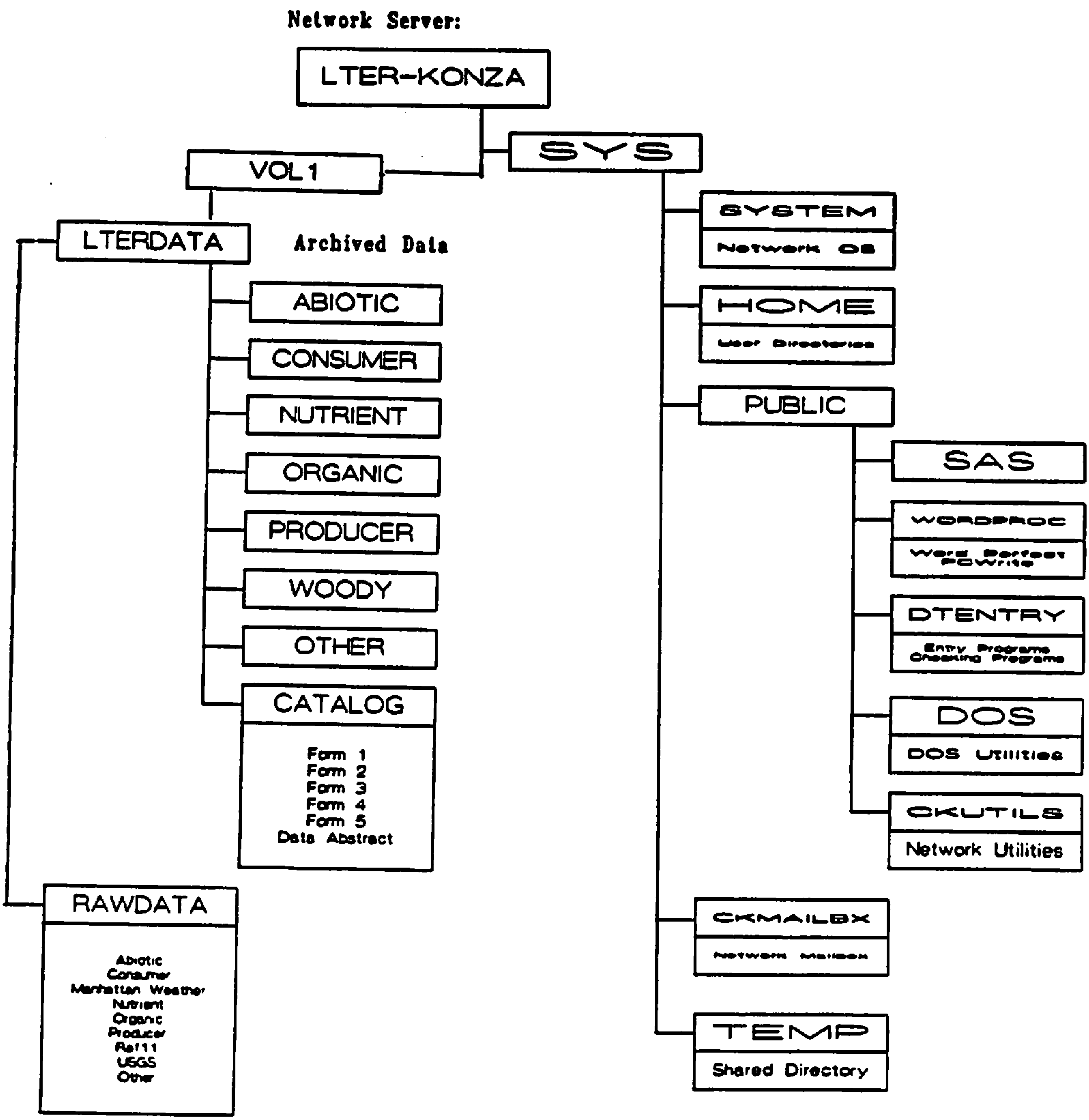


Figure 37. Schematic outline of the Konza LTER data base and associated files that on the Local Area Network.

Table 3. Computer Software and Hardware Equipment List

Image Processing and GIS Laboratory:

1-Sun 4/110 color workstation with 8Mb RAM, 900Mb disk, and 1/4" tape cartridge with ARC/INFO 5.0
1-8 mm Exabyte Cartridge Tape subsystem
1-Calcomp 8-pen plotter
1-Compaq 386/25 with 5 Mb RAM, 320 Mb disk with ERDAS 7.3
1-Cipher 6250 BPI 1/2" tape drive
1-Cipher 1600 BPI 1/2" tape drive
1-Tektronix 4696 Color jet printer
1-Video Digitizer
1-Altek 32" X 24" digitizer

PC Computers in Konza Prairie LTER Microcomputer Lab:

1-Zenith 386/33 with 2 Mb Ram, 150 Mb disk and VGA video
2-IBM AT's with 2046 RAM, 20 Mb disk and EGA video
1-Ultra Comp 80286 with 1Mb RAM, 50 Mb disk and VGA video
1-Ultra Comp 80286 with 640k, 50Mb disk and EGA video
1-Jameco 80286 with 640k, 80Mb disk and monochrome video
1-Zenith 158-3 with 512k, 20Mb disk and monochrome video
Computer Languages--Basic, Pascal, C and Assembler
Statistical Packages--SAS, RS/1
Graphics--SAS/GRAPH, 123, Slide Write, Quattro, Surfer
GIS/Image Processing--ERDAS, ARC/INFO, P-Map, Idrisi, MAP
Word Processing--Word Perfect, Wordstar, PC-Write
Database Management--DBASE IV

Network Hardware and Gateways:

1-Equinox Data Switch (allows gateway to campus IBM mainframe, Computer Science VAX 11/780 and Telenet)
1-Zenith 386/25 with 4 Mb RAM and 320 Mb disk (serves as Novell file server) with Novell's Advanced Netware/286
1-Summus GigaTape 8mm tape subsystem used for backups
1-UPS

Peripherals:

1-HP Laserjet II printer
1-HP 7475 Plotter
1-Data Products Postscript laser printer
1-Oki 393 24 pin dot matrix printer
1-IBM Quietwriter printer

Other Konza Prairie LTER hardware computer equipment
Most investigators associated with Konza Prairie LTER have an IBM-PC type machine in their office. By the end of this year, all will be connected to local area network in the microcomputer lab and to the campus-wide ethernet.

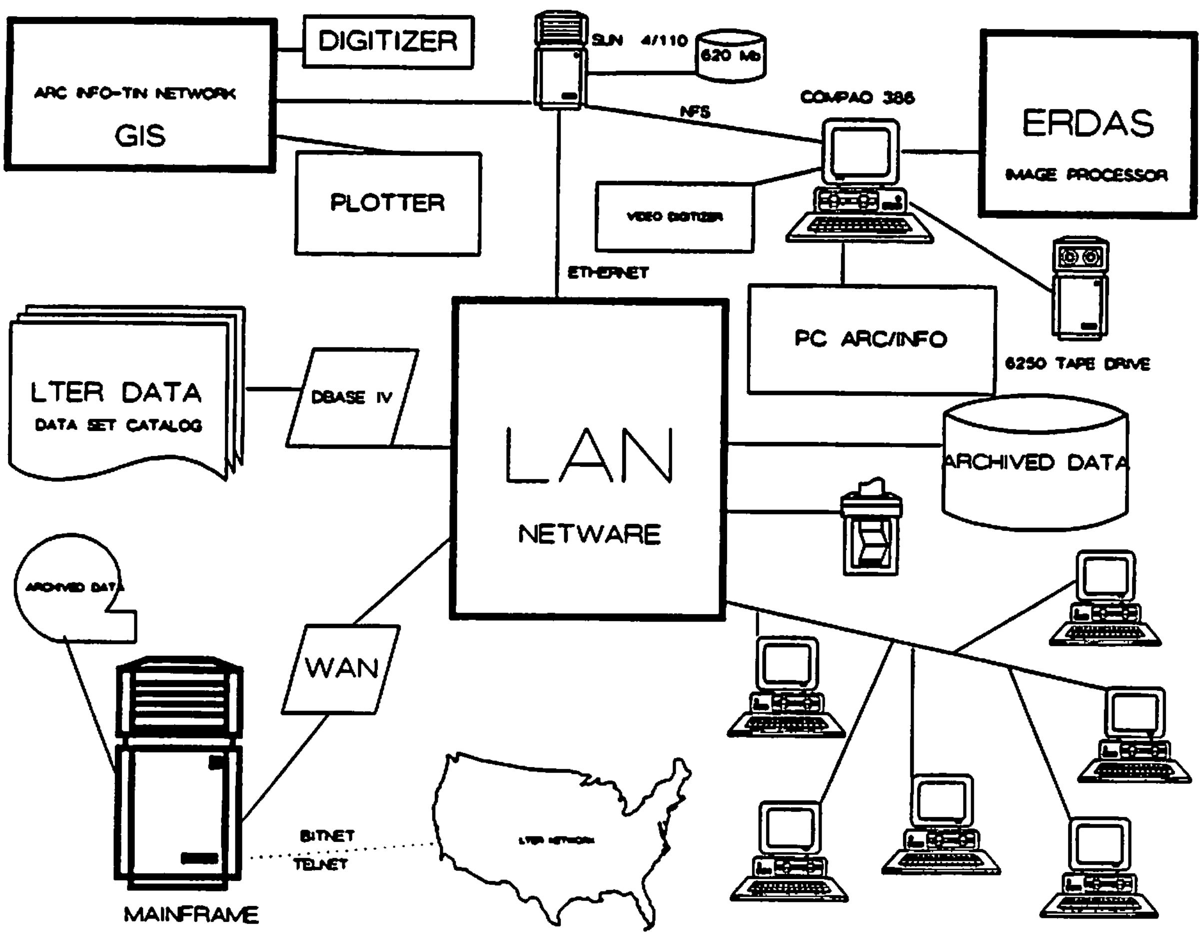


Figure 38. Diagram of the computer facitilies available to the Konza LTER research staff.

an extensive GIS database that we are just now beginning to exploit (Nellis and Briggs 1989). The GIS database linked to the Konza Prairie LTER database will increase our ability to address landscape-level questions and conduct complex, interactive modeling.

Konza Prairie Database

The list of 70 LTER data sets which are being maintained by the LTER staff are shown in Appendix C. Those data sets without an end date are presently on-going. In addition to the online data set catalog and data documentation, the Konza Prairie LTER staff has maintained a methods manual since 1981. This important manual (currently a 147 page document) details how each LTER data set is collected. It includes items such as precise maps of the vegetation survey, sample data sheets, and very detailed procedures on instrument installation and use. This manual provides the necessary details to interpret the more extensive data documentation files maintained for each data set. This document is updated yearly and a complete revision manual is produced every 5 years.

The Konza Prairie LTER data base requires a large investment in time and money to maintain. A large amount of time is spent constantly updating existing data sets and documenting new data sets. This is particularly true with the turnover of investigators at our site coupled with the new projects started on Konza and with the increase of investigators not affiliated with Kansas State University.

We have developed an user-interface to our LTER database to facilitate proper and prompt data documentation by the current LTER researchers to aid us in this job. Currently, we are using DBASE IV to store and retrieve documentation forms. A menu-driven format allows us to update, add or browse data documentation. We have developed data entry programs and data checking programs to aid us in our effort to maintain data integrity. We store all archived files (files that have been entered and thoroughly checked) on 1/2" magnetic tapes on the mainframe. In addition, we have multiple back-ups of the magnetic tapes. We are assuming that the 1/2" magnetic tapes will last 4-5 years and are rotating them under that assumption. Furthermore, we have weekly backups of our PC Network and Sun 4/110 using 8mm tape. Thus, we have at least three electronic backups of our LTER database at all times. Once a universal hardware standard for optical disks is established, we will replace the 1/2" magnetic tapes with optical disks. We are also storing the original data/field sheets. All data is stored in ASCII form for maximum portability to statistical and graphical systems of the investigator's choice or to outside investigators. The storage of data in ASCII form worked very well with the FIFE experiment on Konza, when during that time frame (1987-1988), we handled over 30 requests for Konza LTER data from scientists all over the world.

With the addition of remote sensing, GIS and modeling to the KPLDM, procedures are underway to determine the proper protocol necessary to store such items. Some of the procedures have been discussed with data managers from other LTER sites, but no firm decisions have been made. Presently, all satellite derived images of Konza are stored on 1/2" magnetic tape using band sequential format. Each image has an ASCII file with it, indicating information such as date, platform (i.e. SPOT, TM, etc), ground control points and the method of geometric correction. Future plans also include sharing bibliographic database (starting with the Konza Prairie Publications list) across the local area network with the goal of expanding this to all the LTER sites. We are presently exploring the software options available and again we have been in contact with data managers at the other LTER sites.

The number of requests (45) involving the access of archived data in 1989 has increased 50% over previous years. We have developed a protocol which was implemented in 1983 that has alleviated concerns expressed by investigators. We have three levels of access restrictions: unrestricted, limited restriction, and full restriction. Briefly, unrestricted--archived data sets with access to all current Konza Prairie researchers upon notification of the data manager. This is read-only access: it is understood that any errors discovered (or suspected) in an unrestricted data file must be brought to the immediate attention of the data manager, who will confer with the investigator. Limited restriction--archived data sets with read-only access available to current Konza LTER researchers or to outside researchers upon written permission of the current LTER PI(s) and the data set investigator for the time period of data requested. The PI(s) may deem that the investigator's approval is not necessary if he/she has waived that privilege, is deceased, or cannot be reached within a reasonable amount of time. Restricted--these data are accessible only to the investigator or persons designated by the investigator. These may be raw data files or other data files which are considered incomplete, unverified or otherwise uncertain as to their correctness. Our goal is to have all LTER data archived and in the unrestricted category within one year after the last datum is collected. These restrictions apply to data sets only after they are archived, before that, the data are entirely the responsibility of the investigator(s). Regardless of access restriction, no researcher outside of Konza Prairie LTER will be given access to LTER data without written approval of the LTER principal investigator. In addition we have adopted the following guideline for the release and citation of data collected as part of the Konza Prairie LTER project to individuals not directly associated with the Konza Prairie LTER project.

Data Requests at this time must include:

1) Formal written request and a statement of intended use.

2) Approval of the investigator and/or the Konza Prairie LTER Principal Investigator.

3) Request must be filed with the Konza Prairie LTER data manager.

4) Release of data (following approval) should include a cover letter specifying that: The data are released for your use only and for the purposes outlined in your request.

5) Manuscripts using the data are to be provided to the Principal Investigator, LTER, Division of Biology, Ackert Hall, Kansas State University, Manhattan, KS 66506 so that he/she may notify the appropriate investigators.

6) Publication of these data are allowed by the expressed permission of Konza Prairie LTER investigators named, who have primary responsibility for the data sets.

7) Acknowledgment should be made to recognize the contribution of data by Konza Prairie LTER. In addition, the format shown below is also to be included with the letter. Citation of a data set should use the following format: "Data from the Konza Prairie Research Natural Area were collected as part of the Konza Prairie LTER program (NSF grants DEB-8012166 and BSR-8514327), Division of Biology, Kansas State University, Manhattan, KS. Data and supporting documentation are stored (Data Set Code(s)=_____) in the Konza Prairie Research Natural Area LTER Data Bank." Additionally, specific investigators might be cited for their contributions to the paper.

With the initiation of our third round of funding, the following data management policy will be implemented: "Accepting support from LTER includes the acknowledgment that the investigator agrees to archive all Konza LTER data in the Konza LTER database, and that this data will eventually be available to others. The investigator will have exclusive rights to such data for a maximum of three years from the time of data collection. Thereafter, the data manager shall have the right to provide these data to others. Permission

Table 4. Title, leaders, and status of major ongoing and proposed research projects involving 5 or more sites.

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1. Decomposition

a. Fine litter exchange experiment
Melillo (HFR), Harmon (AND - coordinator), Parton (CPR). A 21-site litter decomposition experiment in terrestrial systems is getting underway. A proposal for further work is in preparation.

b. Coarse woody debris
Harmon (AND), Schowalter (AND). Preliminary study of log decomposition based on periodic destructive sampling of a collection logs which were fresh when placed on the ground in 1985. Supported by a NSF grant. Support for a 5-site network is pending.

c. Litter decomposition in aquatic systems
Meyer (CWT). Proposal based on approach used in terrestrial fine litter exchange experiment to be developed ca. 1991.

2. Modeling Vegetation Dynamics in Forests and Grasslands
Shugart (VCR), Lauenroth (CPR), Parton (CPR). The approach is to utilize simulation models to investigate behavior of ecosystems over a range of sites in North America. Individual-based vegetation models and soil process models will be used to 1) account for existing patterns in ecosystems under a spectrum of environmental regimes arrayed along temperature and water gradients, and 2) to make predictions about the response of these ecosystems to environmental change. Test applications began in earnest in 1989 under several NSF grants. NSF proposal submitted 12/89 and some commitment made in appropriate LTER site proposals.

3. Climate Change Effects on Site Hydrology at Plot to Landscape Scales Grant (AND), Caine (NWT). A hydrology model (probably Precipitation-Runoff Modeling System (PRMS)) would be used in comparative analysis of hydrology, including effects of climate change. This would be done in cooperation with George Leavesley (US Geological Survey) who developed the model. Discussions of the project have been held with USGS. Use of PRMS is underway at AND and NWT.

4. Space/Time Variability in Diverse Systems
Magnuson (NTL), Kratz (NTL), and others. Variance in data from at least 5-yr and 5-location measurements of physical and biological variables are analyzed to characterize contrasting systems in terms of temporal and spatial sources of variance. Originally funded by senior investigator, Coordinating Committee, and site funds. Further work planned based on funding from latter two sources.

5. Ecosystem Properties Across Environmental Gradients
Tilman (CDR), Zack (CDR)--coordinators. Ten-site-comparison of soil nutrient dynamics, productivity, and plant life forms across environmental gradients in the US. Funded by Coordinating Committee and individual site grants.

6. Plant Demography, Especially Mortality
Harmon (AND), Franklin (NET), and others. A specific work plan for intersite comparative analysis of existing data will be developed at the tree mortality workshop at AND in April 1990.

from the original investigator will be requested, but after three years this request shall be considered a courtesy and not a prerequisite to data transferal."

The data manager will inform the LTER PI(s) regarding the annual status of data set entry and necessary documentation forms. Investigators not submitting data and supporting documentation collected with LTER funds shall be given reduced funding priority. LTER support to Konza Prairie researchers is based on their commitment to document and archive data and not to support their specific research interests.

5. Synthesis and Modeling

To date, we claim a BioScience article, several isolated book chapters and a large portion of one book (Collins and Wallace 1990) as examples of our efforts to synthesize our research projects. A book on Konza Prairie that made extensive use of LTER information was written by a colleague (Reichman 1987). The 11th North American Prairie Conference (Bragg and Stubbendieck 1989), a volume dedicated to the memory of the Director of Konza Prairie, L.C. Hulbert, contained substantial Konza Prairie information, including an important synthetic effort (Evans et al. 1989). Additional chapters and review articles have been published, and interest has been indicated in publishing several books during the proposed funding period. We acknowledge the need for such syntheses, but also point out that Konza Prairie, unlike other LTER sites, is of relatively recent origin and has not had an interdisciplinary focus until the current funding period.

Our site had essentially no mathematical modeling activities through 1985. Beginning in 1986, however, Koelliker used a hydrologic model to focus his research (e.g., Bartlett 1988, Koelliker 1988). The CENTURY model developed by W. Parton, CSU (e.g., Parton et al. 1987), was adapted to tallgrass prairie and used to predict effects of fire and fire frequency (Ojima 1987, Ojima et al. 1990). LTER data were used to parameterize the model and Ojima was hired as a consultant to develop a life-form version of CENTURY. The model predictions provided the focus for the ecosystem research conducted on Konza for the last several years. The success of CENTURY and its usefulness to the LTER effort convinced us of the need for a full-time modeler. Consequently, Henebry joined our program in June of 1989.

W. Lauenroth (CSU) and H.H. Shugart (U.VA) have an ongoing modeling effort in which Henebry has and will continue to participate. Among the objectives of this effort include many of our within-site questions:

Table 5. Federally funded research projects on Konza Prairie (1986-present)[1]

Investigator (University)	Title (Co-Principal Investigators, Agency)
Firestone, M.F.* (U.Cal. Berkeley)	Interaction of soil nitrogen and water cycles as control of N-gas production. (NSF)
Gray, L.J. (Ottawa Univ.)	Biotic export of energy and nutrients from a prairie stream ecosystem. (NSF)
Groffman, P.J.* (U. Rhode Island)	Denitrification, nitrous oxide, carbon dioxide and moisture dynamics at the landscape level using remote sensing techniques. (NSF and NASA)
Hartnett, D.C. (KSU)	Effects of bison herbivory on two tallgrass prairie species: The influence of fire, competition and pattern of defoliation on plant responses. (NSF)
Havlin, J.L. (KSU)	Synchrony and contribution of legume nitrogen for grain production under different tillage systems. (C.W. Rice, USDA-LISA)
James, S.W. (KSU)	Impact of a changing earthworm fauna on decomposition and mineralization processes of tallgrass prairie. (T. Seastedt, NSF)
Kanemasu, E.T. (U.Ga)	Canopy photosynthesis and resistance measurements for FIFE. (J.L. Norman, NASA)
Keeler, K.* (U. Nebr.)	Polyploid polymorphism in big bluestem. (NSF)
Knapp, A.K. (KSU)	Non-steady state responses in net photosynthesis and stomatal conductance during periods of variable sunlight. (NSF)
Lauenroth, W.K* (CSU)	Plant community structure across resource gradients from grassland to forest. (H.H. Shugart, NSF)
Norman, J.L. (U.WI)	Measuring and modeling of near surface reflected and emitted radiation fluxes at the FIFE site. (B.L. Blad, E.A. Walter-Shea, NASA)
Parton, W.J.* (CSU)	Interactions of fire and grazing on landscape patterns in tallgrass prairie (D. Schimel, C. Owensby, NSF)
Schimel, D.S.* (CSU)	Biological control of land-atmosphere exchange: an ecosystem study. (A. Knapp, W. Parton, T.Seastedt, C. Wessman, NSF)
Schimel, D.S. (CSU)	Surface biophysical properties and trace gas exchange in the tallgrass prairie. (W.J. Parton, R.G. Woodmansee, NASA)
Seastedt, T.R. (KSU)	Effects of invertebrates and small mammals on the productivity and nitrogen dynamics of tallgrass prairie. (E. Evans, L. Hulbert, D. Kaufman, S. James, NSF).
Seastedt, T.R. (KSU)	The influence of grazing on land surface climatological variables. (M.I. Dyer and C.L. Turner, NASA)

"1. Investigate the two-way interactions between ecosystem processes (carbon balance, nitrogen cycling and water relations) and vegetation structure (life form and species composition, physiognomy, size and age-class distributions).

2. Determine the pattern of environmental constraint on ecosystems in terms of the relative importance of light, water, nutrients and temperature in controlling ecosystem processes and vegetation structure.

3. Explore the importance of disturbances as system constraints that interact with ecosystem processes and vegetation structure.

4. Assess the direction and magnitude of ecosystem response to climatic change, with explicit consideration of the significance of short-term transient behavior" (W.K. Lauenroth, pers comm).

Given the large amount of overlap between these modeling questions and our empirical efforts, Konza Prairie has much to offer this modeling project in terms of calibration and validation of data. The project emphasizes integration of life-form vegetation models, STEPPE (Coffin and Lauenroth in press) and a new generation of FORET models developed by Shugart's group (e.g., Urban et al. 1987), with abiotic process models (e.g., CENTURY). We expect that their end product will complement the biophysical emphasis of our own integrated modeling effort. Together these models will provide Konza with a singularly robust framework within which to generate and evaluate hypotheses.

6. Intersite and Network Activities

Researchers from our site were among the first to participate in multisite studies. Gurtz (1986) helped develop the data management system now used at a number of LTER sites. Tate spent two years on a NSF Fellowship comparing the nitrogen and phosphorus sensitivity of streams in five different biomes. Seastedt et al. (1989) expanded upon an intersite research project of Schowalter and compared densities and indices of species diversity of fauna in decaying wood. The list of ongoing multisite projects and investigators involving Konza Prairie and LTER investigators is rapidly increasing. Table 4 illustrates the proposed and ongoing projects at five or more LTER sites. Eight of 19 federally supported projects on Konza Prairie during the current five year period have involved at least one additional site (Table 5). In addition, we know of at least eight multisite projects involving Konza Prairie that are pending at NSF (Table 6). We strongly concur with the statement of commitment of intersite research prepared by Cohort I LTER sites (Table 7).

Table 5 cont. ------Federally supported research on Konza Prairie, 1986-present, cont.----

Sharpe, P.J.H.* (Tex. A&M)	Spatial relation, resources and disturbance: A comparative ecosystem study. (NSF)
Tate, C.M.* (U. WI)	Seasonal response of stream periphyton to nutrient enrichment in five biomes. (NSF)
Thurman, E.M. (USGS, Lawrence)	Organic groundwater chemistry of various aquifers beneath tallgrass prairie. (USGS)

1. Projects as of January 1990, exclusive of airborne or off-Konza NASA-FIFE studies.
* Multisite projects.

Table 6 .Current and pending *multi-site* research projects on Konza Prairie. (see also Table 4.)

Investigator (Institution)	Title (Initiation date of project)
----------current projects----------	
Schowalter, T.D. (Oregon State U.)	Cross-site comparison of wood decomposition. (1987)
Harmon, M.A. (Oregon State U.)	Litter decomposition study (materials collected 1989)
Tiezsen L. (Augustana)	Comparative analysis of soil organic matter with stable C and N isotopes at several LTER sites. (1989)
----------pending projects----------	
Bledsoe, L.J. (U. Wash.)	Biogeochemical cycles across the LTER network.
Dahm. C.N. (U. New Mex.)	Comparative analysis of methane flux in small order streams.
Grimm. N.B. (Ariz. State U.)	Hydrologic and biogeochemical linkages between the hyporheic and surface zones of streams.
Huntly, N. (U. Idaho)	Patterns, scales and mechanisms of influence of spatially explicit animal-generated disturbances on plant community structure.
Myrold, D.D. (Oregon State U.)	^{15}N tracer studies of soil microbial dynamics in forest and prairie.
Lauenroth, W.J. (Colo. State U.)	Coupling ecosystem processes and vegetation structure across environmental gradients.
Fahey, T.J. (Cornell U.)	Fine root dynamics, a cross-ecosystem study.

We are currently working at three spatial scales above our individual site. We are developing a tallgrass prairie regional network, which includes a network of tallgrass prairie sites (including at present: Fermilab (IL), Tucker Prairie (MO), The Land Institute (KS), and the Nebraska sites, Allwine Preserve, Arapaho Prairie and the Niobrara Preserve), as well as a group interested in comparing prairie and agroecosytem properties (e.g., Havlin and Rice's LISA study, Seastedt and Brigg's proposal to MAB). An example of this regional interaction occurred in 1986-87, when LTER data sets were used in a preliminary evaluation of the status of nearby tallgrass prairie sites used for military training activities (Schaeffer et al. in press). The next spatial scale includes the North American grassland and arid-lands study, a program currently lead by the CADRE effort of Colorado State University. We provide an eastern link to their network.

The largest scale involves the participation of our personnel in the LTER and associated networks, and our group is involved at this level. Tate was invited to the Third Cary Conference and was an author on "The Ten Commandments of Comparative Analyses" (Tate and Jones, in press). Active collaboration currently exists for several initiatives, including modeling (Henebry), data management (Briggs), stable isotope and stream studies (Tate), remote sensing/GIS (Nellis and Briggs), decomposition and organic matter dynamics (Rice), and global climate change (Knapp and Seastedt).

7. Related Research Projects

Additional non-LTER studies are listed in Table 8 (also see Tables 4-6). The NASA FIFE project (1987-present) represents a study of a size and scale previously unknown to ecologists; it dwarfs even the grasslands IBP work in terms of number of scientists involved, funding, data acquisition and data management (Appendix D). The significance of this effort to current LTER efforts cannot be overstated. If ecologists are to become realistic and active participants in the global change arena, they must be able to interact with this group (biophysicists and atmospheric scientists) and be capable of providing data appropriately scaled for vegetation-atmosphere studies. Biological processes and ecological constraints have extremely large influences on regional climate, both on the short and long-term (e.g., Figures 2,39). This fact has yet to be integrated into general circulation models. Until such information is incorporated, these models cannot provide realistic long-term predictions.

Table 7.

Statement of Committment to LTER Intersite Research and Coordination, for the LTER III Proposals of Cohort 1 Sites (Andrews, Central Plains, Coweeta, Konza, Niwot, North Inlet, Temperate Lakes).

The seven Cohort 1 LTER Sites have prepared this statement to define our committment to common intersite research and coordination activities. The magnitude of our past, present, and proposed intersite activity reflects our belief that these activities produce important results in ecological science. Further, the LTER Network makes possible collaborative research that would otherwise be extremely difficult or impossible.

The similarities of broad themes among individual site proposals (e.g. global change effects, ecosystem processes at multiple scales) lead naturally to identification of these intersite projects. Perspectives gained from intersite comparative studies and from pooling talent from multiple sites strengthens the research programs of individual sites. This interplay of site- and intersite-research is particularly important and effective in long-term research.

Listed in Table 4 are intersite activities in various stages of development. Many of these activities involve other (non-Cohort 1) LTER and non-LTER sites. In addition to the relatively extensive intersite research projects listed here, our sites participate in approximately two dozen research projects involving several sites each. Details of on-going and proposed activities are contained in individual site proposals, the Coordinating Committee proposal, work plans, and other documents. In some cases, the specifics have not been determined yet. Approaches to organizing and funding these activities vary in relation to their magnitude and stage of development. Approaches include funding from sites, the Coordinating Committee grant, and other NSF and non-NSF sources.

Given the rapid pace of change in ecological sciences, we expect that some of the most important intersite research to be developed over the six-year grant period are impossible to anticipate at this time.

Thus, our group has an important responsibility to the scientific community. First, we must provide proof-of-concept projects and studies using the FIFE data, and secondly, we must preserve the FIFE data base (FIS; Strebel et al. 1989) to guarantee its availability to ecologists. Our current cooperative study with Schimel et al. at CSU, and our own NASA projects should contribute towards the first goal. We are exploring avenues of obtaining a functional archive of FIS with Strebel and other personnel at NASA.

A list of federally funded projects on Konza Prairie for the period 1986-1990 that heavily utilized LTER data bases and/or experimental designs are shown in Table 5. Only those projects currently (1990) funded are briefly described here.

An NSF funded Doctoral Dissertation Improvement Grant to S. Glenn and S. Collins focuses on factors affecting small-scale patch dynamics in undisturbed tallgrass prairie. Removal of little bluestem from study plots at Konza and El Reno, Oklahoma, was completed in February 1989. Data are being analyzed to determine the effects of removing a dominant matrix-forming competitor on the patch dynamics of non-matrix species.

A NSF funded research project to D.C. Hartnett focuses on understanding plant growth, physiological and demographic responses to bison herbivory in two dominant grasses, big bluestem and switchgrass. This study is designed to determine how fire, plant competition and the spatio-temporal patterns of defoliation influence the continuum of negative to positive plant responses to grazing. Tiller growth, seed production, clonal spread and survivorship of the two grasses are being measured over several seasons in replicate grazed and ungrazed, and frequently and infrequently burned watersheds. A series of 25 m^2 exclosures is also being used to experimentally manipulate the temporal pattern of defoliation and to provide additional ungrazed control plants within grazed watersheds. Although forbs are generally avoided by bison in favor of the dominant warm season grasses, their abiotic environment and competitive neighborhood is altered by the activities of bison. Thus, the growth, reproductive and demographic responses of forbs to bison activity will also be studied.

These studies will test the hypothesis that the effects of fire and biotic neighborhood variation alter plant responses to grazing and that the relative grazing tolerances of different species change under different fire regimes. They will further our understanding of the potential long-term effects of bison herbivory on individuals and populations, the proximal effects of grazing on important tallgrass prairie species, and the interaction of grazing and fire effects at the plant population level. These studies will complement the proposed LTER studies

Table 8. Additional Non-LTER Ongoing Studies at Konza Prairie

Name & Institution	Project Title
Benedix, James Kansas State University	An analysis of the social system of plains pocket gopher.
Benning, Tracy Kansas State University	Fire frequency and topoedaphic control of productivity of tallgrass prairie
Brillhart, Dennis Kansas State University	Food habits of the coyote (<u>Canis latrans</u>) in tallgrass prairie Use of dropping boards as an indicator of tree use by <u>Peromyscus leucopus</u>
Brock, Brent Kansas State University	Physicochemical factors influencing migration of fishes in an intermittent stream
Cerling, Thure Kansas State University	Paleosols as indicators of paleoclimates: oxygen and carbon isotopes in pedogenic carbonate
Christensen, Martha Univ. of Wyoming, Laramie	Fungi in ecosystems
Cink, Calvin Baker Univ, Kansas	Breeding ecology and behavior of the Common Poor-will
Davis, Lawrence Kansas State University	Search for fast-growing rhizobia that nodulate soybeans
DeLucia, Evan Dept. Plant Biol., Urbana, IL	Water and nitrogen-use efficiency and species distribution in tallgrass prairie
Engman, Edwin USDA-ARS, Beltsville, MD	Hydrologic application of microwave measured soil moisture
Fay, Phil Kansas State University	Cynipid gall manipulations with <u>Silphium integrifolium</u> Gall insect population and plant-insect interactions on tallgrass prairie
Finck, Elmer Emporia State University	Behavioral observations and time budget studies of bison Census of greater prairie chicken on leks
Fisher, Diane Univ. of Colorado, Boulder	A comparison within and between populations of tallgrass prairie species from Konza Prairie and Boulder
Gosz, James & Dahm, Cliff Univ. of New Mexico	Trace gas measurements using FTIR on tallgrass prairie
Gray, Lawrence Ottawa Univ., KS	Biotic linkages between terrestrial lotic habitats
Harris, Marion Kansas State University	Factors initiating dispersion between <u>Artemisia ludoviciana</u> patches in the specialist grasshopper
Healy, Richard USGS, Lakewood, CO	Temporal variability in infiltration rates as affected by root activity
Irons, James NASA/Goddard Space Flight Center, MD	Remote determination of surface albedo using multiple direction observation
James, Sam Kansas State University	A long-term study of below-ground earthworm response to bison dung pats
Jeffrey, Jay Kansas State University	Ecological studies of Konza herps
Jekanoski, Robert Kansas State University	Canopy use by small mammals in tallgrass prairie
Jennings, Dianne Kansas State University	Nocturnal use of structure during foraging, by <u>Peromyscus maniculatus</u>

on plant populations and communities by providing an understanding of the plant physiological, life history and demographic responses causing observed long-term patterns in plant species relative abundances, productivity and community structure.

A USDA-CSRS LISA (Low Input Sustainable Agriculture) funded project to J. L. Havlin and Rice is located on the cultivated land of the Konza Prairie. This research project focuses on the use of different legumes for supplying the N to wheat and grain sorghum. The project examines the synchronization of legume N mineralization and soil N cycling in relation to crop N uptake to maximize N use and minimize N losses. The database from LTER being developed is useful in understanding the close coupling of soil cycling and plant N needs that exists in the native tallgrass prairie ecosystem when compared to agroecosystems. The use of residue management (tillage) can manipulate the soil N dynamics to better couple the soil N dynamics with the plant N needs. The LTER climatic database will be used for eventual modeling efforts.

Collaborative research (funded by NSF) with D. Schimel (CSU) involving Knapp and Seastedt is examining the influence of tallgrass prairie biota on CO_2 and H_2O exchange with the atmosphere. This examination is at a finer scale than the FIFE project and thus complements and builds upon that experiment. Measurements of foliage N content, leaf chlorophyll, plant water status, net photosynthesis, transpirational water loss and aboveground biomass have been made on transects spanning topographic gradients. These data are being correlated with canopy spectral reflectance measurements made by C. Wessman (Univ. of Colorado) to provide the key links in the modeling efforts of Schimel and colleagues at CSU. The influence of fire on these relationships is also being studied. Ultimately, these data will be combined with land-use patterns to develop a regional model of biosphere-atmosphere interactions that can be nested within global climate models.

We have made arrangements for S. Hamburg (Univ. Kansas) to test his time-domain reflectometry (TDR) system in conjunction with the Schimel et al. transect studies. TDR provides real-time measurements of soil moisture along a topoedaphic gradient, and these data, in conjunction with photosynthesis, water stress, production and nitrogen data should provide a robust perspective of plant-nitrogen-water relationships, as mediated by the Flint Hills topography. Should the system provide useful data not obtainable with current methods (neutron probes; Figure 40), we will attempt to install a system for the LTER transects.

Table 8 cont.

Name & Institution	Project Title
Merrill, Gary Kansas State University	Effects of fire and competition on establishment and long-term survival of prairie moss species Supplemental to LTER plant species composition study: Bryophytes
Muhtasib, Hala Kansas State University	The cost and benefit of silica to grasses
Parrish, J.A.D. Univ. of Illinois	Timing of pollination and seed set in prairie forbs
Peck, Eugene Hydex Corporation, VA	Alternative approach to ground truth soil moisture
Pournazai, Mohsen Kansas State University	Spatial variability of nitrogen mineralization on tallgrass prairie
Reichman, Jim Kansas State University	Pocket gopher ecology Caching behavior in woodrats
Smith, Christopher Kansas State University	Reproductive strategies of wind-pollinated trees in the temperate deciduous forest biome
Spratt, Jr., Henry Southeast Missouri State, MO	Sulfur biogeochemistry in stream sediments on the Konza Prairie Research Natural Area
Striegl, Robert USGS, Denver, CO	Methane consumption in prairie soils: Effects of biomass burning
Tieszen, Larry Augustana College, SD	Stable isotopes in vegetation and soil to assess vegetation changes in N.A. prairies
Turner, Clarence Kansas State University	Influence of grazing on surface climatological variables
Vinton, Mary Ann Kansas State University	Bison grazing patterns and plant responses on Konza Prairie
Wehmeueller, William SCS, Manhattan, KS	Geary County Soil Survey
Wetzel, Peter NASA/GSF Center, MD	Testing a regional evapotranspiration model over heterogeneous surfaces
Wickham, Susan Univ. of Oklahoma	Patch dynamics in North American tallgrass prairie plant communities
Wong, James NASA/Goddard Space Flight Center, MD	A study of the variations of soil moisture and other surface parameters obtained from airborne and satellite visible IV, and microwave sensor data
Wooster, David Kansas State University	Influence of temperature on caching behavior in woodrats, <u>Neotoma floridana</u>
Wright, Valerie Kansas State University	Management of stored-grain insects: Lesser grain borer population

Research initiated in 1989 by Knapp (and funded by NSF in 1990) is examining ecophysiological responses in tallgrass prairie plants to environmental variability. Results from other ecosystems suggest that, in some species, intermittent sunlight (due to clouds or within canopy shading) may enhance plant water status and total carbon gain compared to constant sunlight (Knapp and Smith in press). Preliminary data from prairie grasses and forbs show similar trends. This positive response to environmental variability at the leaf level parallels results from studies of production responses to infrequent burning (Figure 15).

Collins, S. Glenn and S. Pickett recently received support from NSF to conduct a study entitled, "Phase-space ordination and the complexity of successional trajectories". The complexity of the successional trajectory will be quantified using long-term data sets at Konza Prairie, Cedar Creek, MN, and elsewhere.

An effort is underway by USGS and State of Kansas Cooperative Studies to characterize soil water and groundwater conditions in the N04D watershed. Four transects perpendicular to the stream channel were instrumented with 58 lysimeters and 20 observation wells in late winter of 1988. Lysimeters were installed in the A, B and C soil horizons to sample unsaturated zone, and observation wells were installed in the Morrill and Eiss Limestone Members (Lower Permian). Water samples analyzed for dissolved organic carbon (DOC) and nitrate found concentrations to be greater in the unsaturated zone than in groundwater, indicating a decrease in these constituents during transport from soil to groundwater. Future work will focus on the reasons for the DOC and nitrate decrease and the identification of DOC biomarkers that can be used as tracers in the transport of water and natural compounds from the soil to groundwater.

8. Archives and Inventories

a. Data archives (described above).

b. Sample archives. The following data sets include soil or tissue sample archives in addition to data archives: OGD01, OPD01, PAB01, PBB01, PBB02, PGL01, NPL01, NSC01

At present about 2,000 samples are stored in paper or plastic sacks in filing cabinets, in insect-free rooms. Earliest samples are from 1981. Tree ring analysis is planned beginning in 1990 that will provide us with another form of sample archive. Root window tracings have been archived so that retrospective analyses are also possible. A photographic archive has also been established.

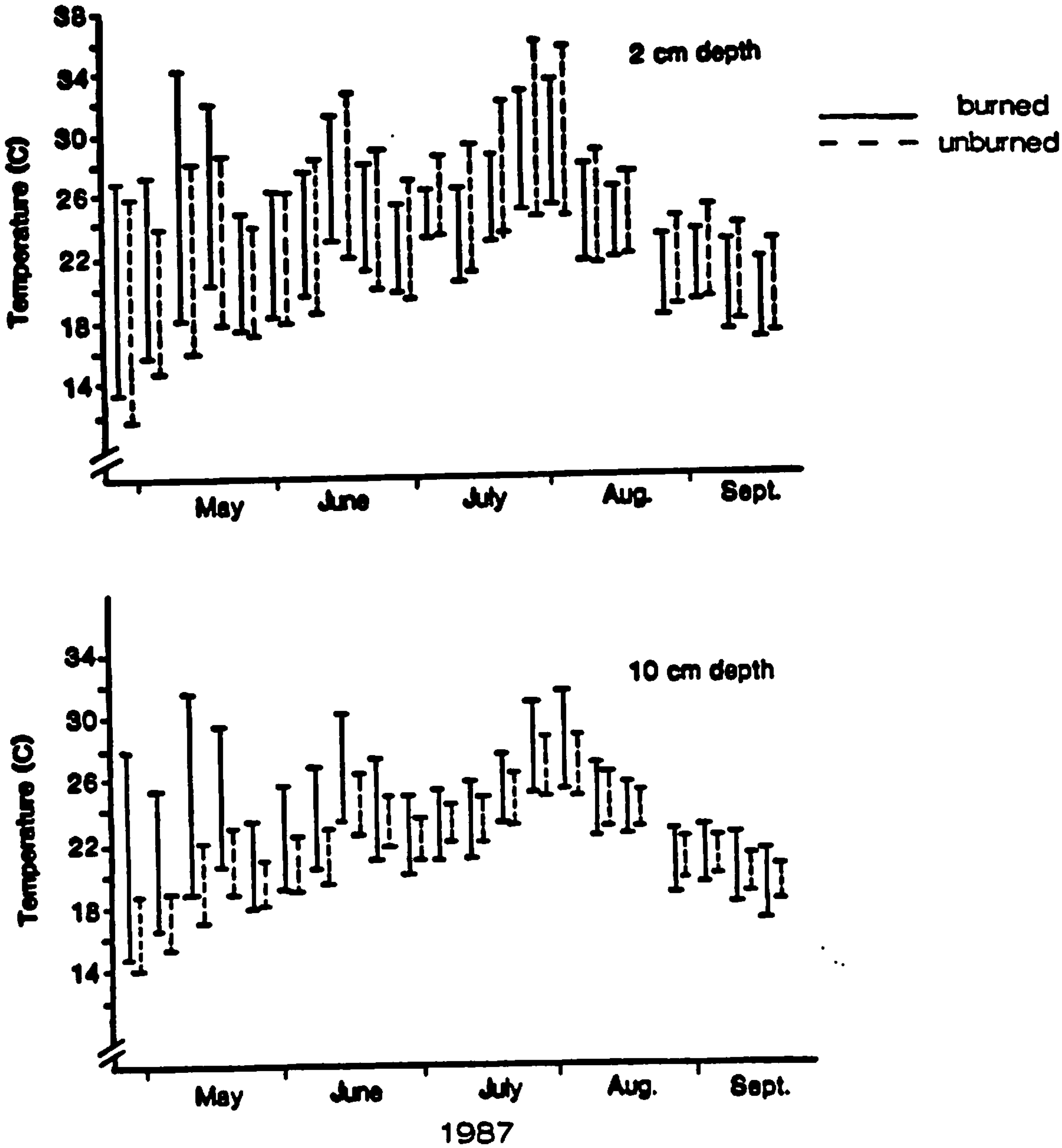

Figure 39. Weekly min-max temperatures at 2 cm and 10 cm soil depths on annually burned and unburned plots.

These results (data set AST01) are significant for several reasons. These are microsite measurements that appear directly related to watershed values, as shown by satellite images of canopy brightness (Figure 2). Also, these data demonstrate that the effects on canopy temperatures caused by fire (Figure 2) are related to soil temperatures via plant effects on soil moisture. In July and August, soil temperatures at 2 cm show similar patterns to those observed in the canopy (e.g., the canopies of burned sites are, in normal years, cooler due to increased evapotranspiration). However, at 10 cm, soil temperatures are relatively warmer on the burned sites. This is caused by the reduction in soil moisture and the reduction in thermal capacities of the drier soils on the burned watersheds.

The influence of plant vigor on both soil temperatures and soil moistures has important consequences to soil biotic processes. We have expanded these measurements to include clipped plots as well.

9. Leadership, Management and Organization

Konza Prairie was an initial LTER site selected in 1980 because of the research potential offered by its watershed-level experimental design. Konza Prairie and KSU had no history of previous interdisciplinary research, and the LTER research evolved as KSU personnel changed. The original research had a strong organismic emphasis. As knowledge of the system progressed, gaps in knowledge were addressed by adding new researchers. Process-level phenomena (NPP, organic matter dynamics, nutrient cycling and hydrology) were emphasized in the second funding cycle of the LTER. The development of a strong landscape, hydrologic and modeling component to the LTER allows for a state-of-the-art synthesis of structure-function relationships. Our LTER program has become a multi-dimensional, multi-investigator effort that exhibits considerable diversity and balance (Figure 41). In addition to our LTER support, the Kansas Agricultural Experiment Station has played a significant role in the development of Konza Prairie as a national and regional research site. This has come through general support of Konza Prairie management and operations, and support of the research efforts of many investigators associated with the LTER effort.

Administrative leadership has been transferred with each LTER funding cycle, and we plan to continue to rotate this position. Intellectual leadership is shared among the group. Our site has undergone a large change in personnel; only one individual's name (Zimmerman) has been appeared in all LTER proposals. Knapp, who participated as a researcher in the first LTER (1983-1985), returned as a faculty member in August, 1988; C. Rice also joined the faculty on that date. While a central theme of Konza research (fire) has remained constant, many approaches, questions and levels of resolution have changed, in part due to changes in personnel and emergence of new technologies, but also in response to objectives and criteria provided by the intersite-LTER coordinating committee and research initiatives suggested by National Academy of Science and other blue-ribbon committee reports.

The multiple-authored publication record of Konza Prairie researchers is perhaps the best indication of the functional working groups and interactions within the project. Groups are fairly easily identified from Figure 41. There exists the "wet group", those individuals involved in hydrologic studies. The "belowground group" consists of those individuals involved in belowground plot experiment and related soils studies. The "populations group" retains the traditional biology focus of the research, and the "modeling and landscape

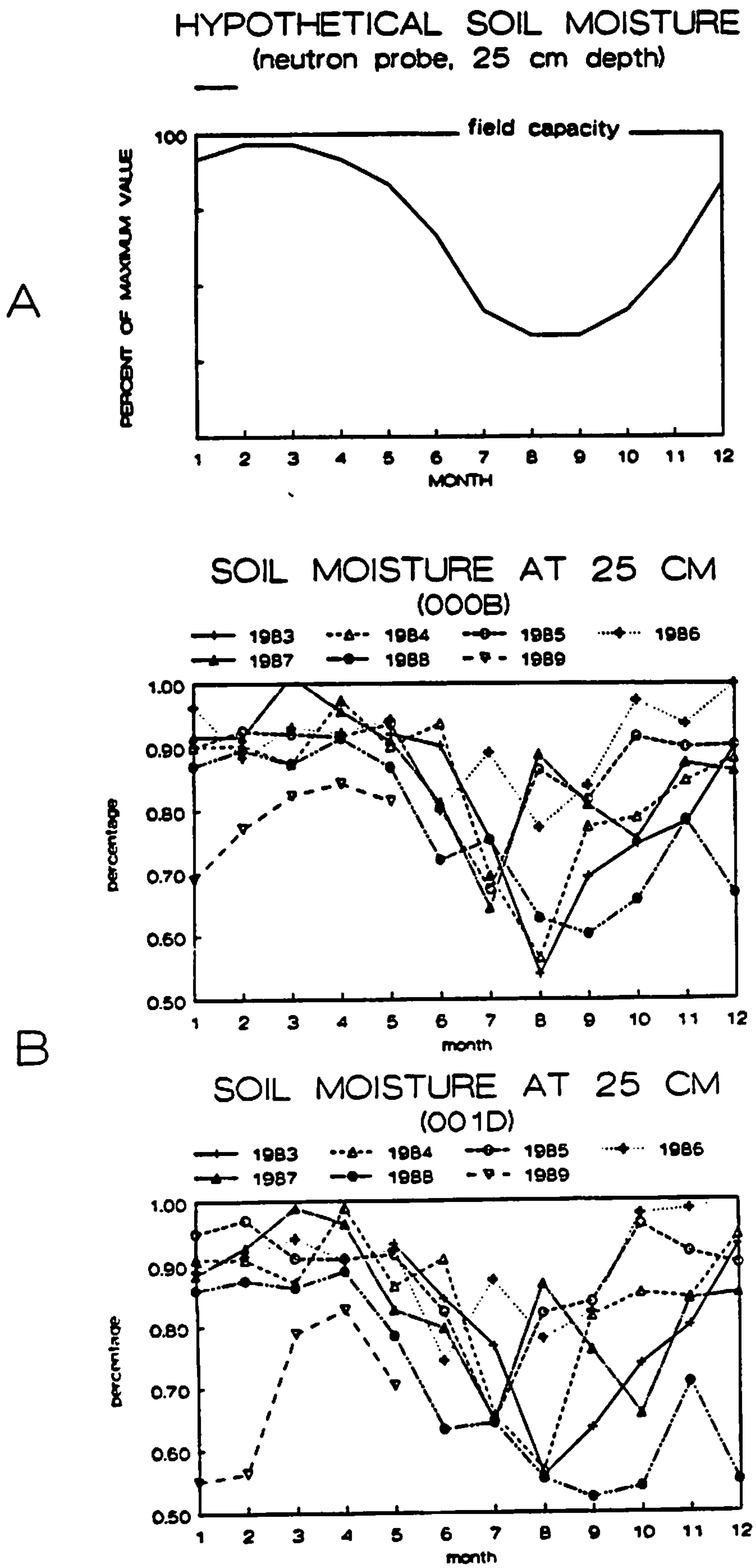

Figure 40. Percent soil moisture on the prairie usually begins the growing season at field capacity. Evapotranspiration may result in substantial plant water stress by mid summer (See Fig. 21). If rain does not occur, early senescence of the vegetation occurs.

B. Seasonal pattern in soil moisture (expressed as % of field capacity) in unburned (000B) and annually burned (001D) sites exhibit considerable year-to-year variation, with substantial summer recharge occurring in three of the seven years of record. Note that soil water tends to be higher later in the spring on unburned sites. Also note the unusually dry conditions that occurred in the spring of 1989.

These data (ASM01) will be used along with soil temperature data to help interpret canopy brightness using the thermal channel of the TM satellite.

group" may incorporate data from any of the other groups to characterize the system. Many of us are active in several research areas. All groups directly or indirectly use the data management and technical staff (Brown, Kinderknecht, Ramundo and their student assistants), and the experimental design for the research is supported by the Konza Prairie management team, a group funded by the State of Kansas.

The "wet group" is new; only two researchers (Koelliker, Tate) were involved in Konza Prairie studies prior to the autumn of 1989. With a group size of six and with collaborative efforts with the USGS groundwater study, this group is now the largest subgroup within the Konza Prairie LTER program. Moreover, their landscape-level approach to the study of hydrologic and geomorphologic processes epitomizes our objective of providing a true interdisciplinary and synthetic perspective. Also, their intensive site, watershed N04D, has been an intensive study site for all other LTER measurements. We will therefore be able to relate topographic and geomorphic features with, for example, soil chemistry, NPP, plant species composition and other "traditional" LTER measurements.

We have used several mechanisms to coordinate and inform LTER members about on-going research. Our LTER program held a review by our External Review Committee [Paul Risser (Chair), James Gosz, Richard Root and Richard Wiegert] in early 1987. Our site was reviewed by an NSF review team in late 1988. Written reviews were provided from both meetings. The Konza Prairie research group, an organizational entity larger than the LTER group, held weekly meetings in 1989. Informal research presentations were made by LTER personnel and others at those meetings. We held our first (annual) LTER workshop, a two-day event, at Konza Prairie headquarters in summer 1989 (Appendix E). A benefit of this group presentation in late summer is that material for the annual report can be simultaneously obtained, and funding priorities established for subsequent years. Moreover, this format (as opposed to single, monthly presentations) appears to be more productive in terms of the stimulation of research ideas, synthetic efforts and group projects. We therefore propose to continue both the informal meetings (albeit at a less-frequent interval) and the annual workshop.

With the increase in intersite activities and coordination committee meetings, the need for frequent external review is lessened. Given the increased complexity of the LTER effort, however, we recognize the need to bring in specialists to evaluate specific portions of the project. We can do this in part on an informal basis using our departmental seminar program, as well as make direct use of consultants for advice on specific topics.

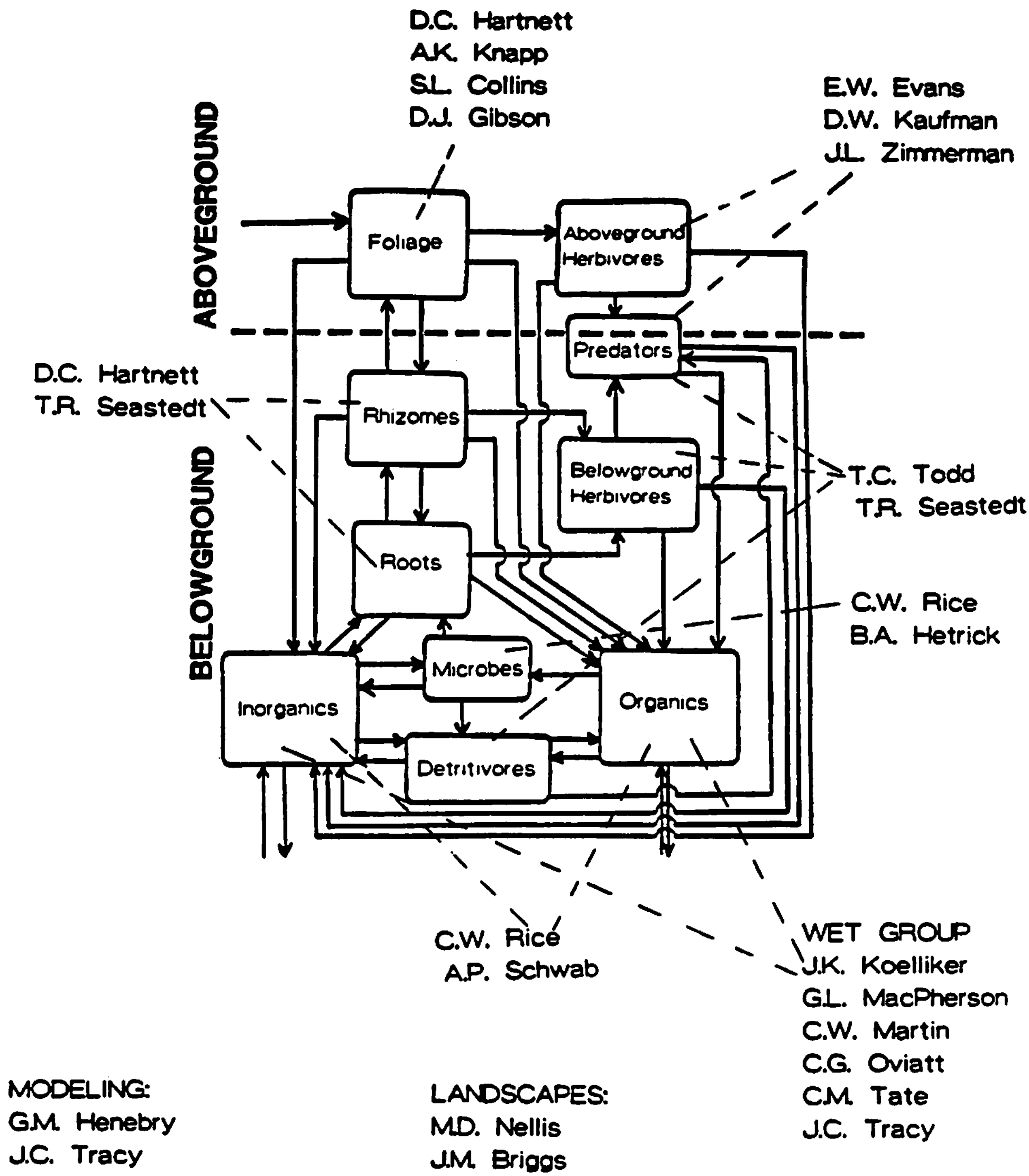

Figure 41.

INVESTIGATORS INVOLVED IN LANDSCAPE, ECOSYSTEM AND BIOTIC STUDIES AS PART OF THE KONZA PRAIRIE LTER EFFORT

D. Schimel (CSU) has been here every summer since 1985, and his advice regarding biogeochemical studies is always solicited and welcomed. This year we had B. Milne (UNM) evaluate the landscape aspects of the project, while W. Abrahamson (Bucknell U.) reviewed some of the plant population studies. We propose to have our external review team meet with us at our annual workshop during year three (1993) for an evaluation of our project. We assume that this meeting will occur two years prior to a formal NSF review in 1995.

10. New Projects and Technologies

The availability of GIS and remote sensing techniques now allows us to make full use of Konza's robust experimental design, and several projects are already underway. A Konza Prairie geomorphology map (Figure 42) will be digitized onto the GIS in 1990. Maps indicating soils, elevation, slope and aspect, and watershed boundaries are already on the GIS. Our current holdings of satellite images (Table 2) will be augmented with additional SPOT and TM scenes for 1989. We will continue to acquire as much satellite data as possible.

We are very interested in obtaining a functional archive of the FIFE data set (FIS; Strebel et al. 1989), which contains over 30 gigabytes of data on Konza and adjacent areas. We recognize that we will have to acquire additional funding for this effort (Figure 43). In conjunction with this project, we wish to re-establish some of the high temporal resolution biophysical measurements of mass, energy, momentum and CO_2 flux originally obtained by the FIFE project. The cost of equipment and permanent staff to operate this equipment is too large to be supported with existing funds. We will, however, continue to attempt outside support. As evidence of this effort, members of our LTER group submitted proposals or preproposals in autumn 1989, to five different programs in NSF (Ecology, Dissertation Improvement, BBS Training Grant, Conservation Biology, REU) and to MAB. A preproposal to form the equivalent of an "earth science center" has also been sent to State funding agencies. The BBS training grant, submitted as a joint proposal through U. Nebr., was one of 60 programs selected for further consideration.

Our experiences with FIFE have convinced us that biotic processes are under-emphasized in current climate interaction studies. We are attempting to educate NASA biophysicists involved in atmosphere-climate interactions that "ecological constraints" (specific biotic communities or ecological treatments) are responsible for imposing potentially large constraints on the instantaneous measurements of energy and trace gas flux using remote sensing methods (Shugart 1986, Seastedt and Briggs 1990; Figures 2,6). Just as biologists are often guilty

Figure 42. Preliminary geomorphology map of Konza (Smith 1990). A final version will be digitized into our GIS data base in 1990.

of "black-boxing" abiotic system components, investigators involved in climate change scenarios appear guilty of "black-boxing" the biota. Consideration for biologically-induced hysteresis is a serious deficiency in most current climate models.

An analysis of gallery forest wood growth dynamics will begin in 1990. This dendrochronological study will allow us to compare forest wood production with our prairie foliage NPP record, and test several predictions regarding controls on the respective systems (Briggs et al. 1989). The dendrochronological analysis will also complement LTER studies on the dynamics and spatial patterns of woody plants by providing information on wood, plant population structure and past recruitment patterns. These data will also be integrated with climate/hydrological pattern issues studied by the "Wet Group".

As was mentioned in the synthesis/modeling section, spatial modeling at the landscape or regional scale demands a high degree of concurrent (parallel) processing in order to simulate efficiently (and naturally) the nested spatiotemporal hierarchies intrinsic to ecological processes. Accordingly, we intend to implement our integrated soil-water-vegetation model on a fine resolution parallel processor. Through the National Center for Supercomputing Applications (NCSA), we have access to a Connection Machine (Hillis 1985), a single-instruction multiple-data (SIMD) computer with 32,768 processors and distributed memory (8K per processor), 1024 32-bit floating-point accelerators (one for every 32 processors), and a 10-gigabyte disk array for additional workspace. We shall be able to map the Konza landscape into the CM-2 by specifically programming the topology of the processors to mimic our link-node representation of Konza watersheds. Climatic variables, disturbances and other forcings are introduced into the CM-2 "landscape" through a host computer. The Connection Machine represents a cutting-edge technology that holds great promise for ecological modeling.

Another significant new approach that will be developed during LTER III is the use of cellular automata in ecological modeling. Cellular automata (Toffoli and Margolus 1987, Farmer et al. 1984) are discrete dynamical systems in which behavior is determined by local topology. They are the discrete analogue to the class of continuous dynamical systems defined by partial differential equations. According to Toffoli and Margolus (1987), a cellular automaton can be thought of as a stylized universe in which space is a uniform grid with each grid site or cell containing a few bits of data. As time progresses in discrete steps, the system evolves according to a set of simple relationships that computes the new state of a particular cell from that of its close

Figure 43. Example of the equipment required for energy, trace gas and momentum studies such as those conducted by NASA-FIFE on Konza Prairie during 1987-1989. We estimate that three or four of these stations operating continuously over the growing season would require about 300k per year for equipment and personnel.

neighbors. The laws of the universe are thus local and uniform but are sufficient to generate rich hierarchies of structure and phenomena.

To facilitate experimentation with cellular automata, we have on order (delivery expected 2nd-quarter 1990) a high-performance cellular automata machine, the CAM-6. The principal data structure in the CAM-6 is an array of 256 x 256 cells, each holding four bits of information. All 256K bits of cell-state memory are updated 60 times per second with output piped directly to the color monitor. The update of each bit is the result of a table-lookup operation based on up to 13 neighborhood inputs. The high-speed display of the CAM-6 permits the user to observe system dynamics interactively. External data sets can be loaded into the CAM-6 for initial conditions or perturbations.

The use of cellular automata and the CAM-6 in the modeling efforts at Konza will have, at least, two major applications, 1) generation of *dynamic* neutral spatial models, and 2) development of large-scale coarse-grained spatial simulation models that can readily use remotely-sensed data (e.g., TM images) and GIS maps (raster-based) for initial conditions, calibration and validation. This linkage of remote-sensing, GIS and simulation modeling offers some exciting possibilities.

11. Dissemination of Information

Konza Prairie is well known. The site was written up in Science (Kolata 1984), and television programs about Konza Prairie have appeared in the US, Japan and England. The FIFE project resulted in CNN and CBC news stories. A natural history/ecology text on Konza Prairie has been written by O. J. Reichman (1987). We hope that we are reaching the scientific community with our publications and presentations at national meetings. We have a variety of reference material available such as the standard site brochures (Appendix F). Konza Prairie supports an educational coordinator, who solicits other faculty and staff to direct tours and provide talks. During 1989, for example, talks were given to 48 groups while tours were provided for 25 individuals, 27 small groups, and 37 classes. Every other year we provide a "Konza Prairie Visitors Day", which draws ca. 1200 people to the one-day event. There is also a self-guided nature trail that is frequently hiked, especially on weekends, but we have no data on vistors' use.

Literature Cited
(See also Konza Publication List and Theses and Dissertations)

Aber, J.D., K.J. Nadelhoffer, P. Steudler and J.M. Melillo. 1989. Nitrogen saturation in northern forest ecosystems. BioScience 39: 378-386.

Albertson, F.W., G.W. Tomanek and A. Riegel. 1957. Ecology of drought cycles and grazing intensity on grasslands of central great plains. Ecological Monographs 27:27-44.

Aldous, A.E. 1934. Effect of burning on Kansas bluestem pastures. Kansas Agric. Exp. Stn. Tech. Bull. 38. Manhattan, KS.

Allen, T.F.H. and T.B. Starr. 1982. Hierarchy: Perspectives for Ecological Complexity. Univ. of Chicago Press, Chicago.

Anderson, J. P. E. and K. H. Domsch. 1975. Measurement of bacterial and fungal contribution to respiration of selected agricultural and forest soils. Can. J. Microbiol. 21:314-322.

Anderson, R.C. 1982. An evolutionary model summarizing the roles of fire, climate, and grazing animals in the origin and maintenance of grasslands:an end paper. In: J.R. Estes, R.J. Tyrl and J.N. Brunken (eds.). Grasses and grasslands: systematics and ecology. Univ. of Okla. Press, Norman. pp. 297-308.

Bark, D. 1987. Konza Prairie Research Natural Area, Kansas. In: D. Greenland (ed.). The Climates of the Long-Term Ecological Research Sites. Inst. of Arctic and Alpine Res. Occas. Paper No. 44, Univ. Colo., Boulder. pp.45-50.

Bergelson, J. M. and J. M. Crawley. 1988. Mycorrhizal infection and plant species diversity. Nature (London) 344:202.

Bolan, N.S., A.D. Robson and N.J. Barrow. 1987. Effects of vesicular-arbuscular mycorrhiza on the availability of iron phosphates to plants. Plant and Soil 99:401-410.

Bragg, T.B. and L.C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. J. Range Manage. 29:19-23.

Bragg, T.B. and J. Stubbendieck (eds.). 1989. Proceedings of the 11th North American Prairie Conference. Univ. of Nebraska, 7-11 August 1988.

Briggs, J.M. and D.J. Gibson. submitted. Effect of fire on tree spatial patterns in a tallgrass prairie landscape. J. Ecology.

Briggs, J.M. and A.K. Knapp. submitted. Estimating aboveground biomass in tallgrass prairie with the harvest method: Determining proper sample size using jackknifing and monte carlo simulations. S.W. Natur.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. Am. Nat. 124:255-279.

Burke, I.C., D.S. Schimel, C.M. Yonker, W.J. Parton, L.A. Joyce and W.K. Lauenroth. in press. Regional modeling of grassland biogeochemistry using GIS. Landscape Ecology.

Caine, N. and Swanson, F. J. 1989. Geomorphic coupling of hillslope and channel systems in two small mountain basins. Zeitschrift fur Geomorphologie 33:189-203.

Chapin, F.S., D.M. Vitousek and K. Van Cleve. 1986. The nature of nutrient limitation in plant communities. Am. Nat. 127:48-58.

Chen, C.W. and G.T. Orlob. 1972. Ecological simulation for aquatic environments. Final Report to the Office of Water Resources Research, U.S. Dept. of Interior. OWRR C-2044. 156 pp.

Clark, B.K. and D.W. Kaufman. submitted. Response of small mammals to experimental fire in tallgrass prairie. Can. J. Zool.

Clayton, L. and J. R. Tinker, Jr. 1971. Rates of hillslope lowering in the badlands of North Dakota. Research Project Technical Completion Report, North Dakota Water Resources Research Institute, OWRR Project No. A-012-NDAK, 36 p.

Coffin, D.P. and W.K. Lauenroth. In press. A gap dynamics simulation model of succession in a semi-arid grassland. Ecol. Modelling

Cole, C.V., G.S. Innis and J.W.B. Stewart. 1977. Simulations of phosphorus cycling in semi-arid grasslands. Ecology 58:1-15.

Collins, S. L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. Ecology 68:1243-1250.

Collins, S. L. 1990. Fire as a natural disturbance in tallgrass prairie ecosystems. *In*: S. L. Collins and L. L. Wallace, eds. Fire in tallgrass prairie ecosystems. Univ. Oklahoma Press, in press.

Collins, S. L. and S. M. Glenn. submitted. Spatial and temporal analysis of species distribution and abundance. Ecology.
Collins, S.L. and L.L. Wallace. 1990. Fire and tallgrass prairie. Univ. Oklahoma Press, Norman, OK.
Connell, J.H. and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111:1119-1144.
Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.
Connell, J.H. and W.P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. Am. Nat. 121:789-824.
Coughenour, M.B. 1984. A mechanistic simulation analysis of water use, leaf angles, and grazing in east African graminoids. Ecol. Modelling 26:203-230.
DuBois, J.D. and L.A. Kapustka. 1983. Biological nitrogen influx in an Ohio relict prairie. Amer. J. Bot. 70:8-16.
Emmett, W. W. 1974. Channel aggradation in western United States as indicated by observations at Vigil Network sites. Zeitschrift fur Geomorphologie, Supplement Band 21(2):52-62.
Emmett, W. W. and Hadley, R. F. 1968. The vigil network: Preservation and access of data. U. S. Geological Survey Circular 460-C, 9 p.
Evans, E.W. and T.R. Seastedt. In press. Relations of phytophagous invertebrates and rangeland plants. In: D.J. Bedunah (ed.). Management of Grazing Lands: Importance of Plant Morphology and Physiology to Individual Plant and Community Response. Society for Range Management.
Everritt, B. L. 1968. Use of cottonwood in an investigation of the recent history of a floodplain. American Journal of Science 266:417-439.
Farmer, D., T. Toffoli and S. Wolfram, (eds.). 1984. Cellular Automata. North-Holland Physics Publ. 247 pp.
Franklin, J.F. 1989. Importance and justification of long-term studies in ecology. In: G.E. Likens (ed.). Long-term studies in ecology: Approaches and alternatives. Springer-Verlag, New York. pp. 3-19.
Franklin, J.F., H.H. Shugart and M.E. Harmon. 1987. Tree death as an ecological process: The causes, consequences, and variability of tree mortality. BioScience 37:550-556.
Gerdemann, J.W. 1968. Vesicular-arbuscular mycorrhiza and plant growth. Annual Rev. Phytopathol. 6:397-418.
Gleason, H.A. 1913. The relation of forest distribution and prairie fires in the middle west. Torreya 13:173-181.
Glenn, S. M., S. L. Collins and D. J. Gibson. submitted. Disturbances in tallgrass prairie: local versus regional effects on heterogeneity. Ecology
Griffith, D.A. 1988. Advanced Spatial Statistics. Kluwer Academic Publ. 273 pp.
Grime, J. P. 1973. Control of species diversity in herbaceous vegetation. J. Environ. Manage. 1:151-167.
Grime, J. P., J. M. L. Mackey, S. H. Hillier, and D. J. Read. 1987. Floristic diversity in a model system using experimental microcosms. Nature (London) 328:420-422.
_____. 1988. Reply. Nature (London) 344:202.
Hamburg, S.P. and R.L. Sanford. 1986. Disturbance, *Homo sapiens*, and ecology. Bull. Ecol. Soc. Am. 67:169-171.
Hanski, I. 1982. Dynamics of regional distribution: The core and satellite species hypothesis. Oikos 38:210-221.
Hartnett, D. C. submitted a. Effects of fire in tallgrass prairie on growth and reproduction of prairie coneflower (*Ratibida columnifera*: Asteraceae). Am. J. Bot.
Hartnett, D. C. submitted b. Size-dependent allocation to seed and vegetative reproduction in four clonal composites. Oecologia.
Hereford, R. 1984. Climate and ephemeral-stream processes: Twentieth-century geomorphology and alluvial stratigraphy of the Little Colorado River, Arizona. Geological Society of American Bulletin 95:654-668.
Hillis, W.D. 1985. The Connection Machine. The MIT Press. 190 pp.
Holland, E.A. and J.K. Detling. In press. Plant response to herbivory and belowground nitrogen cycling. Ecology.
Hulbert, L.C. 1973. Management of Konza Prairie to approximate pre-white-man fire influences. In: L.C. Hulbert (ed.). Proc. 3rd Midwest Prairie Conf. (1972) pp. 14-16.
Huston, M. 1979. A general hypothesis of species diversity. Amer. Nat. 113:81-101.

Huston, M., D. DeAngelis and W. Post. 1988. New computer models unify ecological theory. BioScience 38:682-691.
Jantz, D.R., R.F. Harner, H.T. Rowland and D.A. Gier. 1975. Soil survey of Riley County and part of Geary County, Kansas. Soil Cons. Serv., U.S. Govt. Printing Off. 575-563/90.
Jayachandaran, K., A.P. Schwab and B.A.D. Hetrick. 1989. Mycorrhizal mediation of phosphorus availability: synthetic iron chelate effects on phosphorus solubilization. Soil Sci. Soc. Am. J. 53:1701-1706.
Jenkinson, D. S. and D. S. Powlson. 1976. The effects of biocidal treatments on metabolism in soil. V. Method of measuring soil biomass. Soil Biol. Biochem. 8:209-213.
Knapp, A.K. and W.K. Smith. In press. Stomatal and photosynthetic response to variable sunlight. Physiologia Plantarum
Kolata, G. 1984. Managing the inland sea. Science 224:703-704.
Levins, R. A. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull. Entomol. Soc. Am. 15:237-240.
Leopold, L. B. 1976. Reversal of erosion cycle and climatic change. Quaternary Research 6:557-562.
Leopold, L. B. and W. W. Emmett. 1967. On the design of a Gerlach trough. Revue de Geom. Dynamique. 4:172.
Leopold, L. B., W. W. Emmett and R. M. Myrick. 1966. Channel and hillslope processes in a semiarid area, New Mexico. U. S. Geological Survey Professional Paper 352-G.
Magnuson, J.J., C.J. Bowser and A.L. Beckel. In press. The invisible present long term ecological research on lakes. BioScience.
Margalef, R. 1969. Diversity and stability: A practical proposal and a model of interdependence. Pps. 25-37 *in*: Diversity and Stability in Ecological Systems. Brookhaven Symp. Biol. 22.
McIntosh, R.P. 1985. The background of ecology: concept and theory. Cambridge Univ. Press, NY.
Meyer, J. L., W. H. McDowell, T. L. Bott, J. W. Elwood, C. Ishizaki, J. M. Melack, B. L. Peckarsky, B. J. Peterson, and P. A. Rublee. 1988. Elemental dynamics in streams. Journal of North American Benthological Society 7:410-432.
Milchunas, D. G., O. E. Sala, and W. K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. Am. Nat. 132:87-106.
Myrold, D. D., and J. M. Tiedje. 1986. Simultaneous estimation of several nitrogen cycle rates using 15N: Theory and application. Soil Biol. Biochem. 18:559-568.
Neilson, R.P., G.A. King, R.L. DeVelice, J. Lenihan, D. Marks, J. Dolph, B. Campbell and G. Glick. 1989. Sensitivity of ecological landscapes and regions to global climate change. U.S. Environ. Prot. Agency. EPA/600/3-89/073. 103 pp.
Ojima, D.S., W.J. Parton, D.S. Schimel and C.E. Owensby. 1990. Simulated impacts of annual burning on prairie ecosystems. In: S.L. Collins and L.L. Wallace (eds). Fire and Tallgrass Prairie. University of Oklahoma Press, Norman.
Ojima, D.S., W.J. Parton, D.S. Schimel and C.E. Owensby. 1989. Simulating the long-term impact of burning on C, N, and P cycling on a tallgrass prairie. In: G. Giovannozzi-Sermanni and P. Hammipieri, (eds.). Current Perspectives in Environmental BioGeochemistry, C.N.R.-IPRA VIA NIZZA 128-00192 ROMA. pp 353-370.
O'Neill, R.V., D.L. DeAngelis, J.B. Waide and T.F.H. Allen. 1986. A Hierarchical Concept of Ecosystems. Monogr. in Pop. Biol. No. 23, Princeton Univ. Press, N.J. 253 pp.
Parkhurst, D.L., D.C. Thorstenson and L.N. Plummer. 1985. PHREEQE, a computer program for geochemical calculations. U.S. Geological Survey WRI Report 80-96, 193 p.
Parton, W.J., D.S. Schimel, C.V. Cole and D.S. Ojima. 1987. Analysis of factors controlling soil organic levels of grasslands in the Great Plains. Soil Science Society of America Journal 51:1173-1179.
Patton, P. C. and Schumm, S. A. 1981. Ephemeral-stream processes: Implications for studies of Quaternary valley fills. Quaternary Research 15:24-43.
Paul, E. A., and N. G. Juma. 1981. Mineralization and immobilization of nitrogen by microorganisms. *In*: Terrestrial nitrogen cycles. F. E. Clark and T. Rosswall (ed.) Ecol. Bull. (Stockholm) 33:179-195.
Pickett, S. T. A., J. Kolasa, J. J. Armesto and S. L. Collins. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. Oikos 54:131-139.
Pimentel, R.A. and J.D. Smith. 1986. BIOSTAT I. Sigma Soft, Placentia, CA. 241 pp.

Pons, W.A., Jr. and J.D. Guthrie. 1946. Determination of inorganic phosphorus in plant materials. Ind. Eng. Chem. Anal. Ed. 18:184-186.
Pyne, S.J. 1982. Fire in America: a cultural history of wildland and rural fire. Princeton University Press, Princeton.
Pyne, S.J. 1986. "These conflagrated prairies": a cultural fire history of the grasslands. In: G.K. Clambey and R.H. Pemble, (eds.). Proc. 9th North Amer. Prairie Conf. Tri-College Press, Fargo, ND. pp. 131-137.
Rabinowitz, D., J. K. Rapp, S. Cairns and M. Mayer. 1989. The persistence of rare prairie grasses in Missouri: environmental variation buffered by reproductive output of sparse species. Am. Nat. 134:525-544.
Ramundo, R.A. and T.R. Seastedt. submitted. Seasonal bias in NADP wetfall ammonia estimates. Atmos. Environ.
Redmann, R.E. 1978. Plant and soil water potentials following fire in a northern mixed grassland. J. Range Manage. 31:443-445.
Robertson, G.P., M.A. Huston, F.C. Evans and J.M. Tiedje. 1988. Spatial variability in a successional plant community: patterns of nitrogen availability. Ecology 69:1517-1524.
Risser, P.G., E.C. Birney, H.D. Blocker, S.W. May, W.J. Parton and J.A. Weins. 1981. The true prairie ecosystem. Hutchinson Ross Publ. Co., Stroudsburg, PA. 557 pp.
Rykiel, E. J., Jr. 1985. Towards a definition of ecological disturbance. Aust J. Ecol. 10:361-365.
Sauer, C.O. 1950. Grassland climax, fire and man. J. Range Manage. 3:16-21.
Schimel, D.S., G.F. Kittel, T.R. Seastedt and W.J. Parton. submitted. Landscape variations in grassland biomass, N and canopy structure: Biogeochemical constraints over interactions with the atmosphere. Ecology.
Seastedt, T.R., J.M. Briggs and D.J. Gibson. submitted. Fire frequency and nitrogen limitation of primary production in tallgrass prairie. Oecologia.
Shugart, H.H. 1986. Discussion. In: C. Rosenzweig and R. Dickinson, (eds.). Climate Vegetation Interactions. UCAR Report OIES-2, Boulder, CO.
Sigafoos, R. S. 1964. Botanical evidence of floods and floodplain deposition. U. S. Geological Survey Professiona; Paper 421-A.
Smith, R. M., P. C. Twiss, R. K. Krauss and M. J. Brown. 1970. Dust deposition in relation to site, season, and climatic variables. Soil Science Society of America Proceedings 34:112-117.
Stanford, G. and S. J. Smith. 1972. Nitrogen mineralization potential of soils. Soil Sci. Soc. Am. Proc. 36:465-472.
Strebel, D.E., J.A. Newcome, J.P. Ormsby, F.G. Hall and P.J. Sellers. 1989. Data management in the FIFE information system. Proc. IGARSS 89:42-44.
Swanson, F.J., T.K. Kratz, N. Caine and R.G. Woodmansee. 1988. Landform effects on ecosystem patterns and processes. BioScience 38:92-98.
Tansley, A.G. 1935. The use and abuse of vegetational concepts and terms. Ecology 16:284-307.
Thiebaux, H.J. and M.A. Pedder. 1987. Spatial Objective Analysis. Academic Press. 295 pp.
Tiessen, H., J.W.B. Stewart and C.V. Cole. 1984. Pathways of phosphorus transformations in soils of differing pedogenesis. Soil Sci. Soc. Am. J. 48:853-858.
Tilman, D. 1982. Resource competition and community structure. Princeton Univ. Press, Princeton.
Toffoli, T. and N. Margolus. 1987. Cellular Automata Machines. The MIT Press. 259 pp.
Towne, G. and C. Owensby. 1984. Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie. J. Range Manage. 37:392-397.
Tracy, J.C. and M.A. Marino 1987. Seepage into variably-saturated porous medium. J. Irrig. and Drain. Eng., ASCE 113:198-212.
Urban, D.L., R.V. O'Neill and H.H. Shugart, Jr. 1987. Landscape ecology. BioScience 37:119-127.
Voroney, R. P. and E. A. Paul. 1984. Determination of Kc and Kn *in situ* for calibration of the chloroform fumigation incubation method. Soil Biol. Biochem. 16:9-14.
Weaver, J.E. 1954. North America Prairie. Johnson Publ. Co., Lincoln, NE.
Weaver, J.E., L.A. Stoddart and W. Noll. 1935. Response of the prairie to the great drought of 1934. Ecology 16:612-629.
Wollum III, A. G. 1982. Cultural methods for soil microorganisms. *In*: A. L. Page et al (eds) Methods of Soil Analysis, Part 2. Chemical and Microbiological Properties. Agronomy 9 (2nd edition):781-802.
Womack, W. R. and S. A. Schumm. 1977. An example of episodic erosion. Geology 5:72-76.

Appendix A.

PUBLICATION LIST, KONZA PRAIRIE RESEARCH NATURAL AREA, 1981-PRESENT
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1981

Knodel-Montz, J. J. 1981. Use of artificial perches on burned and unburned tallgrass prairie. Wilson Bull. 93:547-548.

1982

*Finck, E. J. 1982. Hail damage to breeding birds and their nests on the Konza Prairie Research Natural Area. Kansas Ornithological Society Bull. 33:29-30.

Gurtz, M. E., G. R. Marzolf, K. T. Killingbeck, D. L. Smith, and J. V. McArthur. 1982. Organic matter loading and processing in a pristine stream draining a tallgrass prairie/riparian forest watershed. Kansas Water Resources Research Institute Contr. No. 230. 78 pp.

James, S. W. 1982. Effects of fire and soil type on earthworm populations in a tallgrass prairie. Pedobiologia 24:37-40.

Killingbeck, K. T., D. L. Smith, and G. R. Marzolf. 1982. Chemical changes in tree leaves during decomposition in a tallgrass prairie stream. Ecology 63:585-589.

*Zimmerman, J. L. 1982. Nesting success of dickcissels (*Spiza americana*) in preferred and less preferred habitats. Auk 99:292-298.

1983

*Evans, E. W. 1983. The influence of neighboring hosts on colonization of prairie milkweeds by a seed-feeding bug. Ecology 64:648-653.

*Evans, E. W., R. A. Rogers, and D. J. Opfermann. 1983. Sampling grasshoppers (Orthoptera: Acrididae) on burned and unburned tallgrass prairie: night trapping vs. sweeping. Environ. Entomol. 12:1449-1454.

Hatch, S. A. 1983. Nestling growth relationships of brown-headed cowbirds and dickcissels. Wilson Bull. 95:669-671.

Hetrick, B. A. Daniels, and J. Bloom. 1983. Vesicular-arbuscular mycorrhizal fungi associated with native tall grass prairie and cultivated winter wheat. Can. J. Bot. 61:2140-2146.

Hulbert, L. C., and J. K. Wilson. 1983. Fire interval effects on flowering of grasses in Kansas bluestem prairie. Pages 255-257 *in* Proc. of the Seventh North American Prairie Conference (C. L. Kucera, ed.), Department of Biology, Southwest Missouri State University, Springfield.

*Kaufman, D. W., G. A. Kaufman, and E. J. Finck. 1983. Effects of fire on rodents in tallgrass prairie of the Flint Hills region of eastern Kansas. Prairie Nat. 15:49-56.

*Kaufman, D. W., S. K. Peterson, R. Fristik, and G. A. Kaufman. 1983. Effect of microhabitat features on habitat use by *Peromyscus leucopus*. Am. Midl. Nat. 110:177-185.

Krysan, J. L., R. F. Smith, and P. L. Guss. 1983. *Diabrotica barberi* (Coleoptera: Chrysomelidae) elevated to species rank based on behavior, habitat choice, morphometrics, and geographical variation of color. Ann. Entomol. Soc. Am. 76:197-204.

Petersen, N. J. 1983. The effects of fire, litter, and ash on flowering in *Andropogon gerardii.* Pages 21-24 *in* Proc. of the Eighth North American Prairie Conference (R. Brewer, ed.), Department of Biology, Western Michigan University, Kalamazoo.

Reichman, O. J. and P. Fay. 1983. Comparison of the diets of a caching and a noncaching rodent. Am. Nat. 122:576-581.

*Seastedt, T. R. 1983. The rhinoceros beetle, *Xyloryctes jamaicensis* Drury (Coleoptera, Scarabaeidae): a locally abundant detritivore of a Kansas riparian forest. J. Kansas. Entomol. Soc. 56:543-546.

Simberloff, D., and N. Gotelli. 1983. Refuge design and ecological theory: lessons for prairie and forest conservation. Pages 61-71 *in* Proc. of the Eighth North American Prairie Conference (R. Brewer, ed.), Dept. of Biology, Western Michigan University, Kalamazoo.

*Zimmerman, J. L. 1983. Cowbird parasitism of dickcissels in different habitats and at different nest densities. Wilson Bull. 95:7-22.

*Zimmerman, J. L. and E. J. Finck. 1983. Success in a secondary habitat: the dickcissel in the tallgrass prairie. Pages 47-49 *in* Proc. of the Eighth North American Prairie Conference (R. Brewer, ed.), Department of Biology, Western Michigan University, Kalamazoo.

1984

*Evans, E. W. 1984. Fire as a natural disturbance to grasshopper assemblages of tallgrass prairie. Oikos 43:9-16.

*Finck, E. J. 1984. Observations at a northern harrier nest. Kansas Ornithological Society Bull. 35:24.

*Finck, E. J. 1984. Male dickcissel behavior in primary and secondary habitats. Wilson Bull. 96:672-680.

Hazelton, P. K., and R. J. Robel. 1984. Preferences and influence of paired food items on energy intake of American robins and gray catbirds. J. Wildl. Manage. 48:198-202.

James, S. W. 1984. New records of earthworms from Kansas (Oligochaeta: Acanthodrilidae, Lumbricidae, Megascolecidae). Prairie Nat. 16:91-95.

*Kaufman, D. M., and D. W. Kaufman. 1984. Size preference for novel objects by the eastern woodrat (*Neotoma floridana*) under field conditions. Trans. Ks. Acad. Sci. 87:129-131.

Killingbeck, K. T. 1984. Nitrogen and phosphorus resorption dynamics of five tree species in a Kansas gallery forest. Am. Midl. Nat. 111:155-164.

Killingbeck, K. T. 1984. Direct measurement of allochthonous litter accumulation in a tallgrass prairie stream. Southwestern Nat. 29:357-358.

*Knapp, A. K. 1984. Effect of fire in tallgrass prairie on seed production of *Vernonia baldwinii* Torr. (Compositae). Southwestern Nat. 29:242-243.

*Knapp, A. K. 1984. Postburn differences in solar radiation, leaf temperature and water stress influencing production in a lowland tallgrass prairie. Am. J. Bot. 71:220-227.

*Knapp, A. K. 1984. Water relations and growth of three grasses during wet and drought years in a tallgrass prairie. Oecologia (Berl) 65:35-43.

McGinley, M. A. 1984. Central place foraging for non-food items: determination of the stick size value relationship of house building materials collected by eastern woodrats. Am. Nat. 123:841-853.

Powers, D. H., and E. L. Skidmore. 1984. Soil structure as influenced by simulated tillage. J. Soil Sci. 48:879-884.

*Seastedt, T. R. 1984. Belowground macroarthropods of annually burned and unburned tallgrass prairie. Am. Midl. Nat. 111:405-408.

*Seastedt, T. R. 1984. Microarthropods of burned and unburned tallgrass prairie. J. Kans. Entomol. Soc. 57:468-476.

*Zimmerman, J. L. 1984. Nest predation and its relationship to habitat and nest density in dickcissels. Condor 86:68-72.

1985

*Abrams, M. D. 1985. Fire history of oak gallery forests in a northeast Kansas tallgrass prairie. Am. Midl. Nat. 114:188-191.

*Abrams, M. D. 1985. Age-diameter relationships of *Quercus* species in relation to edaphic factors in gallery forests in northeast Kansas. For. Ecol. Manage. 13:181-193.

Freeman, C. C., and L. C. Hulbert. 1985. An annotated list of the vascular flora of Konza Prairie Research Natural Area, Kansas. Trans. Kans. Acad. Sci. 88:84-115.

*Hayes, D. C. 1985. Seasonal nitrogen translocation in big bluestem during drought conditions. J. Range Manage. 38:406-410.

*Heinrich, M. L., and D. W. Kaufman. 1985. Herpetofauna of the Konza Prairie Research Natural Area, Kansas. Prairie Nat. 17:101-112.

*Hulbert, L. C. 1985. History and use of Konza Prairie Research Natural Area. Prairie Scout 5:63-95.

James, S. W. 1985. An unexpected effect of fall burning on soil organic matter of tallgrass prairie. Am. Midl. Nat. 114:400-403.

*Kaufman, D. W., M. E. Peak, and G. A. Kaufman. 1985. *Peromyscus leucopus* in riparian woodlands: use of trees and shrubs. J. Mammalogy 66:139-143.

Killingbeck, K. T. 1985. Autumnal resorption and accretion of trace metals in gallery forest trees. Ecology 66:283-286.

*Knapp, A. K. 1985. Early season production and microclimate associated with topography in a C_4 dominated grassland. Oecol. Plant. 6:337-346.

*Knapp, A. K. 1985. Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. Ecology 66:1309-1320.

*Knapp, A. K., M. D. Abrams, and L. C. Hulbert. 1985. An evaluation of beta attenuation for estimating aboveground biomass in a tallgrass prairie. J. Range Manage. 38:556-558.

*Knapp, A. K., and F. S. Gilliam. 1985. Response of *Andropogon gerardii* to fire-induced high vs low irradiance environments in tallgrass prairie: leaf structure and photosythetic pigments. Am. J. Bot. 72:1668-1671.

Koelliker, J. K., M. E. Gurtz, and G. R. Marzolf. 1985. Watershed research at Konza--tallgrass prairie. Pages 862-867 *in* Hydraulics and hydrology in the small computer age, Vol. 1 (W. R. Waldrop, ed.), American Society of Civil Engineers, New York.

*McArthur, J. V., M. E. Gurtz, C. M. Tate, and F. S. Gilliam. 1985. The interaction of biological and hydrologic phenomena that mediate the quality of water draining native prairie on the Konza Prairie Research Natural Area. Pages 478-482 *in* Perspectives on nonpoint source pollution, Proc., 1985 National Conference, EPA 440/5-85-001, U.S. Environmental Protection Agency.

McArthur, J. V., G. R. Marzolf, and J. E. Urban. 1985. Response of bacteria isolated from a pristine prairie stream to concentration and source of soluble organic carbon. Appl. Environ. Microbiol. 49:238-241.

*Peterson, S. K., G. A. Kaufman, and D. W. Kaufman. 1985. Habitat selection by small mammals of the tallgrass prairie: experimental patch choice. Prairie Nat. 17:65-70.

Robel, R. J., S. M. Arruda, M. E. Morrow, and D. H. O'Neill. 1985. Chronic effects of a prescribed field application of a carbamate insecticide on bobwhites. The World Pheasant Assoc. 10:47-64.

*Seastedt, T. R. 1985. Canopy interception of nitrogen in bulk precipitation by annually burned and unburned tallgrass prairie. Oecologia (Berl) 66:88-92.

*Seastedt, T. R. 1985. Maximization of primary and secondary productivity by grazers. Am. Nat. 126:559-564.

Webster, J. R., E. R. Blood, S. V. Gregory, M. E. Gurtz, R. E. Sparks, and E. M. Thurman. 1985. Long-term research in stream ecology. Bull. of the Ecological Society of America 66:346-353.

*Zimmerman, J. L. 1985. Birds of Konza Prairie Research Natural Area, Kansas. Prairie Nat. 17:185-192.

1986

*Abrams, M. D. 1986. Historical development of gallery forest in northeast Kansas. Vegetatio 65:29-38.

*Abrams, M. D. 1986. Physiological plasticity in water relations and leaf structure of understory versus open-grown *Cercis canadensis* in northeastern Kansas. Can. J. For. Res. 16:1170-1174.

*Abrams, M. D. 1986. Ecological role of fire in gallery forests in eastern Kansas. Pages 73-80 *in* Symposium on prescribed burning in the midwest (A. Koonce, ed.), University of Wisconsin-Stevens Points, Stevens Point.

*Abrams, M. D., and A. K. Knapp. 1986. Seasonal water relations of three gallery forest hardwood species in northeast Kansas. Forest Sci. 32:687-696.

*Abrams, M. D., A. K. Knapp, and L. C. Hulbert. 1986. A ten-year record of aboveground biomass in a Kansas tallgrass prairie: effects of fire and topographic position. Amer. J. Bot. 73:1509-1515.

Asrar, G., E. T. Kanemasu, G. P. Miller, and R. L. Weiser. 1986. Light interception and leaf area estimates from measurements of grass canopy reflectance. IEEE Trans. of Geoscience and Remote Sensing GE-24:76-82.

Asrar, G., R. L. Weiser, D. E. Johnson, E. T. Kanemasu, and J. M. Killeen. 1986. Distinguishing among tallgrass prairie cover types from measurements of multispectral reflectance. Remote Sens. Environ. 19:159-169.

*Finck, E. J. 1986. Birds wintering on the Konza Prairie Research Natural Area. Pages 91-94 *in* Proc. of the Ninth North American Prairie Conference (G. K. Clambey and R. H. Pemble, eds.), Tri-College University Center for Environmental Studies, North Dakota State University, Fargo.

*Finck, E. J., D. W. Kaufman, G. A. Kaufman, S. K. Gurtz, B. K. Clark, L. J. McLellan, and B. S. Clark. 1986. Mammals of the Konza Prairie Research Natural Area, Kansas. Prairie Nat. 18:153-166.

*Gurtz, M. E. 1986. Development of a research data management program: factors to consider. Pages 23-38 *in* Research data management in the ecological sciences. (W. K. Michener, ed.), Belle Baruch Marine Library in Marine Sciences No. 16. University of South Carolina Press, Columbia.

*Hulbert, L. C. 1986. Fire effects on tallgrass prairie. Pages 138- 142 *in* Proc. of the Ninth North American Prairie Conference (G. K. Clambey and R. H. Pemble, eds.), Tri-College University Center for Environmental Studies, North Dakota State University, Fargo.

*James, S. W., and T. R. Seastedt. 1986. Nitrogen mineralization by native and introduced earthworms: effects on big bluestem growth. Ecology 67:1094-1097.

Killingbeck, K. T. 1986. Litterfall dynamics and element use efficiency in a Kansas gallery forest. Am. Midl. Nat. 116:180-189.

*Knapp, A. K. 1986. Postfire water relations, production, and biomass allocation in the shrub, *Rhus glabra*, in tallgrass prairie. Bot. Gaz. 147:90-97.

*Knapp, A. K. 1986. Ecophysiology of *Zigadenus nuttallii*, a toxic spring ephemeral in a warm season grassland: effect of defoliation and fire. Oecologia 71:69-74.

*Knapp, A. K., and L. C. Hulbert. 1986. Production, density and height of flower stalks of three grasses in annually burned and unburned eastern Kansas tallgrass prairie: a four year record. Southwestern Nat. 31:235-241.

*Knapp, A. K., and T. R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. BioScience 36:662-668.

*Koelliker, J. K. 1986. Notes about sediment in a tallgrass prairie (Konza Prairie site). Pages 35-38 *in* Sediment movement at LTER sites: mechanics, measurement and integration with hydrology. State Water Survey Contract Report 387. Champaign, IL.

McArthur, J. V., and G. R. Marzolf. 1986. Interactions of the bacterial assemblages of a prairie stream with dissolved organic carbon from riparian vegetation. Hydrobiologia 134:193-199.

Nellis, M. D. 1986. Remote sensing for monitoring rangeland management strategies in the Kansas Flint Hills. Int. Arch. Photogramm. and Remote Sens. 26:370-375.

*Seastedt, T. R., D. C. Hayes, and N. J. Petersen. 1986. Effects of vegetation, burning and mowing on soil macroarthropods of tallgrass prairie. Pages 99-102 *in* Proc. of the Ninth North American Prairie Conference (G. K. Clambey and R. H. Pemble, eds.), Tri-College University Center for Environmental Studies, North Dakota State University, Fargo.

Smith, D. L. 1986. Leaf litter processing and the associated invertebrate fauna in a tallgrass prairie stream. Am. Midl. Nat. 116:78-86

Smith, K. G. 1986. Winter population dynamics of three species of mast-eating birds in the eastern United States. Wilson Bull. 98:407-418.

Stapanian, M. A., and C. C. Smith. 1986. How fox squirrels influence the invasion of prairies by nut-bearing trees. J. Mammalogy 67:326-332.

*Tate, C. M., and M. E. Gurtz. 1986. Comparison of mass loss, nutrients, and invertebrates associated with elm leaf litter decomposition in perennial and intermittent reaches of tallgrass prairie streams. Southwestern Nat. 31:511-520

Weiser, R. L., G. Asrar, G. P. Miller, and E. T. Kanemasu. 1986. Assessing grassland biophysical characteristics from spectral measurements. Remote Sens. Environ. 20:141-152.

1987

*Abrams, M. D. 1987. Leaf structural and photosynthetic pigment characteristics of three gallery-forest hardwood species in northeast Kansas. For. Ecol. Manage. 22:261-266.

*Abrams, M. D., and L. C. Hulbert. 1987. Effect of topographic position and fire on species composition in tallgrass prairie in northeast Kansas. Am. Midl. Nat. 117:442-445.

*Bark, L. D. 1987. Konza Prairie, Kansas. Pages 45-50. Chapter 8. *In* The Climate of the Long-term Ecological Research Sites (D. Greenwood, ed.), Inst. Arctic & Alpine Res. Occas. Paper No. 44, Univ. Colorado, Boulder.

Chase, I. D., and S. Rohwer. 1987. Two methods for quantifying the development of dominance hierarchies in large groups with applications to Harris' sparrows. Anim. Behav. 35:113-118.

*Clark, B. K., D. W. Kaufman, G. A. Kaufman, and E. J. Finck. 1987. Use of tallgrass prairie by *Peromyscus leucopus*. J. Mammalogy 68:158-160.

*Evans, E. W. 1987. Dispersal of *Lygaeus kalmii* (Hemiptera: Lygaeidae) among prairie milkweeds: population turnover as influenced by multiple mating. J. Kans. Entomol. Soc. 60:109-117.

*Freeman, C. C., and D. J. Gibson. 1987. Additions to the vascular flora of Konza Prairie Research Natural Area, Kansas. Trans. Kans. Acad. Sci. 90:81-84.

*Gibson, D. J., and L. C. Hulbert. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. Vegetatio 72:175-185.

*Gilliam, F. S. 1987. The chemistry of wet deposition for a tallgrass prairie ecosystem: inputs and interactions with plant canopies. Biogeochemistry 4:203-217.

*Gilliam, F. S., T. R. Seastedt, and A. K. Knapp. 1987. Canopy rainfall interception and throughfall in burned and unburned tallgrass prairie. Southwestern Nat. 32:267-271.

Gotelli, N. J., and D. Simberloff. 1987. The distribution and abundance of tallgrass prairie plants: a test of the core- satellite hypothesis. Am. Nat. 130:18-35.

*Hayes, D. C., and T. R. Seastedt. 1987. Root dynamics of tallgrass prairie in wet and dry years. Can. J. Bot. 65:787-791.

Hooker, K. L., and G. R. Marzolf. 1987. Differential decomposition of leaves in grassland and gallery forest reaches of Kings Creek. Trans. Kans. Acad. Sci. 90:17-24.

*Kitt, D. Gerschefske, B. A. Daniels Hetrick, and G. Thompson Wilson. 1987. Sporulation of two vesicular-arbuscular mycorrhizal fungi in nonsterile soil. Mycologia 79:896-899.

Kraus, K. E., and C. C. Smith. 1987. Fox squirrel use of prairie habitats in relation to winter food supply and vegetation density. Prairie. Nat. 19:115-120.

Lanning, C. R., and L. N. Eleuterius. 1987. Silica and ash in native plants of the central and southeastern regions of the United States. Ann. of Botany 60:361-375.

*McArthur, J. V., and G. R. Marzolf. 1987. Changes in soluble nutrients of prairie riparian vegetation during decomposition on a floodplain. Am. Midl. Nat. 117:26-34.

*Nellis, M. D., and J. M. Briggs. 1987. Micro-based Landsat TM data processing for tall-grass prairie monitoring in the Konza Prairie Research Natural Area, Kansas. Papers and Proc. Appl. Geography Conference 10:76-80.

Reichman, O. J. 1987. Konza Prairie a Tallgrass Natural History. University of Kansas Press, Lawrence. 248 pages.

Robel, R. J., and M. E. Morrow. 1987. Feeding by bobwhites on sprouting corn reduced by bendiocarb. Trans. Kans. Acad. Sci. 90:35-40.

Sanchez, J. C., and O. J. Reichman. 1987. The effects of conspecifics on caching behavior of *Peromyscus leucopus*. J. Mammalogy 68:695-697.

Schmugge, T. J., E. T. Kanemasu, and G. Asrar. 1987. Airborne multispectral observations over burned and unburned prairies. Pages 203-207 *in* Proc. of IGARSS'87 Symposium, Ann Arbor.

Schmugge, T. J., J. R. Wang, and R. W. Lawrence. 1987. Results from the pushbroom microwave radiometer flights over the Konza Prairie in 1985. Pages 877-881 *in* Proc. of IGARSS'87 Symposium, Ann Arbor.

Seastedt, T. R., T. C. Todd, and S. W. James. 1987. Experimental manipulations of soil arthropod, nematode, and earthworm communities in a North American tallgrass prairie. Pedobiologia 30:9-17.

Whitcomb, R. F. 1987. North american forests and grasslands: biotic conservation. Pages 163-76 *in* Nature conservation: the role of remnants of native vegetation (D. A. Saunders, G. W. Arnold, A. A. Burbidge and A. J. M. Hopkins, eds.) Surrey Beatty and Sons Pry Limited in association with CSIRO and CALM.

*Zimmerman, J. L. 1987. Non-passerine breeding birds of Konza Prairie. Kansas Ornithological Society Bull. 38:29-33.

1988

*Abrams, M. D. 1988. Effects of burning regime on buried seed banks and canopy coverage in Kansas tallgrass prairie. Southwestern Nat. 33:65-70.

*Abrams, M. D. 1988. Genetic variation in leaf morphology and plant tissue water relations during drought in *Cercis canadensis* L. Forest Sci. 34:200-207.

*Abrams, M. D. 1988. Effects of prescribed fire on woody vegetation in a gallery forest understory in northeastern Kansas. Trans. Kans. Acad. of Sci. 91:63-70.

Asrar, G., T. R. Harris, R. L. Lapitan and D. I. Cooper. 1988. Radiative surface temperatures of the burned and unburned areas in a tallgrass prairie. Remote Sens. Environ. 24:447-457.

Auen, L. M. and C. E. Owensby. 1988. Effects of dormant-season herbage removal on Flint Hills rangeland. J. Range Manage. 41:481-482.

*Clark, B. K., D. W. Kaufman, G. A. Kaufman, E. J. Finck, and S. S. Hand. 1988. Long-distance movements by *Reithrodontomys megalotis* in tallgrass prairie. Am. Midl. Nat. 120:276-281.

*Evans, E. W. 1988. Community dynamics of prairie grasshoppers subjected to periodic fire - predictable trajectories or random walks in time? Oikos 52:283-292.

*Evans, E. W. 1988. Grasshopper (Insecta: Orthoptera: Acrididae) assemblages of tallgrass prairie: influence of fire frequency, topography, and vegetation. Can. J. Zool. 66: 1495-1501.

*Gibson, D. J. 1988. Regeneration and fluctuations of tallgrass prairie vegetation in response to burning frequency. Bull. Torrey Bot. Club 115:1-12.

*Gibson, D. J., and B. A. D. Hetrick. 1988. Topographic and fire effects on composition and abundance of Va-mycorrhizal species composition in tallgrass prairie. Mycologia 80:433-451.

Gray, L.J. and K. W. Johnson. 1988. Trophic structure of benthic macroinvertebrates in Kings Creek. Trans. Kans. Acad. Sci. 91:178-184.

*Gurtz, M. E., G. R. Marzolf, K. T. Killingbeck, D. L. Smith, and J. V. McArthur. 1988. Hydrologic and riparian influences on the import and storage of coarse particulate organic matter in a prairie stream. Can. J. Fish. Aqua. Sci. 45:655-665.

Gurtz, M. E., and C. M. Tate. 1988. Hydrologic influences on leaf decomposition in a channel and adjacent bank of a gallery forest stream. Am. Midl. Nat. 120: 11-21.

Hall, F. G., D. E. Strebel, and P. J. Sellers. 1988. Linking knowledge among spatial and temporal scales: Vegetation, atmosphere, climate and remote sensing. Landscape Ecology 2:3-22.

*Hetrick, B. A. Daniels, and G. W. T. Wilson. 1988. Suppression of mycorrhizal fungus spore germination in nonsterile soil: relationship to mycorrhizal growth response in big bluestem. Mycologia 80:338-341.

*Hetrick, B. A. Daniels, D. Gerschefske Kitt, and G. Thompson Wilson. 1988. Mycorrhizal dependence and growth habit of warm-season and cool-season tallgrass prairie plants. Can. J. Bot. 66:1376-1380.

*Hetrick, B. A. Daniels, J. F. Leslie, G. Thompson Wilson, and D. Gerschefske Kitt. 1988. Physical and topological assessment of VA-mycorrhizal fungus effects on root architecture of big bluestem. New Phytol. 110:85-96.

*Hetrick, B. A. Daniels, G. Thompson Wilson, D. Gerschefske Kitt, and A. P. Schwab. 1988. Effects of soil microorganisms on mycorrhizal contribution to growth of big bluestem grass in nonsterile soil. Soil Biol. Biochem. 20:501-507.

Hooker, K. L., and M. R. Whiles. 1988. A technique for the collection and study of subterranean invertebrates. Southwestern Nat. 33:375-376.

•Hulbert, L. C. 1988. Causes of fire effects in tallgrass prairie. Ecology 69:46-58.

Jackson, W. M., S. Rohwer, and R. L. Winnegrad. 1988. Status signaling is absent within age-and-sex classes of Harris' Sparrows. Auk 105:424-427.

James, S. W. 1988. The postfire environment and earthworm populations in tallgrass prairie. Ecology 69:476-483.

•James, S. W. 1988. *Diplocardia hulberti* and *D. rugosa*, new earthworms (Annelida: Oligochaeta: Megascolecidae) from Kansas. Proc. Biol. Soc. Washington. 101:300-307.

•Kaufman, D. W., S. K. Gurtz, and G. A. Kaufman. 1988. Movements of the deer mouse in response to prairie fire. Prairie Nat. 20:225-229.

•Kaufman, G. A., D. W. Kaufman, and E. J. Finck. 1988. Influence of fire and topography on habitat selection by *Peromyscus maniculatus* and *Reithrodontomys megalotis* in ungrazed tallgrass prairie. J. Mammalogy 69:342-352.

•Kitt, D. Gerschefske, B. A. Daniels Hetrick, and G. W. T. Wilson. 1988. Relationships of soil fertility to suppression of mycorrhizal big bluestem growth response in nonsterile soil. New Phytol. 109:473-482.

Killingbeck, K. T. 1988. Microhabitat distribution of two *Quercus* (Fagaceae) species in relation to soil differences within a Kansas gallery Forest. Southwestern Nat. 33:244-246.

Koelliker, J. K. 1988. Considerations in modeling the hydrology of Konza Prairie long-term ecological research site. Pages 377-386 *in* Modeling Agricultural, Forest, and Rangeland Hydrology, American Society of Agricultural Engineers, St. Joseph, MI.

•Marzolf, G. R. 1988. Konza Prairie Research Natural Area of Kansas State University. Trans. Kans. Acad. Sci. 91:24-29.

•Nellis, D. M., and J. M. Briggs. 1988. SPOT satellite data for pattern recognition on the North American tall-grass prairie Long- term Ecological Research Site. Geocarto International 3:37-40.

Reichman, O. J. 1988. Caching behavior by eastern woodrats (*Neotoma floridana*) in relation to food perishability. Animal Behavior. 36:1525-1532.

Schmugge, T. J., J. R. Wang, and G. A. Asrar. 1988. Results from the push broom microwave radiometer flights over the Konza Prairie in 1985. IEEE Trans. on Geoscience & Remote Sensing 26:590-596.

•Seastedt, T. R. 1988. Mass, nitrogen, and phosphorous dynamics in foliage and root detritus of annually burned and unburned tallgrass prairie. Ecology. 69:59-65.

•Seastedt, T. R., and D. C. Hayes. 1988. Factors influencing soil and water nitrogen concentrations in tallgrass prairie. Soil Biol. Biochem. 20:725-729.

•Seastedt, T. R., S. W. James, and T. C. Todd. 1988. Interactions among soil invertebrates, microbes and plant growth in tallgrass prairie. Agriculture, Ecosystems and Environment. 24:219-228.

•Seastedt, T. R., R. A. Ramundo, and D. C. Hayes. 1988. Maximization of densities of soil animals by foliage herbivory: empirical evidence, graphical and conceptual models. Oikos. 51:243-248.

Sellers, P. J., F. G. Hall, G. Asrar, D. E. Strebel, and R. E. Murphy. 1988. The first ISLSCP field experiment (FIFE). Bull. Am. Meteorological Soc. 69:22-27.

Shuman, T. W., R. J. Robel, A. D. Dayton, J. L. Zimmerman. 1988. Apparent metabolizable energy content of foods used by mourning doves. J. Wildl. Manage. 52:481-483.

*Travers, S. E., D. W. Kaufman, and G. A. Kaufman. 1988. Differential use of experimental habitat patches by foraging *Peromyscus maniculatus* on dark and bright nights. J. Mammalogy. 69:869-872.

*Wilson, G. W. T., B. A. Daniels Hetrick, and D. Gerschefske Kitt. 1988. Suppression of mycorrhizal growth response of big bluestem by nonsterile soil. Mycologia 80:338-343.

*Zimmerman, J. L. 1988. Breeding season habitat selection by the Henslow's sparrow (*Ammodramus henslowii*) in Kansas. Wilson Bull. 100:17-24.

1989

Asrar, G., R. B. Myneni, Y. Li and E. T. Kanemasu. 1989. Measuring and modeling spectral characteristics of a tallgrass prairie. Remote Sens. Environ. 27:143-155.

*Briggs J. M., and M. D. Nellis. 1989. Landsat thematic mapper digital data for predicting aboveground biomass in a tallgrass prairie ecosystem. *In* Prairie pioneers: Ecology, history and culture (T. B. Bragg and J. Stubbendieck, eds.). Proc. Eleventh North American Prairie Conference, Univ. Nebraska, Lincoln.

*Briggs, J. M., T. R. Seastedt, and D. J. Gibson. 1989. Comparative analysis of temporal and spatial variability in above-ground production in a deciduous forest and prairie. Holarctic Ecology 12:130-136.

Briggs, J. M., and K. G. Smith. 1989. Influence of habitat on acorn selection by *Peromyscus leucopus*. J. Mammalogy 70:35-43.

*Clark, B. K., D. W. Kaufman, E. J. Finck and G. A. Kaufman. 1989. Small mammals in tallgrass prairie: patterns associated with grazing and burning. Prairie Nat. 21:177-184.

Eisele, K. A., D. S. Schimel, L. A. Kapustka, and W. J. Parton. 1989. Effects of available P and N:P ratios on non-symbiotic dinitrogen fixation in tallgrass prairie soils. Oecologia 79:471-474.

*Evans, E. W. 1989. Interspecific interactions among phytophagous insects of tallgrass prairie: an experimental test. Ecology 70:435-444.

*Evans, E. W., C. C. Smith, and R. P. Gendron. 1989. Timing of reproduction in a prairie legume: seasonal impacts of insects consuming flowers and seeds. Oecologia 78:220-230.

*Evans, E. W., E. J. Finck, J. M. Briggs, D. J. Gibson, S. W. James, D. W. Kaufman, and T. R. Seastedt. 1989. Is fire a disturbance in grasslands? *In* Prairie pioneers: Ecology, history and culture (T. B. Bragg and J. Stubbendieck, eds.). Proc. Eleventh North American Prairie Conference, Univ. Nebraska, Lincoln.

*Fedynich, A. M. 1989. Dissolved organic carbon concentrations in soil water collected in Tully soils from a tallgrass prairie. Trans. Kans. Acad. Sci. 92:121-131.

*Gibson, D. J. 1989. Effects of animal disturbance on tallgrass prairie vegetation. Am. Midl. Nat. 121:144-154.

*Gibson, D. J. 1989. Hulbert's study on the effects of fire, mowing, and soil composition of tallgrass prairie. *In* Prairie pioneers: Ecology, history and culture (T. B. Bragg and J. Stubbendieck, eds.). Proc. Eleventh North American Prairie Conference, Univ. Nebraska, Lincoln.

Gray, L. J. 1989. Correlations between stream insect emergence and densities of insectivorous birds in the tallgrass prairie. *in* Prairie pioneers: Ecology, history and culture (T. B. Bragg and J. Stubbendieck, eds.). Proc. Eleventh North American Prairie Conference, Univ. Nebraska, Lincoln.

*Hartnett, D. C. 1989. Density- and growth stage-dependent responses to defoliation in two rhizomatous grasses. Oecologia 80:414-420.

*Hayes, D. C. and T. R. Seastedt. 1989. Nitrogen dynamics of soil water of burned and unburned tallgrass prairie. Soil Biol. & Biochem.

*Hetrick, B. A. Daniels, G. T. Wilson and D. C. Hartnett. 1989. Relationship between mycorrhizal dependence and competitive ability of two tallgrass prairie grasses. Can. J. Bot. 67: 2608-2615.

James, S. W. and M. R. Cunningham. 1989. Feeding ecology of some earthworms in Kansas tallgrass prairie. Am. Midl. Nat. 121:78-83.

Kaufman, G. A. 1989. Use of fluorescent pigments to study social interactions in a small nocturnal rodent, *Peromyscus maniculatus*. J. Mammalogy 70:171-174.

*Kaufman, D. W., and G. A. Kaufman. 1989. Population biology. Pps. 233-270. *in* Advances in the study of *Peromyscus* (Rodentia) (G. L. Kirkland and J. N. Layne, eds.), Texas Tech Press, Lubbock, TX.

*Kaufman, D. W., G. A. Kaufman and E. J. Finck. 1989. Rodents and shrews in ungrazed tallgrass prairie manipulated by experimental fire. *in* Prairie pioneers: Ecology, History and Culture (T. B. Bragg and J. Stubbendieck, eds.). Proc. Eleventh North American Prairie Conference, Univ. Nebraska, Lincoln.

Keeler, K. H., and B. Kwankin. 1989. Polyploid polymorphism in grasses of the North American prairie. Pages 101-127 *in* The Evolutionary Ecology of Plants (J. H. Bock and Y. B. Linhart, eds.), Westview Press, Boulder, CO.

Keeler, K. H. and B. Kwankin. 1989. Polyploid polymorphism in the prairie grass big bluestem (*Andropogon gerardii*). *in* Prairie pioneers: Ecology, history and culture (T. B. Bragg and J. Stubbendieck, eds.). Proc. Eleventh North American Prairie Conference, Univ. Nebraska, Lincoln.

Merrill, G. L. 1989. New records for Kansas mosses. Trans. Kans. Acad. Sci. 92:70-78.

Merrill, G.L. 1989. Bryopyhtes on Konza Prairie Research Natural Area. *in* Prairie pioneers: Ecology, history and culture (T. B. Bragg and J. Stubbendieck, eds.). Proc. Eleventh North American Prairie Conference, Univ. Nebraska, Lincoln.

*Nellis, M. D. 1989. Integrating field experiences with remote sensing for understanding vegetation indices. *in* Current Trends in Remote Sensing Education (M.D. Nellis, R. Lougeay, and K. Lulla, eds.). Geocarto International Centre: Hong Kong.

*Nellis, M. D., and J. M. Briggs. 1989. The effect of spatial scale on Konza landscape classification using textural analysis. Landscape Ecology 2:93-100.

*Ramundo, R. A., T. D. Shapley, C. L. Turner, M. I. Dyer, and T. R. Seastedt. 1989. Effects of burning, mowing and nitrogen fertilizer on chlorophyll, nitrogen and phosphorus content of big bluestem (*Andropogon gerardii* Vitman) at Konza Prairie. *in* Prairie pioneers: Ecology, history and culture (T. B. Bragg and J. Stubbendieck, eds.). Proc. Eleventh North American Prairie Conference, Univ. Nebraska, Lincoln.

Seastedt, T. R., M. V. Reddy, and S. P. Cline. 1989. Microarthropods in decaying wood from temperate coniferous and deciduous forests. Pedobiologia 33:69-78.

*Seastedt, T.R., R.A. Ramundo, and D.C. Hayes. 1989. The effects of foliage removal and root pruning on silica, nitrogen, and phosphorus concentrations and amounts in vegetation of tallgrass prairie. *in* Prairie pioneers: Ecology, history and culture (T. B. Bragg and J. Stubbendieck, eds.). Proc. Eleventh North American Prairie Conference, Univ. Nebraska, Lincoln.

Shuman, T. W., R. J. Robel, J. L. Zimmerman and K. E. Kemp. 1989. Variance in digestive efficiences of four sympatric avian granivores. Auk 106:324-326.

Strebel, D. E., J. A. Newcomer, J. P. Ormsby, F. G. Hall, and P. J. Sellers. 1989. Data management in the FIFE information system. Pages 42-45 *in* Proc. of IGARSS'89 Symposium, Vancouver, B.C.

Stewart, J. B. and L. W. Gray. 1989. Preliminary modelling of transpiration from the FIFE site in Kansas. Agricultural and Forest Meterology 48:305-315.

Tepedino, V. J., A. K. Knapp, G. C. Eickwort and D. C. Ferguson. 1989. Death Camas (*Zigadenus nuttallii*) in Kansas: Pollen Collectors and a Florivore. J. Ks. Entomological Soc. 62:411-412.

*Zimmerman, J. L. 1989. Passerine breeding birds of Konza Prairie. Kansas Ornith. Soc. Bull. 40:23-28.

KONZA PRAIRIE PUBLICATIONS IN PRESS

*Collins, S. L., and D. J. Gibson. Effects of fire on plant community structure in tallgrass prairie. *in* Effects of Fire on Tallgrass Prairie Ecosystems (S. L. Collins and L. L. Wallace, eds.). University of Oklahoma Press, Norman.

Collins, S. L., and S. M. Glenn. A hierarchical analysis of species abundance patterns in grassland vegetation. Am. Naturalist.

Glenn, S. M., and S. L. Collins. Patch structure in tallgrass prairies: dynamics of satellite species. Oikos.

Evans, E. W. and T. R. Seastedt. in press. Relations of phytophagous invertebrates and rangeland plants. *In*: D. J. Bedunah (ed.). Management of Grazing Lands: Importance of Plant Morphology and Physiology to Individual Plant and Community Response. Society for Range Mangement.

*Gibson, D. J., D. C. Hartnett, and G. Smith-Merrill. Fire temperature heterogeneity in contrasting fire-prone habitats: Kansas tallgrass prairie and Florida sandhills. Bull. Torrey Bot. Club.

Gray, L. J. Emergence production and export of aquatic insects from a tallgrass prairie stream. Southwestern Nat.

*Hetrick, B. A. Daniels. Constraints on mycorrhizal acquisition of phosphorus and plant growth responses. *in* Physiology and Ecology of Nitrogen, Phosphorus, and Sulphur Utilization by Fungi. (L. Boddy, R. Marchant, and D. J. Read, eds.). Brit. Mycol. Soc.

*Hetrick, B. A. Daniels, G. W. T. Wilson, and C. E. Owensby. Influence of mycorrhizal fungi and fertilization on big bluestem seedling biomass in tallgrass prairie soil. J. Range Manage.

*Kaufman, D. W., E. J. Finck, and G. A. Kaufman. Small mammals and grassland fires. *in* Effects of Fire on Tallgrass Prairie Ecosystems (S. L. Collins and L. L. Wallace, eds.), University of Oklahoma Press, Norman.

*Kaufman, D. W., and G. A. Kaufman. House mice (*Mus musculus*) in natural and disturbed habitats in Kansas. J. Mammalogy.

Kaufman, D. W. and G. A. Kaufman. Influence of plant litter on patch use by foraging *Peromyscus maniculatus* and *Reithrodontomys megalotis*. Am. Midl. Nat.

Keeler, K. H. Distribution of polyploid variation in big bluestem (Andropogon gerardii, Poaceae) across the tallgrass prairie region. Genome.

*Mushinsky, H. R. and D. J. Gibson. The influence of fire periodicity. *in* Habitat complexity: The physical arrangement of objects in space (S. S. Bell, E. D. McCoy and H. R. Mushinsky, eds.), Chapman and Hall.

Ojima, D. S., W. J. Parton, D. S. Schimel, and C. E. Owensby. Simulating the long-term impact of burning on C, N, and P cycling in a tallgrass prairie. Pages 353-370 *in* Current Perspectives of Biogeochemistry. CNR-IRRA N122A 128-00192.

Schaeffer, D. J., T. R. Seastedt, D. J. Gibson, D. C. Hartnett, B. A. D. Hetrick, S. W. James, D. W. Kaufman, A. P. Schwab, E. E. Herricks and E. W. Novak. Field bioassessments for selecting test systems to evaluate military training lands in a tallgrass prairie. Environmental Management.

*Seastedt, T. R. and J. M. Briggs. Long-term ecological questions and considerations for taking long-term measurements: Lessons from the LTER and FIFE programs on tallgrass prairie. *in* International Workshop on Long-term Ecological Research. (P. J. Risser, and J. Melillo, eds.) SCOPE Publ, Stockholm.

*Seastedt, T. R. and R. A. Ramundo. The influence of fire on belowground processes of tallgrass prairie. *in* Effects of Fire on Tallgrass Prairie Ecosystems (S. L. Collins and L. L. Wallace, eds.), University of Oklahoma Press, Norman.

Tate, C.M. Patterns and controls of nitrogen in tallgrass prairie streams. Ecology.

Tate, C. M. and C. G. Jones. Improving use of existing data. *in* Comparative Analyses of Ecosystems: Patterns, Mechanisms and Theories. (J. J. Cole, S. E. G. Findlay and G. M. Lovett, eds.). Springer-Verlag.

Wang, J. R., J. C. Shiue, T. J. Schmugge, and E. T. Engman. Mapping surface soil moisture with L-band radiometric measurements. Rem. Sens. Environment.

*Wilson, G. W. T., B. A. Daniels Hetrick, and D. Gerschefske Kitt. Suppression of VA mycorrhizal fungus spore germination by nonsterile soil. Can. J. Bot.

*Zajicek, J. M., M. L. Albrecht, and B. A. Daniels Hetrick. Vesicular-arbuscular mycorrhizae and greenhouse production of three native tallgrass prairie forbs. Restoration and Management Notes.

Appendix B.

DISSERTATIONS AND THESES CONDUCTED ON KONZA PRAIRIE (RELATING TO OR SUPPORTED BY LTER PROJECTS)

Hayes, D. C. 1982. Seasonal nitrogen translocation in big bluestem, *Andropogon gerardii* Vitman, in Kansas during a drought year. MS Thesis, Kansas State University, Manhattan, Kansas. 75 pp.

Smith, D. L. 1982. Macroinvertebrates and leaf litter decomposition in a tallgrass prairie stream. PhD Dissertation, Kansas State University, Manhattan, Kansas. 60pp.

Finck, E. J. 1983. Male behavior, territory quality and female choice in the dickcissel (*Spiza americana*). PHD Dissertation, Kansas State University, Manhattan, Kansas. 79pp.

James, S. W. 1983. Effects of burning on populations of three earthworm species in tallgrass prairie. PhD Dissertation, University of Michigan, Ann Arbor, Michigan. 188pp.

Blew, R. D. 1984. Rhizosphere nitrogen fixation (C_2H_2 reduction) associated with the major species of the tallgrass prairie. MS Thesis, Emporia State University, Emporia, Kansas. 58 pp.

Heinrich, M. L. 1984. Herpetofauna of the Konza Prairie Research Natural Area in the Flint Hills region of Kansas with respect to habitat selection. MS Thesis, Kansas State University, Manhattan, Kansas. 49pp.

McArthur, J. V. 1984. Interactions of the bacterial assemblages in a prairie stream with dissolved organic carbon from riparian vegetation. PhD Dissertation, Kansas State University, Manhattan, Kansas. 84pp.

Eisele, K. A. 1985. Effects of fire and N to P availability ratio on dinitrogen fixation in the tallgrass prairie. MS Thesis, Colorado State University, Fort Collins, Colorado. 82pp. (CSU funded)

Gurtz, S. Peterson. 1985. Habitat selection by small mammals: seasonality of responses to conditions created by fire and topography in tallgrass prairie. MS Thesis, Kansas State University, Manhattan, Kansas. 44pp.

Tate, C. M. 1985. A study of temporal and spatial variations in nitrogen concentrations in a tallgrass prairie stream. PhD Dissertation, Kansas State University, Manhattan, Kansas. 93pp.

Hayes, D. C. 1986. Seasonal root biomass and nirtogen dynamics of big bluestem (*Andropogon gerardii* Vitman) under wet and dry conditions. PhD Dissertation, Kansas State University, Manhattan, Kansas. 89pp.

Farley, G. H. 1987. Comparative breeding strategies of two coexisting passerines: Bell's vireo (*Vireo bellii*) and Bewick's wren (Thyromanes *bewickii*). MS Thesis, Kansas State University, Manhattan, Kansas. 52pp.

Hooker, K. L. 1987. Factors affecting the nitrate removal potential of sediments from a tallgrass prairie stream. PhD Dissertation, Kansas State University, Manhattan, Kansas. 107pp.

Loring, D. J. 1987. Observations of fluctuations in population density of two species of crayfish in a tallgrass prairie stream. MS Thesis, Kansas State University, Manhattan, Kansas. 64pp.

Ojima, D. S. 1987. The short-term and long-term effects of burning on tallgrass ecosystem properties and dynamics. PhD Dissertation, Colorado State University, Fort Collins, Colorado. 98pp. (CSU funded)

Bartlett, C. A. 1988. Computer modeling of water yield from Kings Creek watershed. MS Thesis, Kansas State University, Manhattan, Kansas. 95pp.

Gale, W. J. 1988. Canopy net carbon dioxide exchange by burned and unburned tallgrass prairie. MS Thesis, Kansas State University, Manhattan, Kansas. 76pp.

Kavanaugh, J. L. 1988. Community composition and emergence phenology of Chironomidae (Diptera) in prairie streams with different flow regimes. MS Thesis, University of Kansas, Lawrence, Kansas. 77pp.

Mikesell, F. L. 1988. Avian habitat selection in the attenuated riparian forest on the tallgrass prairie. MS Thesis, Kansas State University, Manhattan, Kansas. 57pp.

Su, H. 1988. Detecting soil information on the Konza Prairie using high resolution satellite data. MS Thesis, Kansas State University, Manhattan, Kansas. 109pp.

Clark, B.K. 1989. Influence of plant litter and habitat structure on small mammal assemblages: experimental manipulations and field observations. Ph.D. Disseration, Kansas State University, Manhattan, Kansas. 125pp.

Duell, A.B. 1989. Effects of burning on infiltration, overland flow, and sediment loss on tallgrass prairie. 82 pp.

Hetrick, J.A. 1989. Soil phosphorus chemistry: A systems approach. Ph.D. Dissertation, Kansas State Univ., Manhattan, KS., 118 pp.

Klittich, W. M. 1989. A comparison of soil hydraulic properties on Konza Prairie burning treatments. PhD Dissertation, Kansas State University, Manhattan, Kansas. 87pp.

Smith, G. N. 1990. Geomorphology and geomorphic history of the Konza Prairie Research Natural Area, Riley and Geary Counties, Kansas. M. S. Thesis, Kansas State University (in preparation).

GRADUATE PROJECTS IN PROGRESS WITH PARTIAL LTER SUPPORT

M.B. Brown: Effects of simulated bison grazing as influenced by time since fire and plant competition.

T.L. Benning: Fire frequency and topoedaphic controls of NPP in tallgrass prairie: development and tests of remote sensing indices.

S.H. Bixler: Population ecology of the prairie vole (*Microtus ochrogaster*) in ungrazed tallgrass prairie.

S. Bentivenga: Effect of management practices on inoculum potential (IP) of vesicular-arbuscular mycorrhizal fungi in tallgrass prairie.

J. Fahnestock: Responses of tallgrass prairie forbs to bison herbivory: Influence of topographic location on carbon and water relations.

P.A. Fay: Effects of gall wasp infestations on *Silphium integrifolium* in

F. Garcia: Nitrogen transformations in Konza tallgrass prairie. tallgrass prairie.

K. Jayachandran: Influence of iron chelation on phosphorus availability to prairie mycorrhizal plants.

L.K. Ramey-Gassert: Dendrochronological analysis of gallery forest trees on Konza Prairie: Reconstruction of climate, fire, and population history.

C.L. Turner: The influence of grazing on land surface climatological variables.

M.A. Vinton: Patterns of bison herbivory on Konza Prairie and initial responses of *Andropogon gerardii* and *Panicum virgatum* to bison grazing.