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REQUESTED AMOUNT \$ 4,200,000	PROPOSED DURATION (1-60 MONTHS) 72 months			REQUESTED STARTING DATE October 1, 1998		
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Summary

In 1987 we initiated a Long-Term Ecological Research Project in Field Crop Ecosystems to examine basic ecological relationships in field crop ecosystems typical of the U.S. Midwest. Our goal was -- and is -- to test the long-term hypothesis that agronomic management based on knowledge of ecological interactions in cropping systems can effectively replace management based on chemical subsidies. To test this hypothesis we established a series of sites comprising 11 different cropping systems and successional communities, corresponding to different levels and types of ecological disturbance. Within these communities we test hypotheses related to the patterns and processes that underlie ecosystem productivity and nutrient retention. Working hypotheses are built around the general topic areas of plant community dynamics, soil microbial populations, the dynamics of insect consumers, and nutrient availability/soil organic matter.

Over the past funding period we have made substantial progress towards addressing many of the initial hypotheses set out a decade ago. During this period we have developed biologically-based cropping systems with acceptable yields, successfully tracked both changes in the various taxons that appear to be important to row crop functioning as well as changes in important ecosystem-level attributes, and identified a number of questions related to understanding the key relationships in field-crop ecosystems.

With this proposal we present a plan to continue to investigate the significant portions of our long-term hypotheses, and to add two new components: a comprehensive watershed dynamics component to incorporate biogeochemical processes at a scale larger than individual fields, and a social component in recognition of the fact that many of the controls on ecological processes in agricultural ecosystems are human. We also lay out a brief plan to begin to regionalize the project by examining relationships between climate and productivity across the entire North Central Region.

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1.0 Results from Prior Support

1.1 Overview

In 1987 we established the KBS LTER site to provide a context for examining the ecological basis of commercial row-crop agriculture. The rationale was simple: most of what is known about agronomic systems stems from narrowly defined, highly disciplinary studies of specific properties and processes conducted in isolation from one other. As a result, our ecological understanding of row crop systems — arguably the most important ecosystem in human-dominated biomes (Matson et al. 1997) — is fragmented and incomplete. Our aim as a site has been to help remedy this situation by providing a physical context in which integrative ecological research in row-crop ecosystems can be carried out on a long-term, comparative basis. Our research strategy has targeted the examination of key components of these ecosystems, conducted in a comparative framework that integrates results from experimental studies at several scales with a multi-decade record of relevant baseline data.

The KBS LTER is located in the eastern portion of the U.S. corn belt (Fig. 1.1) and is comprised of a replicated series of annual row-crops, perennial forage crops, and unmanaged successional and older-growth communities used for ecological and historical comparisons. We have been conducting experiments designed to address interactions among four central processes within the row crop ecosystem: 1) nutrient availability, 2) herbivory and disease, 3) plant competition, and 4) crop productivity. During the first decade of the study we have used a taxon-based approach to conceptualize relationships (Fig. 1.2). Interactions among these components form the basis for understanding the regulation of crop productivity and the environmental impact of row crops within the larger landscape.

Our original global hypothesis is that agronomic management based on ecological knowledge can effectively substitute for reliance on chemical subsidies in modern high-yielding row crops. As noted below (Section 1.2), we have made substantive headway towards addressing both this hypothesis and its corollaries (Table 1.3), though we remain far from a comprehensive understanding of most of the underlying mechanisms that allow for substitution.

Most of our hypotheses to date have been addressed in the context of a simple experimental design established in 1989: replicated experimental treatments in a single field coupled with an additional successional community on a nearby never-tilled soil of the same series (Figure 1.4). This design (Figure 1.5) provides four annual cropping systems managed with a range of chemical-input intensities (from full to zero chemical inputs); two perennial cropping systems (one herbaceous [alfalfa] and the other woody [*Populus* sp.]); and two successional communities (one historically tilled and one never tilled). In 1993 we added three additional communities to the design, for a total of 5 unmanaged communities that now include three later successional old fields abandoned from cropping 40-60 years ago, three planted conifer stands, and three older-growth hardwood stands. The power of this design lies in its provision of a wide range of replicated communities with the same pedogenic history that differ in key ecological characteristics (e.g. plant species diversity, productivity, litter quality, microclimate). This allows us to test specific hypotheses from which we can better infer mechanisms operating in row-crop ecosystems – mechanisms that can then be tested with specific manipulative experiments. Baseline measurements are taken from all 11 community types, but not all communities are used to test every project hypothesis.

We have organized the project into groups led by Co-PI's with expertise in the topic areas that follow.

1.2 Net Primary Production

Aboveground net primary production (ANPP) and its translation to agronomic yield is a central focus of the KBS LTER site. High yields in our standard-management agronomic treatments can establish our credibility as a project with relevance to U.S. agriculture, and high yields in our biologically-based treatments

can validate our global hypothesis, i.e. that ecological knowledge can substitute for chemical inputs in high-yield cropping systems.

Corn yields on the KBS LTER from our two standard chemical input treatments have consistently been close to average yields for both Kalamazoo county and for the 12-state North Central Region as a whole, except for a localized drought year when KBS and county yields were both low (Fig. 1.6). This has also been true for yields from our biologically based treatments, but only for the past 4 years. For the first five years, yields on our biologically-based cropping systems were around 50% of the county mean (Fig. 1.7) -- except in one soybean year when yields were equivalent to county levels. Since 1994, however, yields for all three crops in these treatments have been equivalent to county means. This is agronomically significant because we appear to be achieving these yields consistently and without the organic supplements (e.g. manure) used in many low-input operations. It is experimentally significant because it allows us to ask questions from the standpoint of "why *DO* these systems work" rather than "why *DON'T* they work."

How does ANPP in our biologically managed systems compare to ANPP in the unmanaged successional sites? During non-drought years, total ANPP of corn averages 15-20 MT·ha⁻¹ in our standard chemical-input treatments (Fig. 1.8). This contrasts with <5 MT·ha⁻¹ in the successional fields, and ca. 10 MT·ha⁻¹ in the deciduous forest sites. This contrast emphasizes the impact of management on ANPP and underscores the high level of ecosystem services that can be provided by intensively managing organisms -- rather than chemicals -- in our biologically-based management treatments. In 1993 ANPP in the low and zero input cropping systems was ca. 12 MT·ha⁻¹, ca. four times greater than in the successional plots (T7) on the same site (ca. 3 MT·ha⁻¹), even when these are fertilized (see Fig. 1.10 below).

Most ANPP in annual cropping systems occurs during an 8 week period in midsummer, placing intense demands on soil resources and making rainfall during this period a potentially critical factor. In 1996, for example, rainfall in June-August was 60% of normal and yields dropped 40% -- but only in the standard input treatments (Fig. 1.9). In the low-chemical input treatments, yields were substantially higher. What confers drought protection in the biologically-based treatments? We can infer from our soil nitrogen measurements an interaction between nutrient and water availability. The chemical input treatments rely on rainfall during a 3-week window to deliver nitrogen to the root zone, whereas in the biological input treatments nitrogen is provided by microbes and soil invertebrates that decompose soil organic matter (SOM) -- including the winter cover crop -- earlier in the season when soil moisture is not limiting. This suggests an unexpected environmental service -- protection from some climate anomalies -- that is provided by biologically based management. This is the sort of finding that requires long-term, comparative measurements to detect, parallel studies to deduce mechanisms, and follow up experiments to test. We now have a fully synchronized annual crop rotation (1993-96) for a period when our biologically-based treatments consistently challenge ANPP in our conventional management treatments (since 1993), together with comparative data for unmanaged sites (since 1993), all of which combine to provide a powerful ecological context for examining the structure and functioning of differentially managed cropping systems.

1.3 Plant Community Dynamics

Our examination of the factors that regulate ANPP at KBS has included a focus on the dynamics and diversity of these communities. Determining the factors that influence the structure and diversity of plant communities has been a question of long-standing interest for ecologists (e.g. Huston 1994, Rosenzweig 1995, Tilman & Pacala 1993). Increasing concern about the effects of human influences on landscapes has motivated research to examine how the composition and diversity of communities affects ecosystem functions and the services provided by these communities (Vitousek et al. 1997). Because the KBS LTER is a matrix of cultivated and successional fields and older-growth forests, we have the opportunity to examine specific hypotheses about the factors influencing diversity, its relationship to ANPP, and the consequences of diversity for ecosystem processes in a variety of systems.

Successional grassland communities at KBS span a wide-range of ANPP (up to 10-fold), and both seedling recruitment, particularly of native species, and species richness varies with site productivity (Foster and Gross 1997, 1998, Gross et al. 1998). Enhancement of productivity with nitrogen fertilizer in these communities significantly reduces seedling recruitment and consequently the diversity of these fields (Foster and Gross 1998). Reduced diversity with increased productivity in grass-dominated sites appears due to both increased litter production and reduced light availability at ground level. Interestingly, we have observed a different response to fertilization in successional communities that are dominated by dicots rather than grasses (Huberty et al. 1998). Although N-addition in dicot communities significantly increased ANPP, there was no effect on either successional dynamics or diversity (S or H'; c.f. Figure 1.10), perhaps because the relatively high fertility of these sites limited their response to N-addition. However, a meta-analysis done by Gough et al. (1998) of the results of fertilization studies from seven LTER sites (including KBS) found that initial site fertility did not explain variation among studies in the effect of N-addition on species diversity. This analysis (and others, see Tilman 1993) suggests that local and regional factors that influence species composition of a site may influence the response to short term perturbation experiments such as fertilization. Different factors may control the relationship between ANPP and diversity at larger scales (Mittelbach et al. 1998, Gross et al. 1998).

The establishment of woody species - and thus the transition from old-fields to successional forests - also appears to be driven by both local and regional processes at this site. The temporal pattern of colonization by woody species with different dispersal modes (wind, bird, mammal) in the experimental successional treatment is very predictable and consistent across replicates (see Fig. 1.11). However, the spatial distribution of these species is variable. Early-arriving wind dispersed species (e.g. *Populus*) are randomly dispersed in these fields, whereas bird-dispersed species are highly clumped in space and associated with the distribution of clonal shrubs (e.g. *Rhus*; Table 1.12).

1.4 Insect Consumers

Management of agricultural systems without chemical subsidies relies on the capacity of beneficial organisms to regulate herbivore populations (Vandermeer 1995) and on an understanding of the ecological factors that enhance their abundance and persistence in the landscape (Pimentel 1960). Successional and forest communities in an agricultural landscape provide alternate sources of food and shelter to maintain beneficial organisms in the system (VanEmden 1990, Ostrom et al. 1997). Although many studies have shown the benefits of within-field or field-edge plant diversity on the maintenance of beneficial insects (e.g. Marino and Landis 1996, Marino et al. 1997), agricultural practices impact the structure of the landscape at many scales (Fig. 1.13), and the effects on landscape diversity on beneficial organisms may differ.

At KBS we have compared the response of two major groups of beneficial insects that differ in mobility to landscape structure: plant-dwelling predatory ladybird beetles (Coccinellids) that are highly mobile, and ground-dwelling predaceous beetles with more limited mobility (Burel 1989). We have found that the abundance and diversity of both ground beetles and Coccinellids varies in relation to the complexity of the agricultural system (Clark et al. 1997; Colunga-Garcia and Gage 1998). For example the most abundant of these species at KBS, *Coleomegilla maculata lengi*, occurs more frequently in the simplified habitats of the standard chemical input conventional tillage treatment, whereas another species, *Coccinella septempunctata*, is most abundant in the more structurally complex biologically-managed systems (Figure 1.14). The crop rotation itself also affects the composition of the ladybird beetle community at this site. *Coleomegilla maculata lengi* was the dominant species in corn whereas *Coccinella septempunctata* was dominant in soybean, illustrating the importance of habitat heterogeneity for providing sufficient diversity to allow function (pest protection) to persist through multiple crop rotations (Colunga-Garcia 1996).

Incorporating woody crops and successional plant communities in agricultural landscapes increases plant diversity and provides alternate habitats for predators, as well as increases the diversity of these

species in field crops (Maredia et al. 1992b, Colunga-Garcia et al. 1997). Changes in the composition and size of the dominant plant species in these communities also can drive changes in the insect community. For example, we observed a succession of dominant species within the ladybird beetle complex as *Populus* aged (Fig. 1.15). Dominant beetle species in young poplar plantations (one to four years) were also dominant in the adjacent field crops. Thereafter, the dominant ladybird beetle species in poplar were species typical of deciduous habitats. The species diversity and abundance of Coccinellids also changed over time in the experimental successional communities (Fig. 1.16). We observed the highest diversity of predatory species after the sixth year, but population numbers are low. These findings have significant implications for the implementation of ecologically-based cropping practices (Colunga -Garcia 1996).

1.5 Microbial Community Dynamics and Soil Organic Matter (SOM)

The diversity of cropping systems and plant communities at the KBS LTER has provided us with unique opportunities to examine the effects of plant diversity and agronomic management on soil communities and the processes they regulate. Our work has focused on the development of both concepts and novel techniques for studying the composition and function of soil microorganisms (Paul et al. 1998a, Horwath and Paul 1994, Thorn 1997), including molecular techniques (e.g. Zhou et al. 1994, Cavigelli et al. 1995, Bruns et al. 1998). This work also has had applications for bioremediation (e.g. Thorn et al. 1997, Ka & Tiedje 1994).

Microbial biomass, as measured by fumigation, has remained relatively constant over time in the agronomic treatments and successional communities (Horwath et al. 1996, Harris et al. 1998; Table 1.17). Microscopic estimates of abundance have revealed an increase in numbers in the Poplars between 1993 and 1996, corresponding to an increase in fungal biomass that is attributable to a switch from arbuscular to ectotrophic mycorrhiza (Paul and Clark 1996, Horwath et al. 1994). Bacterial growth rates in the agronomic treatments (measured by ^3H thymidine incorporation) show the conventional tillage treatment to have bacterial turnover times of 160 days relative to the 107 days of the higher biomass never-tilled successional site (Harris and Paul 1994). These slow turnover rates are reflected in our C budgets for this site (Paul et al. 1998b) and help explain many of the other microbiological measurements and their effect on ecosystem productivity.

Nitrification is an especially important ecosystem process in agricultural systems because of its role in making nitrate available to plants, denitrifiers, and hydrologic export (Paul & Clark 1996, Robertson 1998). The microbes that mediate this process are sensitive to environmental changes, and changes in their species composition may affect changes in nitrification rates. Nitrification potentials differ among many of our communities (Table 1.17). Although there are differences in the diversity of nitrifiers isolated from these treatments, diversity appears to be independent of function. *Nitrosospora* dominated both the agronomic treatments and the Poplars, where nitrification rates were 4 times lower. The historically-tilled successional communities also have low nitrification, but contain a variety of nitrifiers, including two *Nitrosospora* spp., one *Nitrosomonas* sp., and an unidentified deep clade (Bruns 1996) measured by a variety of techniques (Fig. 1.17) including 16sRNA-PCR. Denitrifier populations also vary by community; using FAME analysis and anaerobic isolation techniques Cavigelli (1998) found 22 taxa in the conventionally tilled site vs. 17 in the never-tilled successional community, with only 12 taxa in common.

Understanding the processes that regulate the dynamics of soil-C is essential for ecosystem stability and the long-term sustainability of agricultural systems. We have shown that these soil-C dynamics can be analytically determined by a combination of tracers, laboratory incubation, and physical and chemical fractionation (Paul et al. 1995). For example, non-hydrolysable C comprises 56% of the soil carbon in standard input CT plots and has a mean residence time (MRT) of 1435 yr compared to 465 yr for the total soil (Table 1.19). The non-hydrolysable pool of the never-tilled successional site has a MRT of 170 y, reflecting the larger proportion of recent C. Laboratory incubations that allow microbial enzymes to fractionate the soil C show the never-tilled successional sites to have significantly higher CO_2 evolution on a soil

weight basis (Fig. 1.20, top). The historically-tilled successional sites have the same respiration rate as the never-tilled successional site on a per unit C basis, reflecting the recent accumulation of active and slow fractions (Fig. 1.20, bottom). The small active pool has MRT's of 100's of days while the larger slow pool has field MRT's of 13 yr for the CT and 9 yr in the successional sites (Table 1.21). Expansion of our analysis to a regional basis (Collins et al. 1998) shows our coarse-textured LTER site to have lower MRT's than those of other corn belt soils with more clay and silt. The soil C at depth is very old, but has active and slow pools with MRT's equivalent to surface soils (Collins et al. 1998; Paul et al. 1998c).

1.6 Biogeochemical Fluxes

Two major biogeochemical questions are implicit in our global hypothesis: 1) What controls nutrient (especially nitrogen) availability in our cropping systems and how do these controls relate to the differential productivity of our treatments, and 2) What is the biogeochemical impact of cropping systems on downstream water bodies (including groundwater) and on trace gas fluxes to the atmosphere? Ecologically important questions of nutrient availability in our systems are largely microbial, related in particular to the timing and quantity of SOM turnover. As noted above, we are making substantive progress towards understanding how microbial community composition and SOM quality affect soil nutrient flux. We highlight here recent progress in understanding the impact of management on solution N and trace gas fluxes.

That high-input cropping systems leach large quantities of nitrate to groundwater is well known; countless studies since the 1950's have documented losses of 20-60% of nitrogen applied as fertilizer (e.g. Robertson & Paul 1998). It is less well known how biologically-managed systems lose N: Are N needs in high-yield low-input systems met through better N retention (less leaching and denitrification) or through more effective N acquisition (e.g. N₂ fixation) and utilization (e.g. the timing of N mineralization).

Our work shows clearly that low-input cropping systems can leach nitrate as effectively as high-input systems (Harris et al. 1994, Boles et al. 1997, Fig. 1.22, left). Suction lysimeters show the lowest concentrations of nitrate in soil solution beneath successional fields and perennial crops (flux calculations await our water budgets, under development), with an order of magnitude or higher concentrations beneath the annual crops, including the low-input treatments. Nitrate, however, is not the whole story. It is commonly assumed that dissolved organic nitrogen (DON) is a minor constituent of solution nitrogen loss from ecosystems in general and cropped ecosystems in particular. In 1995 we installed DON-permeable Teflon lysimeters in all LTER treatments to test this assumption directly and have found it unwarranted. Unlike NH₄⁺, many DON species are uncharged and appear to flow freely with wetting fronts; in all of our annual cropping systems DON concentrations were close to those of nitrate until mid-growing season (Fig. 1.22, right), when concentrations fell to <10% of total solution N concentrations. In our perennial and unmanaged systems, DON predominated solution concentrations throughout the year – comprising 50-90% of total solution concentrations at depth. Experiments are now underway to determine the reasons for these differences.

Measurements of trace gas fluxes across all treatments (including the successional and forested sites) are providing important insights into patterns and controls on trace gas fluxes in agricultural landscapes. Our N₂O measurements show that the historical impact of cultivation may far exceed that of fertilizer use on fluxes of N₂O from agronomic systems. Results from our intensive measurement program (completed in 1997) show that rates of N₂O flux from our noncultivated sites are 2-3 times lower than rates from the annual cropping systems (Table 1.23). Furthermore, the fluxes in the biologically-based management systems (our low and zero input treatments) are as high or higher than fluxes in the standard chemical input systems. Likewise, we now have an exceptionally well-documented case that agronomic activity depresses CH₄ uptake in terrestrial communities (Fig. 1.24), and that – as for N₂O fluxes – biologically-based management does not appear to attenuate fluxes from annual cropping systems. Results from comparative studies of agronomic vs. unmanaged sites on the same soil are rare, but very important for gauging the historical impact of agriculture on trace gas fluxes globally (Smith et al. 1995, IPCC 1996).

1.7 Publications of the KBS LTER Site

1.71 Journal Articles Since 1992

Asterisks denote articles associated with specific LTER hypotheses developed in earlier proposals.

- Aiken, R. M., and A. J. M. Smucker. 1996. Root system regulation of whole plant growth. *Annual Review Phytopathology* 34: 325-347.
- Ambus, P., and G. P. Robertson. 1998. Automated near-continuous measurement of CO₂ and N₂O fluxes with a photoacoustic infra-red spectrometer and flow-through soil cover boxes. *Soil Science Society of America Journal*, in press.
- Ambus, P., and G. P. Robertson. 1998. Fluxes of CH₄ and N₂O from Poplar stands grown under ambient and twice-ambient CO₂. *Atmospheric Environment* (submitted).
- Bossart, J. L., and J. M. Scriber. 1995. Maintenance of ecologically significant genetic variation in the tiger swallowtail butterfly through differential selection and gene flow. *Evolution* 49: 1163-1171.
- Bruns, M. A., J. A. Fries, J. M. Tiedje, and E. A. Paul. 1998. Functional gene diversity among terrestrial ammonia oxidizing bacteria. *Applied Environmental Microbiology*. (submitted)
- *Clark, M. S., S. H. Gage, and J. R. Spence. 1997. Habitats and management associated with common ground beetles *Coleoptera: Carabidae* in a Michigan agricultural landscape. *Environmental Entomology* 26: 519-527.
- Chiu, T. C., and K. Sarabandi. Electromagnetic Scattering from short branching vegetation. *IEEE Trans. Geosci. Remote Sensing*. (submitted)
- *Collins, H. P., E. A. Paul, R. L. Blevins, L. G. Bundy, D. R. Christenson, W. A. Dick, D. R. Huggins, D. J. Lyon, S. E. Peters, and R. F. Turco. 1998. Carbon pools and dynamics in Corn Belt agroecosystems. *Soil. Sci. Soc. Amer. J.* (in press).
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1.74 Other Publications — Published Abstracts from National and International Meetings

KBS LTER research results have been presented at over 150 national and international meetings over the 1992-98 period. On our web site (<http://lter.kbs.msu.edu>) we list over 100 published abstracts from these meetings, which include publications in bulletins or proceedings from various national societies including the Ecological Society of America (17 abstracts), the American Society of Agronomy (28 abstracts), the Weed Science Society, the Soil Ecology Society, the American Society of Entomology, the American Society of Microbiology, The Geological Society of America, and the Botanical Society of America, among others.

1.8 Data Sets Available Electronically

Data Sets produced and managed by the KBS LTER project and available 1/98 on-line via the KBS WWW Server (<http://lter.kbs.msu.edu>) except as noted. Unrestricted access.

Weather

- LTERR Main Site Weather Station (searchable database: 3693 daily records)
 - Daily Precip/AirTemperature (from 1988)
 - Daily Solar/Wind Direction and Speed (from 1992)
 - Daily Evapotranspiration
- Pond Lab Weather Station (searchable database: 5347 daily records)
 - Daily Air and Soil Temperatures, RH, and Precipitation (from 1983)
 - Daily Solar/Wind Direction and Speed (from 1983)
- KBS National Weather Service Station (searchable database: 20,000 + daily records)
 - Daily Maximum/Minimum Air Temperatures/Precip (1980-1997).
 - Monthly Maximum/Minimum Air Temperatures/Precip (1980-1997).
 - Daily Maximum/Minimum Air Temperatures/Precip/Snow (1948-1997).
 - Monthly Maximum/Minimum Air Temperatures/Precip/Snowfall (1948-1997).
- National Atmospheric Deposition Program/National Trends Network (NADP/NTN) at KBS (via link to KBS files at <http://nadp.nrel.colostate.edu/NADP>)
 - Weekly, Monthly, and Annual Precipitation Chemistry
 - Ion Concentrations (mg/L)
 - Annual and Seasonal Total Deposition for N , S (kg/ha)
- Kalamazoo Hospital National Weather Service Station (>300,000 daily records)
 - Daily Maximum/Minimum Air Temperatures/Precip/Snow (1887-1987).
 - Monthly Maximum/Minimum Air Temperatures/Precip/Snowfall (1887-1987)
 - Summary Figures (3 graphs)

Spatial Variability (initial site survey)*

- Soil Physical Properties (65 files)
- Soil Chemical Properties (58 files)
- Soil Biological Properties
 - Microbial Populations and Processes (89 files)
 - Nematode Trophic Groups (44 files)
- Plant Biomass and CN Content (24 files)

Net Primary Productivity and Species Diversity (1989-present)

- Annual Systems - Treatments 1,2,3,4 (82 files)
- Perennial Crops - Treatments 5,6 (135 files)
- Perennial Systems - Treatments 7,8,CF,DF,SF (74 files)
- Agronomic Yields - All main site treatments (1989-1997: 17 files)
- Species Lists (46 files)

Soil Properties for all LTER treatments

- Total Carbon & Nitrogen (1989-1995: 14 files)
- N mineralization (1989-1995: 11 files)

Microbial Biomass

- Chloroform Fumigation-Incubation (1989-1996: 21 files)
- Epifluorescence Microscopy (1990-1996: 16 files)
- Bulk Density (1996; searchable database: 334 records)
- Moisture (1990-1996; searchable database: 2,824 records)

Insect Populations (42 data files)

- Aerial (Sticky-trap) Network (1989-1994)
- Soil (Pitfall-trap) Network (1993-1994)

Trace Gas Fluxes: N₂O, CO₂, CH₄

- N₂O, CO₂, CH₄ extensive site sampling (from 1992; searchable database, 1852 records)
- N₂O, CO₂ hourly sampling (data under review, >10,000 records to be posted 3/98)

Biodiversity

- Insects (8 files)
- Microbes & Invertebrates (2 files)
- Plants (1989-1996: 98 files)

Geographical Data

- Remotely Sensed Images (satellite, aerial at scales 1/2500; 1/250; 45 files)
- GIS Data
 - KBS Proper (soils, vegetation, infrastructure; 10 files)
 - Four-Township GIS Database (via link to <http://topos.geo.msu.edu/~kbs/>)¹
 - Aerial Photography
 - Elevation (digitized 1:24,000 maps)
 - Surface Waters (streams, lakes, National Wetland Inventory)
 - Subsurface Flow Patterns (water table elevation)
 - Land use
 - Population
 - Transportation

¹ The four-township GIS database is a cooperative effort between KBS, the KBS LTER project, the Department of Geography, the MSU Center for Remote Sensing, and the governments of the 4 townships that surround KBS. It has been under development for 2 years as a prototype for other township groupings in Michigan, and will be on-line in March 1998.

Section 2 – Proposed Research

2.1 Overview

The long-term core hypothesis of the KBS LTER (Table 1.3), can be recast as two simple questions:

- What are the ecological relationships in row-crop ecosystems that can be managed to provide ecosystem services typically provided by external chemical subsidies, and
- To what extent can the environmental impact of agriculture be minimized without jeopardizing high crop yields?

During our first decade of research on-site we have learned much about the taxa and processes important for the high ANPP of our row crops, much of this via field experiments and comparisons with nearby unmanaged sites in different stages of secondary succession. We have also learned much about the environmental consequences of different management strategies. In particular, we have learned that row crop ecosystems are as ecologically complex as other early successional ecosystems, that chemical subsidies are not needed to provide economically acceptable ANPP, and that biologically-managed systems are not necessarily more environmentally benign than their chemical-based counterparts.

For the second decade of research at KBS we will continue our core, long-term examination of ecological interactions in field crop agriculture and its impact on the environment by concentrating on identifying the mechanisms that underly patterns that emerged during the project's initial years. We add two major refinements to this endeavor:

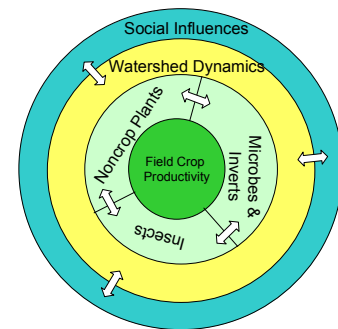
- A focus on biological diversity as an organizing concept for both the basic and the more applications-oriented portion of the project. Scientifically, we have converged on the realization that most of our questions have a major biodiversity component -- How and why is plant community diversity related to ANPP and nutrient retention? How is the structure of soil microbial communities related to SOM, and does diversity affect nutrient flux? What is the scale at which habitat diversity affects the diversity of predatory insects and their ability to disperse and colonize new cropping systems? At all levels, most of our core questions can be reduced to questions about the patterns, causes, and consequences of biological diversity. Cropping systems, because of their explicit management of plant diversity, may be ideally positioned to answer some of the emerging questions about the role of diversity in ecosystem function (Chapin et al. 1998, Robertson & Paul 1998).
- Our second major refinement is a conceptual expansion of the project to better encompass landscape-level questions and to incorporate explicitly the human social dimension of row-crop agriculture and its biological management:
 - Landscape dynamics are important to row-crop ecology at a variety of levels, and many of our prior hypotheses have had implicit landscape components. With this renewal we strengthen the landscape components of our population- and community-level questions (e.g. landscape influences on local insect and plant diversity) and initiate a new biogeochemical component to focus on landscape-level biogeochemistry.
 - Likewise, we have added a new human social component to the project in recognition of the fact that we need to explicitly address the human dimensions of agricultural systems, i.e. the social phenomena that drive many of the ecological interactions that occur in cropping systems; these include both the social barriers to the adoption of ecological technology (e.g. biologically based agronomy) as well as the external socioeconomic forces (such as land use policy and exurbanization trends) that shape growers' decisions to maintain a particular management system.

By necessity and design, the questions we address below are highly intertwined. Ecological interactions occur both within the field crop ecosystem and within larger landscape units, and at all levels interactions are

affected by (and affect) human activities. A highly simplified conceptual diagram identifies the levels of these interactions (Fig. 2.1). We organize the remainder of this section around these components.

2.2 Plant Community Dynamics

Our work to date in this area has focused on comparing species abundance and composition in our different managed and unmanaged plant communities, and on examining the determinants of diversity in our successional sites. We plan to expand the scope of this work to examine directly the patterns and consequences of plant diversity in the agronomic treatments and compare this to both early successional and more established communities in the region that represent a broad range of ANPP and a variety of disturbance types relevant to our agronomic sites. We plan work in four major areas: 1) the importance of seed banks as reservoirs of plant diversity, 2) the relationship between productivity and diversity in successional communities, 3) scales and patterns of diversity among different managed and unmanaged communities, and 4) the consequences of plant diversity in row crop rotations.



The composition and diversity of soil seed banks

The soil seed bank is viewed as a 'reservoir of species diversity' in many types of plant communities (Leck et al. 1989) because it can provide a mechanism for species to persist in temporally variable environments. In agricultural systems, the soil seed bank can preserve part of the "biological legacy" of a site, reflecting changes in crop rotations, tillage, and chemical inputs that can affect the weed species that emerge in different years (Cavers and Benoit 1990). Making predictions about the distribution and abundance of weeds from information about the seed bank can be difficult because there is tremendous spatial heterogeneity in the distribution and abundance of seeds in the soil (Gross 1990, Thompson 1994). Also, a variety of factors interact to determine species survival in soil and emergence from the seed bank (Leck et al. 1989). Understanding the factors that determine the composition and diversity of soil seed banks, and the potential for species emergence, has important implications for the management of plant species diversity in agronomic systems.

We have sampled the soil seed bank in each of the treatments on the LTER main site at 2-3 yr intervals since the inception of the project, initially as part of the spatial variability sampling (1988) and then again in 1990, 1993, 1996. Quantifying the composition of the seed bank is notoriously difficult, but we have developed an elutriation method that works well for documenting the key species in our agronomic communities (Gross and Renner 1989). In successional communities seed bank diversity and composition is best quantified by direct germination methods, but this is time-consuming and appears to be not well related to the above-ground community (e.g. Gross 1990). For example, over the past 8 years the abundance of annual monocots has increased steadily over years on tilled microplots in the successional treatment (from 10 % in 1989 to 90% in 1997), yet the seed bank at this site is dominated by annual dicots (Figure 2.2).

In the agronomic treatments we have seen changes in both the abundance and composition of the seed bank among treatments. Originally, the seed bank on the entire site was dominated by annual dicots (reflecting the multiple years of high-input corn crops; Robertson et al. 1997). In 1990 (one year after treatment establishment), there were no differences in the abundance or composition of the seed bank among the 4 row-crop treatments (Table 2.3). In the successional plots seed numbers in the upper 15 cm of soil had increased 35-fold (from a mean of 1,873 to over 67,000 m⁻²). This rapid increase in abundance reflects the substantial weed pressure potentially facing the biologically-based (low- and zero-chemical input) treatments.

In 1993 we found significant differences among the 4 agronomic treatments in seed number (Table 2.3),

weed seed numbers in the biologically based crop treatments were greater than in the conventional and no-till treatments. Management differences were also apparent in the emergent weed community among the four row-crops -- the low and zero-input treatments had a greater number of weed species in 1993 than did the chemically-based (conventional- and no-till) treatments (Fig 2.4). Interestingly, by 1996 seed densities were not significantly different in these treatments, although densities in the low-input plots were twice those in the other agronomic treatments (Table 2.1). In both the successional and poplar plots seed densities declined over this period (Table 2.3).

The dramatic changes in seed numbers and diversity in the low and no-chemical input treatments may reflect the change in weed management (discontinuation of herbicides) or differences in crop rotation. Over the first 5 years of the project, only the biologically based treatments included winter-wheat and hairy-vetch in the rotation. This difference in crop rotation appears to have influenced the composition of the weed seed bank as winter annuals dominated the soil seed banks of these treatments. Many of the weed species that emerged in these treatments in 1993 (with the corn crop) were winter annuals such as chickweed (*Stellaria media*) that were not present in the conventional- and no-till treatments.

Our results to date have confirmed that crop rotation and weed management can strongly influence the composition and diversity of the weed seed bank in agronomic systems. There have been changes both in the overall composition of the community, as well as changes in the abundance of specific species (Renner et al. 1998) can also affect these patterns. This is an extremely valuable long-term data set from our site because rarely have studies of weed seed banks been performed across this range of agronomic treatments or for such an extended period of time. We plan to continue to monitor the soil seed bank in these treatments, but at a reduced frequency (every 6 years, so again in 2002) as we expect that the long-term value of this data set can be maintained at this level. At that time we will extend this work to include an analysis of factors influencing the spatial heterogeneity of the weed community in the agronomic treatments (see below).

Productivity and diversity in successional communities

Our experimental work in the historically-tilled successional communities established in 1989 (T7 in Figure 1.2) have shown that nitrogen addition increases ANPP, but has no apparent effect on species diversity (Huberty et al 1998; see Figure 1.10). This result is in contrast to conventional wisdom, which holds that fertilizing herbaceous communities should decrease diversity (Gough et al. 1998), particularly in old-fields (Tilman et al. 1996). One explanation for our lack of fertilizer response is the moderately high fertility of KBS soils relative to soil fertility at most sites at which this question has been examined. The mechanism accounting for the low diversity in response to high fertility is that reduced light levels in higher ANPP communities increase competition for light, resulting in competitive exclusion (Tilman 1993, Reynolds and Pacala 1994). If poor light-competitors are already excluded from a high ANPP site, then further increases above some threshold will not much affect diversity regardless of any effect on ANPP. Because most studies of old-field succession have been conducted on depauperate soils (land that has been abandoned from farming for economic rather than for scientific reasons), this phenomenon – if generalizable – will be a significant contribution to ecological knowledge as well as illustrate the value of ecological work in arable systems.

We initiated a study in 1997 to examine whether the timing of N-fertilizer addition might affect the magnitude of fertilizer ANPP and diversity response. Timing could be especially important if the principle mechanism that depresses the response is competition for light, which will change during the growing season as the plant canopy develops. We added N as a single pulse (as in our previous studies, Fig.1.10) and as a split pulse (half in early May, half in June). This split timing of N-addition is similar to that used at the CDR LTER (Tilman 1998) and by Foster & Gross (1998) at KBS, in studies that have shown a strong effect of fertilization on diversity. To rule out competition for phosphorus as an explanation for the lack of a nutrient response, we also included in this design a P-addition treatment. Preliminary results indicate that

the timing of N-addition can indeed strongly influence the magnitude of the ANPP response to fertilization, and consequently subcanopy light levels (Fig 2.5). Addition of P, alone or with nitrogen, had no effect. The timing of nutrient pulses and the effect of the dominant species on light availability may be critical for mediating competitive interactions in these early-successional systems. These results should be directly relevant to our biologically managed cropping systems -- keeping the canopy as closed as possible until the dominant (the crop) is well-established may be crucial for excluding weeds in the absence of herbicide.

We will maintain the N, P addition experiment in the successional treatment for the next three years to confirm and further explore the relationship between nutrient release, light availability, and ANPP and diversity. Additionally we will test these mechanisms in the agronomic treatments to explore how variation in the dominant plant (via crop rotation) affects the depletion of light (% PAR to ground level) and subsequent competition pressure.

Scales and patterns of diversity: Successional and agronomic landscapes

How patterns and processes change with the scale of observation is a key question in ecology and central to much of our work on plant communities at the KBS LTER. This question is especially important for our investigations of interactions among major taxa in our systems: plant-microbe and plant-insect interactions are likely to be very different at different scales, with different consequences for ecosystem function. Species area relationships can be used to define the appropriate scale for examining diversity. Both the size of the sampling unit (*grain*) and the area over which a pattern is expressed (*extent*) affects estimates of diversity (White and Walkert 1997, Allen and Hoekstra 1992). The *focus* of the analysis -- the inference space over which the pattern is being examined (e.g. fields or community types; Sheiner et al. 1998). What is the appropriate scale at which to measure diversity? And how does scale affect relationships among variables that affect diversity such as ANPP, and other ecosystem characteristics that may be affected by diversity (e.g. nutrient turnover and retention)?

At a recent NCEAS workshop to examine the relationship between diversity and ANPP across a wide variety of ecosystems including many LTER sites it became clear that the relationship between ANPP and diversity is highly dependent on the scale of analysis. For example, within grasslands at 4 LTER sites (fields within community type) there was generally no relationship between ANPP and diversity (Fig. 2.6), and those significant relationships that were detected were linear and negative. Only when the *extent* of the analysis was increased to all North American grasslands did we observe the quadratic relationship between diversity and ANPP presumed generally to be the norm (Fig. 2.7; Rosenzweig 1996, Huston 1995). What causes this effect -- are different processes determining the relationship between ANPP and diversity at different scales (e.g. Moore and Keddy 1993)? Or does the shape of the species-area curve vary with ANPP and consequently determine these patterns (see Pastor et al. 1995, Oksanen 1996, Rapson et al. 1997)? Understanding how the relationship between species diversity, sampling area and extent, and ANPP varies in the agronomic and successional communities in our site is critical for our ability to scale up such knowledge to the larger landscape.

Patterns among and within old fields: Our estimates of diversity within and among fields at KBS have come largely from the dispersed quadrats we use to measure ANPP, limiting our ability to measure precisely the species-area relationship in these sites (see Rosenzweig 1996). This year we also determined species-area curves using belt transects (1 x 10 m) in both the historically-tilled early successional (T7) and never-tilled (T8) treatments to compare patterns from our dispersed quadrats to the more refined patterns possible with transects. Early results show that our scattered quadrats capture more of the heterogeneity in species composition across these sites (and thus are appropriate for estimating ANPP), and also confirm that even when finely resolved, diversity differences do not appear to be related to ANPP across our site.

In the coming year we will extend the range of sites in this analysis to include both higher and lower ANPP sites within the larger landscape. This will allow us to examine the potential threshold effect of fertility

on the ANPP-diversity relationship, and also how this relationship is affected by the grain, extent, and focus of analysis. Additionally, we will examine more explicitly the relationship between plant diversity and within-field resource heterogeneity by using autocorrelation techniques to relate the range of spatial dependence for N availability and SOM turnover to within- and between- field diversity (Robertson & Gross 1994).

Patterns among and within agronomic systems: As one should expect, the productivity of non-crop plants in our four annual-crop treatments differ, though the magnitude of these differences varies across years (Fig 1.8). Biologically-based systems rely largely on competitive interactions (from cover crops and the cash crop) and on frequent disturbance (i.e. tillage and rotary-hoeing) as the primary means of weed control, and this may either be less effective than herbicides or stimulate germination of more or different species from the seedbank. In fact, it is striking to note the exceedingly high plant diversity that is present in the low- and zero-chemical input treatments (our biologically based treatments) over a full 3-yr rotation (e.g. 1993-95; Fig. 2.8). The numbers of plant species in the no-input treatment over this period (~60) is similar to that encountered over all replicates of the successional fields (~70) at the same spatial and temporal scale. A crucial difference, however, is that the crop is the clear biomass dominant in the agricultural communities (>80% of total ANPP), whereas there are 5-8 species that “dominate” the successional plots and these dominants shift across replicate blocks.

The challenges we now face are to determine the factors that underlie these differences and to scale these results to the larger landscape. In order to translate apparent differences in non-crop diversity and composition to larger landscape units we need to determine species-area relationships in each treatment and among years. We also need to determine the causes and consequences of differences in non-crop species composition and diversity in these treatments. Are they due to greater heterogeneity in the soil seed bank, to greater variation in dominant plant cover (e.g. competitive interactions), or to some other factor (e.g. sub-canopy light levels)?

Using our existing agronomic systems, supplemented with treatments in which we will further manipulate non-crop diversity (see below), we will measure the effects of dominant species on cover and light level, and determine the potential for crop management to affect the diversity of non-crop biomass via competitive interactions from the crop. Based on our work in successional fields in this area, we hypothesize that the intensity of competitive interactions between weeds and different crops will be expressed in such ways as canopy characteristics and the form and amount of litter. Our goal will be both to determine the causes of the greater diversity in the biologically based agronomic treatments and its potential consequences for crop yields – e.g. does non-crop biomass buffer the agronomic treatments from yield variation, insect outbreak, and nutrient loss?

Consequences of diversity

The potential for diversity to enhance ecosystem services has garnered much theoretical and recent empirical attention (e.g. Chapin et al. 1998, Vitousek et al. 1997). Extended to cropping systems, conventional arguments hold that monocultures should be less buffered from insect outbreaks, nutrient loss, and yield variation than more complex agroecosystems (e.g. Altieri 1984, Berendse 1993). Is this true in our treatments? Yes and no. With respect to nutrient loss, our most nitrogen conservative community is also our most botanically simple community – the Poplar treatment has the lowest nitrogen solution losses (Fig. 1.22) and gas losses (Table 1.23) of any of our 11 community types. Even within the annual crop treatments the more diverse, biologically managed treatments appear to have N solution and gas losses that rival those in the standard chemical input treatments. But this is not to say that diversity doesn't provide other important services such as a springtime nutrient pulse from SOM or herbivore protection: we simply don't yet know.

An important objective of the next phase of KBS research will be to identify experimentally the ways in which diversity affects ecosystem function in our agronomic systems. We will do this by establishing a series of different small-plot rotations within one of our standard chemical input treatments and within one of our

biologically-managed treatments. Rotations will be both simpler than our present corn-soybean-wheat rotations (e.g. continuous corn, continuous soybean, and continuous wheat) and more complex than present rotations (corn-soybean-wheat-alfalfa-oats +/- winter cover), and will be conducted at two different fertility levels (high and low N inputs). Our aim will be to test hypotheses about nutrient turnover (timing and rate), microbial and nematode diversity, and ground-dwelling insect predators. This will need to be a long-term experiment with intensive sampling the first, third, and sixth years, initially.

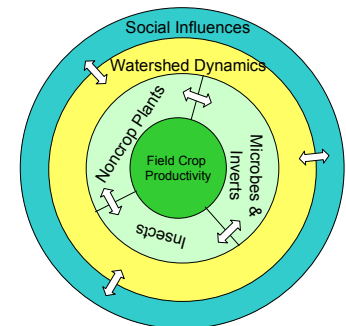
We believe the results from such an experiment will tell us much about the value of plant diversity to ecosystem functioning, especially as the experiment persists through natural drought and insect outbreak years. We also expect to be surprised. For example in our Poplar treatments we have established weed-free and weedy subplots (Table 2.3), and after 9 years have found that C- and N-mineralization rates are higher in the diverse community (Table 2.4) despite the fact that ANPP (Table 2.2) and microbial biomass levels do not differ between subplots. Preliminary genotypic analysis of the soil microbial community suggests 16-S RNA differences between subplots, though there appear to be no differences in phenotypic characteristics such as fatty-acid signatures (FAME) or substrate utilization (*Biolog*) profiles.

2.3 Microbial Community Structure

The diversity and complexity of soil microbial communities present a major challenge to our efforts to understand how biological processes can be managed in agricultural systems. Soil microbial communities are arguably the most diverse communities on earth and the factors that determine this extraordinarily high diversity are not well understood (Caldwell et al. 1997). Torsvick et al. (1994) have shown that in one gram of soil there are billions of individual organisms and thousands of species. What are the ecological consequences of such high diversity at such a small spatial scale? And how does this change across the range of scales that we consider to be important for other organisms (e.g. plants and consumers) and biogeochemical processes? To determine how to manage the biological processes controlled by soil microbes, it is important to understand the patterns, causes, and consequences of microbial diversity and the scale at which microbial communities are structured. Understanding the link between the scale at which the microbial community is structured and the scale at which ecosystem processes occur may itself tell us a great deal about the role of microbial diversity in ecosystem functioning.

The high spatial heterogeneity of soil in an ecological context is well documented (Paul and Clark 1996). Differences among habitats in the degree of soil heterogeneity may influence the diversity of microbes that occur there and their function. For example, our results with nitrifiers and soil C dynamics (Section 1) are best interpreted in relation to differences among treatments in soil heterogeneity (reflecting the availability of microhabitats) and soil organic fractions (reflecting resource heterogeneity; Paul et al. 1998a). Spatial heterogeneity in soil microbial communities occurs at a broad range of scales, from soil particles (e.g. soil macroaggregates), to plant rhizospheres, to field plots, and to the ecosystem and global levels (Tiedje 1994).

At the KBS LTER, we have documented that there is spatially-structured dependence in microbial processes at both a macro- (e.g. 10s of meters, Robertson et al. 1997) and micro- (cm, Cavigelli et al. 1995) scale. We have shown that microbial activity (measured by short-term microbial respiration) varies among and within plant communities; in some sites samples taken only centimeters apart varied by a factor of two. The among-community scale component of this nested variation may be attributable to differences in ANPP and soil physical properties (e.g. depth to the Bt horizon). At the within-community scales, the doubling of microbial activity may be attributable to the distance to the nearest plant. However, we suspect that these



differences may have also been due to heterogeneity in soil structure leading to discontinuous resource availability at the millimeter-scale. This small-scale heterogeneity may be driven by the interaction of plant-derived substrates, such as roots and decaying plant particles, and within-aggregate habitats differences due to clay content, pore sizes, and aeration.

To date, our investigations of soil microbial communities have primarily concentrated on the level and pattern of microbial diversity among the different LTER plant communities. Our results, generated by a variety of phenotypic and genetic approaches, have documented differences in the apparent diversity of whole-soil microbial communities (patterns of bacterial fatty acids, FAMES), as well as for key functional groups, such as denitrifiers (Cavigelli 1998) and nitrifiers (Bruns et al. 1998).

While we will continue our efforts to document the level and patterns of microbial diversity among ecosystems (using strategies such as those outlined in Figure 2.11), we will now begin more intensely to investigate the regulation, maintenance, and consequences of microbial community structure. We hypothesize that the majority of soil microbial diversity is driven by the heterogeneous distribution of resources and habitats in soil. For example, there were a variety of autotrophic nitrifier genera in our never-tilled successional plots (Bruns et al. 1998), all of which grew in the laboratory only at low NH_4^+ concentrations. In contrast, there was a single dominant (*Nitrosomonas*) in our agronomic plots, which was able to use a wider range of NH_4^+ concentrations. These differences in nitrifier diversity could be due to differences in resource availability, and therefore competitive interactions. However, this pattern may also have been generated by the presence of multiple, protective habitats in the never-tilled community. Heterogeneity in soil structure, which may lead to higher levels of microbial diversity, is affected not only by cultivation regime but also by the presence and activity of plants that create biopores and habitat for the mesofauna that are directly responsible for much of the soil structure (Oades 1993).

Clearly, we are at a very early stage in the examination of microbial diversity and community structure. To improve our knowledge of how microbial community structure interacts with the functioning of ecosystems we must obtain a more quantitative knowledge of the interaction between microbes, plant residues and disturbance, at a variety of spatial scales. This will require examining the availability of specific resources (at the substrate level) across multiple spatial scales. We will continue to use our association with the NSF Center for Microbial Ecology (CME) at MSU to explore microbial diversity and variability with a variety of approaches (see Fig. 2.11). Concurrently, we will begin specific experimental efforts to determine causes, and potential consequences, of microbial diversity and community structure among and within a variety of plant communities.

During the next phase of KBS LTER research we will concentrate our research on microbial communities in three areas:

1. We will investigate the availability and spatial structure of microbial resources (substrates) through continued studies on the pools and fluxes of soil organic matter;
2. We will examine the scales at which carbon turns over in soils from the microaggregate (mm) to the landscape (km); and
3. We will continue our examination of the diversity and structure of specific groups of soil microbes across the 11 different communities on the KBS LTER, focusing now on a group that is responsible for significant carbon turnover in soil (Basidiomycete fungi).

Microbial populations, activities, and diversity on soil fractions

Soil aggregates are comprised of different fractions arranged in a defined spatial structure (Paul and Clark 1996, Christensen 1996). These soil fractions may be partitioned into different habitats by microbes. Soil fractions, defined based both on size and position within the soil structure, are an appropriate scale for the examination of microbial diversity and ecosystem-level processes such as soil C turnover. We (Collins et

al. 1998) and others (Golchin et al., 1994, Gregorich 1994) have shown that the mean resident times of individual soil fractions are very different than that for total soil C.

Fractionation of the soil by density separation and wet sieving (Golchin et al. 1994) allows for the collection of the light fraction (Bremer et al. 1994), which is composed of nonaggregated, decaying plant residues, as well as aggregates of different particle size. The microorganisms and their activities will be estimated for the different fractions, as well as the concentric C and microbial gradients within the aggregates (Smucker et al. 1998). The availability of carbon in both individual fractions and the total soil will be measured by incubation, allowing for microbial enzymes to identify the active and slow fractions, followed by curve fitting (Collins et al. 1998). The $\delta^{13}\text{C}$ signature of the individual fractions will also be measured by stable-isotope mass spectrometry.

The bacterial and fungal biomass of different soil fractions will be measured by automated microscopic techniques (Paul et al. 1998b). Microbial biomass will be related to the respiration of CO_2 from individual fractions, incubated with and without substrates, in order to generate metabolic quotients, which are an excellent indicator of activity (Anderson 1994). Bacterial 16S rRNA from the soil fractions (Zhou et al. 1996) will be PCR amplified with both general bacterial primers and those targeting more specific phylogenetic groups. The T-RFLP method (Liu et al. 1997) will be used to assess genetic diversity, and appropriate similarity indexes will be generated. In order to distinguish between the actively reproducing and inactive members of the microbial community, before fractionation and subsequent DNA extraction we will incubate the soil in $^{32}\text{PO}_4$. After the incubations ATP will be isolated by thin layer chromatography, its $^{32}\text{PO}_4$ radioactivity determined, and turnover rates calculated (Karl 1993).

Patterns of microbial diversity in different communities

Microbial community structure and diversity may be driven by differences in either the type or amount of resources available. Across the 11 different community types on the KBS LTER, resource differences for heterotrophic bacteria and fungi may be driven by either the diversity or productivity of the plant community. Field surveys are important in the generation of patterns regarding these relationships: for example, does microbial diversity increase in consort with plant diversity? However, the elucidation of specific mechanisms driving patterns of diversity may not be achievable from field surveys or studies. To begin addressing the role of plant diversity in structuring the soil microbial community we will focus on one aspect of the plant community: the effect of plant residue inputs into the soil on the microbial community. Patterns of bacterial phospholipid fatty acids (PLFA) will be used as a phenotypic fingerprint to compare communities in tandem with estimates of microbial substrate utilization (*Biolog*). This study will provide evidence for the role of plant composition and productivity in structuring the soil microbial community.

Basidiomycetes diversity

The importance of basidiomycetes in soils is well recognized (Domsch et al. 1993), but there is little known about the diversity of these organisms. Past studies of their abundance and distribution have relied on counts of above-ground fruiting bodies (Clark 1980, Gourley 1983). Fungal fruiting structures are restricted to a narrow range of temporal and environmental conditions, and there is no evidence that all soil-inhabiting basidiomycetes produce fruiting bodies. Field investigations of basidiomycetes have been limited to above-ground wood decomposing fungi that are able to modify lignin. Soil basidiomycetes have been largely ignored because when cultured on most selective media, other fungi (e.g. zygomycetes, deuteromycetes, ascomycetes) tend to overgrow them. When basidiomycetes have been successfully cultured in the laboratory, the identification of these isolates has been extremely difficult due to a lack of reliable techniques.

Our past investigations of diversity in soil microbial communities have focused on taxa with specific, narrowly defined functions, e.g. nitrifiers and denitrifiers. We now are ready to expand this work to a more taxonomically complex group of organisms that play a major role in a more broadly shared ecosystem

function, C mineralization. We have developed a selective method for the isolation of soil basidiomycetes. Particle washing, selective inhibitors, and the use of commercial lignin as a primary C source have allowed us to isolate 67 soil basidiomycetes representing 51 morphogroups (Thorn et al. 1996). The majority of these could not be classified utilizing traditional taxonomy, however rDNA sequencing has allowed us to characterize previously undescribed species and genera (Thorn et al. 1996). We will use phylogenetic analysis of fungal isolates to determine the relationships among these groups and apply that information to analyze the diversity of the whole soil fungal DNA. We will use fungal rDNA primers to PCR-amplify base pairs of the 5' end of the 25S rDNA molecule from each isolate (Smalla et al. 1993). The resultant PCR products will be subjected to amplified ribosomal DNA restriction analysis (ARDRA). The resulting restriction fragment-length polymorphism (RFLP) of each isolate will provide resolution to at least the genus level. Further resolution to the species level will require the sequencing of an informative stretch of rDNA (Chapela et al. 1994). For whole soil DNA, we will extract and concentrate fungal hyphae using the sieve and float method (Bingle and Paul 1986). DNA will be extracted (Selenska-Pobell 1995, Van Elsas and Smalla 1995) and we will use basidiomycete-specific primers to amplify a base stretch of informative DNA. The products of this reaction will then be used as substrate for a second PCR reaction. Unique PCR products can be separated from each other via denaturing gradient gel electrophoresis (DGGE) that separates polynucleotides of equal length based on their guanine plus cytosine (G+C) content (Muyzer et al. 1992). The DGGE patterns can then be used to profile the basidiomycete community from different soils.

Integration

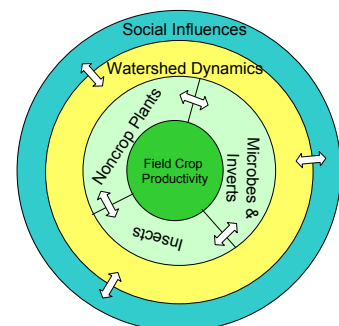
The use of microscopic, physiological, phenotypic, and molecular techniques to assay microbial communities across a variety of scales, from millimeters to field plots, will continue to provide information on changes in our long-term treatments as they mature. Measurements at the within-aggregate and specific-substrate level are essential for providing the resolution needed for microbial community analysis. Soil samples at the plot scale average across the many microhabitats that may be crucial in determining soil microbial diversity. At the same time we will be making measurements at the plot and landscape scale to help identify the spatial scale at which controls on diversity are operating. We are proposing approaches that lend themselves to automation and can handle the large number of samples that must be analyzed to discern both spatial and temporal variability.

The measurement of both C turnover and microbial community structure on the same samples will allow us to relate activity and diversity in all 11 of our community types. The integration of the information from the basidiomycete study with data on decomposition rates, CO₂ flux, and fungal biomass should provide substantive insight into how soil basidiomycete species richness impacts decomposition processes. Specific follow-on experiments will test the relationships inferred from patterns across our landscape.

2.4 Insect Consumers

Ecological management of agricultural systems relies heavily on the potential for beneficial organisms to regulate pest populations (Vandermeer 1995). Agricultural systems generally have lower trophic complexity than natural systems and as a consequence are more prone to pest outbreaks (Risich 1987, Stinner and Stinner 1989). This characterization of agricultural systems is based on management practices that predominated in the '70's and 80's and assumes that farms are monocultures of high-yielding hybrids grown under intense chemical inputs provided by the farmer (Bird 1994).

However, there is a growing awareness that agricultural systems are part of a complex landscape of vegetation types that span the plant to the landscape level (Levins and Wilson 1980, Risser 1986) and that herbi-



vores and beneficial insects respond to variation at different scales (Kogan 1986, Vandermeer 1995).

Our work to date on consumer dynamics at the KBS LTER has focused principally on examining a specific group of predators, Coccinellids, because they are mobile, plant-dwelling predators that use a broad range of habitats during their life cycle (Hodek 1973). Our past work has shown that these species respond to changes in prey and habitat that can be related to agricultural management and successional dynamics in these systems (Section 1). In this renewal we propose to continue to monitor the dynamics of key consumer groups in relation to habitat complexity. We will also expand the spatial scale of our analysis to include a broader geographic range that include regions with less habitat complexity. Finally, in recognition that regional weather patterns can strongly effect the dispersal and regeneration of insects, we will examine how such factors influence the abundance of targeted species that are important agricultural pests.

Predator-landscape dynamics

An increase in the diversity of vegetation has been considered as a necessary step to enhance natural regulation of pests (Pimentel 1960), presumably by providing beneficial organisms with alternate sources of food and shelter necessary to maintain them the landscape (Dover 1989, vanEmden 1990). Most of these studies have focused on within-field or field-edge diversity (Altieri 1994). However, agricultural activities can impact habitat diversity at variety spatial scales and so affect communities of natural enemies (Colunga-Garcia 1996, Marino and Landis 1996). An aspect of landscape diversity that has rarely been addressed is how the spatial patterning of a mosaic of patches of crop fields and uncultivated habitats influences consumer dynamics. Knowledge obtained at this scale is critical for understanding the factors that influence dynamics of natural enemies in a particular landscape and how these results may differ in landscapes with other patterns of landscape diversity.

The spatial diversity of an landscape can be characterized in terms of landscape heterogeneity -- the number, size and spatial arrangement of different landscape types (crop land, old fields, wood lots, residential etc). Temporal diversity in an agricultural landscape can occur at several different time scales. Landscape change resulting from the conversion of woodlands or grasslands to agricultural areas (or the reverse) or the conversion of agricultural land to residences occurs on the time scale of decades. However, within agricultural landscapes there can be annual changes in landscape characteristics depending on the degree of crop rotation. If the same crop is grown every year in the same place, the chain of disturbances associated with such practices become predictable, and certain populations can adapt to these dynamics. By rotating crops we promote change in the landscape that can effect the composition and diversity of the plant community (see Fig. 2.8). Such changes in the plant community may favor different consumers and thus prevent the buildup of herbivores highly specialized on a certain crop. When a previously disturbed patch (crop field) is left undisturbed (old field) then temporal changes faced by the arthropod community are now due to successional changes in species composition and changing plant architecture (Southwood et al. 1979).

Our analysis of more than 550,000 field observations at 210 positions in the KBS landscape has provided us with a substantive understanding of the population dynamics of predatory organisms in agricultural landscapes and how they may substitute for chemical inputs (see Section 1). For example, we have observed a succession of Coccinellid species dominance in *Populus*, fluctuations in species diversity and abundance in early secondary succession, and changes in species composition in corn-soybean rotation and in response to different levels of chemical inputs. In this next phase of the LTER we plan to build on this effort in three ways:

1. We will continue our assessment of abundance and species composition of 15 species of Coccinellids in the landscape to maintain the long-term assessment. In the agricultural treatment and successional treatments we will focus our monitoring on specific time periods that our past work has shown are the critical for measuring population abundance in these systems. In the *Populus* treatments, we will monitor the plots after they are harvested (planned for winter 1999) as we expect

there may be important responses in the consumer to this change in the age structure and architecture of the plots. Of particular interest to us will be determining the response of the current native species assemblage to the invasion of two exotic species of Coccinellids, *Coccinella septempunctata* and *Harmonia axyridis*, which have recently moved into Michigan.

2. We plan to expand the types of insect predators we are monitoring in these communities to include several other plant dwelling species in the families Shyrphidae, Chrysopidae, and Lampyridae. This will allow us to determine whether these other groups – which are also important in the control of herbaceous pests – show similar patterns of response to landscape heterogeneity as the Coccinellids. Adults of these families will be sampled using the same sampling protocol as for Coccinellids. Including Shyrphidae in the analysis will add an important dimension to our study because the larvae are predators, whereas the adults feed on nectar. Thus the presence of wildflowers in the landscape – or nectar producing crops such as alfalfa -- should influence the distribution of adults and the response to herbivore outbreaks.
3. We will expand our landscape observation network to a regional scale to determine how important landscape diversity is for maintaining predator populations. For this work we will contrast the results we have for the KBS area, in which agricultural fields are interspersed with a variety of plant communities (old fields, deciduous forests and conifer plantations; Burbank et al. 1992) with a region close to Michigan's Saginaw Bay (Fig. 2.12). This area is highly agricultural with less forest than the KBS landscape. Based on our work at KBS we hypothesize that agricultural fields in the Saginaw Bay will have both reduced species diversity and abundance of beneficial insects. During the first year of the project we will conduct a comparison of the landscape diversity between the two regions to characterize the level of diversity and the patchiness in each region, followed by a 2-year monitoring effort using the design of the KBS trap network.

Climate change as a factor in predator-herbivore interactions

Insect pest outbreaks are rarely due to a single factor (Ferro 1987). They are caused by the interactions of biotic and abiotic stresses that facilitate the unique combination of historical and current climatic and ecological circumstances predisposing the community to serious defoliation (Strong et al. 1984, Barbosa and Schultz 1988). Differences in pest abundance between structurally and taxonomically diverse vs. simple annual cropping systems have been explained by the dynamics of herbivore movement or by changes in herbivore reproductive behavior (rather than by the activities of predators; Risch 1987). Mature crop rotations in diverse landscapes appear to have a greater potential for predatory insects to maintain herbivore populations below economic thresholds and thus fewer outbreaks (Altieri 1994).

The effectiveness of predators in regulating a pest population can be severely attenuated by several weather-related phenomena (Strong et al. 1984). Weather can influence both the flow of insects into a region (e.g. on weather fronts; Carlson et al. 1992) and their reproductive capacity (for instance, from wet to dry cycles; Wallner 1987). In addition, insect populations are likely to be very responsive to the increases in temperature and changes in rainfall patterns that are predicted in climate change models (e.g. Mellillo et al. 1995). This includes a gradual movement of lower latitude species into higher latitudes after a series of warmer years (Wellington and Trimble 1984, Scriber and Gage 1995). These long-term phenomena may be as important as local interactions in the persistence of predator populations in the landscape.

We plan to examine two questions in relation to climate change effects on insect consumers using a retrospective analysis based on data collected over the past decade on insect dynamics on the KBS LTER and weather patterns locally and in the region:

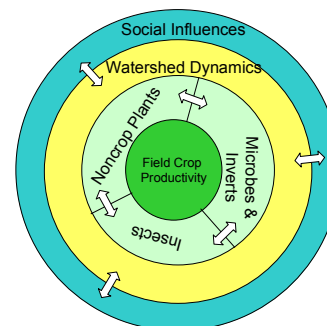
1. Many herbivores do not over-winter in Michigan, but are periodically transported into the Great Lakes region from southern parts of the country via weather fronts. The potato leafhopper (*Empoasca fa-*

bae) is representative of such a species (Carlson et al. 1992). This herbivore has been the only species that has required us to use pesticides to prevent crop (alfalfa) loss, in four of the past nine years at our site. We have collected data for the past 8 years on leaf hopper abundance (May-August) at 210 sites in the main LTER site. We now have a sufficient time series to determine the frequency of long-range transport events of this organism into the region and to relate characteristics of weather fronts during May and June associated with infestation levels of this species. We can obtain daily wind speed and direction information at 850 and 1000 Mb during April-June for the period 1989-1997 from the historical upper airways database archived by the National Climate Data Center. We will use these data to conduct a back trajectory analysis from the KBS LTER southward to 100 upper air monitoring locations to determine the potential source of the immigrant population.

2. Changes in weather patterns can change the competitive balance between plants, herbivores, and predator, favoring the outbreak of the herbivore populations. Factors such as previous periods of drought, decreased storminess, and increased atmospheric circulation or combinations of drought and excessive moisture are often followed by insect outbreaks (Wallen 1987). The occurrence of periods of drought are one of the mechanisms that triggers outbreaks of important herbivore species such as grasshoppers (Gage and Mujerki 1978), armyworms (Haggis 1996), spruce budworm (Thomson et al 1984), and European corn borer (Durant et al 1986). Although outbreaks of European corn borer last only a few years, they can severely affect crop productivity. The questions we ask are: 1) what outbreak-prone organisms are indicators of climate change, 2) what are the climatic conditions that trigger insect outbreaks, and 3) to what extent do changes in climate patterns produce herbivore outbreaks at regional scales?

2.5 Watershed Dynamics /Landscape Biogeochemistry

Our previous LTER research has substantially improved our comprehension of the biogeochemistry of terrestrial environments, where the dominant land use remains agricultural. One of the main ways in which environments interact at the landscape scale is through the fluxes of water by surface and subsurface pathways. We propose to broaden our research at the landscape scale by studying how current and future land use and landscape patterns affect the fluxes of water and nutrients from upland areas to water bodies. This work relates directly to the core hypothesis of the KBS LTER because it deals with the environmental impact of agriculture as well as other forms of land use that will become increasingly prevalent in the future.



Surface waters -- including lakes, wetlands, and streams -- are prominent in the glacial landscape around KBS (Fig. 2.13). The water quality and fisheries in local lakes and streams are strongly valued by local residents, as is typical throughout the upper Midwest. The water quality of local streams is also of regional significance because they flow into Lake Michigan, a regionally important water body for fisheries, aesthetic and recreational values, and water supply. The Kalamazoo River watershed, which includes the landscape around KBS, has been designated by the Environmental Protection Agency as a Lake Michigan Area of Concern due to its water quality problems (EPA/Canada, 1995), which include industrial contaminants (especially polychlorinated biphenyls) in addition to excessive phosphorus loads.

Land use in rural areas distant from surface waters impacts water quality mainly via groundwater flow routes because the permeable glacial drift promotes rapid infiltration of precipitation and lateral movement of groundwater across the gently undulating terrain (Rheume 1990). Most local water bodies interact with the groundwater, serving as points of recharge or discharge, or of groundwater through-flow. A hydrologic budget for Augusta Creek, the drainage just east of the main LTER site, revealed that 75% of the annual

stream discharge was supported by groundwater (Rheaume 1990). Gull Lake, the largest lake in the region, receives at least 40% of its annual water inputs by direct inflow of groundwater, with stream inflows supported largely by groundwater discharge contributing another 35% (Tague 1977). Smaller lakes and many wetlands are likely to receive an even larger proportion of their water from groundwater.

The surface water bodies also affect the quality of groundwater by altering the nutrient composition of water that passes through them before infiltrating to the ground water. The role of wetlands in intercepting nitrate before groundwater enters streams has been demonstrated locally by previous LTER-supported research (Hedin et al. 1998, Hedin and Brown 1994), and has been well-documented elsewhere (e.g. Peterjohn and Correll 1984, Morris 1991). Wetlands also retain or remove nutrients by trapping of sediment and by biological assimilation (Maltby et al. 1996).

Past limnological studies by KBS researchers have produced a detailed understanding of local lakes, with over a hundred publications that have examined Gull, Wintergreen, and Lawrence lakes. Augusta Creek has also been studied extensively (e.g. Minshall et al. 1983). This research has established that primary productivity in local lakes and streams is generally limited by phosphorus availability, and that increased inputs of P will result in enhanced algal growth, leading to eutrophication (Moss et al. 1980, Wetzel 1989, Tessier and Lauff 1992). Phosphorus is also the most limiting nutrient for algae in Lake Michigan (EPA/Canada 1995). Thus the management of lakes and streams to avoid eutrophication should emphasize the control of excessive inputs of P.

Phosphorus is not readily transported in groundwater flow paths because of the relative immobility of P compounds in soils, particularly when calcium carbonate is abundant (as in southern Michigan). The most important pathways by which P is transported to surface waters are not well known in the local area, and P loads of streams and rivers are difficult to estimate because most of the P is particle-bound, often in association with carbonate solids. The prevalence of calcite precipitation in lakes during the summer further reduces P availability by co-precipitation and sedimentation of inorganic P (Wetzel 1989). Phosphorus transport from land to surface waters probably occurs primarily as soluble and particulate forms carried by overland runoff from nearby areas (Soranno et al. 1996). Birds such as the Canada Goose, which tend to feed in agricultural fields and roost in the lakes, are also potentially significant sources of P input to lakes (Manny et al. 1975).

Another major water-quality problem in the Midwestern U.S. besides P enrichment of surface waters is nitrate contamination of groundwaters used for water supply. Rheaume (1990) presented evidence that groundwater NO_3^- concentrations have increased substantially throughout Kalamazoo County during the past few decades, and formulated a nitrogen budget that implicates agricultural fertilizers as the primary cause of the contamination. Our previous LTER-supported research has included detailed studies of N leaching from the rooting zone in experimental and natural vegetation plots, and this work has revealed large N losses from fertilized agricultural fields and yielded insight into the controls on N leaching (Section 1.6). Although we have learned a great deal from these studies of N export from the rooting zone and from the previously cited work on denitrification along a headwater stream, our understanding of the overall transport of N through the landscape remains incomplete. For example, we lack information on the fluxes and transformations of N along groundwater flow paths, and we know little about the fate of excess N reaching lakes and wetlands, or the ecological impacts of the increasing N loading to these ecosystems (Morris 1991).

Future changes in land-use patterns and water availability are likely to alter the nutrient fluxes from the land surface to water bodies in several ways. Land conversion to residential development is forecast to continue its upward trend, increasing the human population density but reducing the area of land used for agriculture and creating a mosaic of residential development amidst remnant agricultural land and woodlots. A report by the Michigan Society of Planning Officials (MSPO 1995) showed that the four-township area around KBS increased in population by 60% between 1960-90, and further increases are projected as people live further from the cities where they work, and the average number of people per household continues to

fall. The increasing N contamination of aquifers will lead to increased N loading to surface waters, as older groundwater is replaced by water from recent decades of increasing fertilizer use (Rheaume 1990, Bolke and Denver 1995).

Climate change is expected to produce increasingly warmer and drier summers, with predicted decreases in soil moisture during the growing season as high as 60-80% in scenarios of doubled atmospheric CO₂ (Melillo et al. 1995, Mortsch and Quinn 1996). Water levels in Lake Michigan are predicted to fall 1-2.5 m with doubled CO₂ (Mortsch and Quinn 1996), and inland waters are likely to be drawn down as well, resulting in the disappearance of many shallow lakes and wetlands. The reduced soil moisture will increase the need to irrigate certain crops (particularly corn and golf-course turfgrass in the KBS area), which is a consumptive use of groundwater.

All of these changes will be gradual and barely perceptible at first, but by the time the cumulative impacts generate obvious water-quality problems in surface waters, it will be very difficult to resolve the problems. Thus the challenge is to develop a scientific understanding of how spatial patterns of land use and landscape diversity affect nutrient fluxes to surface waters, so policymakers can utilize that understanding to plan development in the most ecologically sustainable manner possible. The landscape around KBS is an ideal location to study land-water linkages because we already have a rich body of existing knowledge on the terrestrial and aquatic ecosystems, and it is logistically feasible to collect the remaining information needed to produce an integrated picture of nutrient fluxes. This research would not only contribute to our understanding of the interplay among natural and human-influenced ecosystems on glacial landscapes, which are widespread in North America and Eurasia, but it would also yield general insights into the effects of landscape heterogeneity on land-water linkages.

Hypotheses

We can combine our understanding of land-water nutrient fluxes and nutrient limitation of aquatic primary production with the prospects for continuing changes in land use and landscape patterns to hypothesize that the increasing conversion of rural land to residential use will alter the magnitudes and relative proportions of nitrogen and phosphorus fluxes from the land surface to lakes, streams, and wetlands. Several corollaries follow from this central hypothesis:

Corollary 1: On an areal basis, nitrogen contamination of the groundwater from residential land use will be lower than an equivalent area of row-crop agriculture. This may not necessarily be true if all of the residential land were planted in turfgrass and over-fertilized, but the current trend is for many homeowners to own large lots and leave much of their land as natural vegetation.

Corollary 2: Land conversion to residential areas will enhance the flux of phosphorus from the land to water bodies by facilitating surface transport routes that bypass the retention capacity of the soil and groundwater flow paths, and by creating new sources of P contamination located close to water bodies. The surface transport routes include storm runoff from impervious surfaces and soil erosion in riparian areas (most of which are not presently used for agriculture). Additional sources of P loading include lawn fertilizers and septic systems in the riparian areas that are favored as sites of residential development.

Corollary 3: The changes in water availability that result from the increasingly warmer climate will exacerbate water-quality problems because of reduced contact of runoff with wetlands, changes in the seasonal patterns of runoff, and increased withdrawal of groundwater for irrigation.

We propose to carry out a comprehensive water sampling program that is designed to test these hypotheses and provide a detailed understanding of the current nutrient fluxes from the landscape to surface waters. The study area is defined as a watershed subunit that encompasses the LTER site and is bounded by Gull Lake on the west and Augusta Creek on the east (Fig. 2.14). The northern and southern limits encompass a diversity of land-use types as well as lake shoreline and reaches of two stream systems where

groundwater is discharged. Gull, Wintergreen, and Lawrence lakes are included within the subunit.

We are assembling a detailed Geographic Information System database for the four townships surrounding KBS that includes topography, land use, soils, population, surface waters, wetlands, and subsurface runoff patterns. We produced a digital elevation model (DEM) from 1:24,000 topographic maps, and Figures 2.13 and 2.14 are degraded images from this model. A DEM of the water table is under development using well logs from county records. In addition, we will compile statistics on the addition of nutrients to the various land-use categories, including agricultural fertilizers, lawn fertilizers, septic-system sources, land disposal of sewage sludge, and livestock and horse populations.

The proposed water sampling program is designed to track the hydrochemical changes in water as it falls on the land surface, infiltrates to the water table, passes through the glacial-drift aquifers, enters streams and lakes, and resides in local waterbodies (Table 2.15). The available information on the hydrochemistry of these waters is summarized in Table 2.16. Precipitation chemistry is monitored at KBS by weekly sampling at the center of the study area (Fig. 2.14) as part of the National Atmospheric Deposition Program/National Trends Network (NADP/NTN), and has been sampled since 1979. Water that infiltrates the surface soils can be monitored in the quartz suction lysimeters that are presently being sampled only for nitrogen species (Section 1.6); lysimeters are located in each experimental treatment as well as in the unmanaged vegetation sites of the LTER study (successional fields, coniferous and deciduous forests). We will also install several additional lysimeters beneath turfgrass in residential lawns. Lysimeters will be sampled monthly, although they do not always yield water.

Groundwater in the glacial drift will be sampled initially in bimonthly surveys of domestic wells, which are amply distributed along the roads marked in Fig. 2.14. The wells will be sampled upstream of any water treatment and pipes will be flushed until several minutes after the water reaches a constant temperature before collecting a sample. The water-table DEM and information on potential nutrient sources will help us to define the exact location of well samplings, but an approximate distribution is shown in Fig. 2.14. Groundwater emerging into streams can be readily sampled at springs, which are common along Augusta and Prairieville creeks and flow throughout the year. Along Gull Lake and the smaller lakes, shoreline piezometers will be employed to obtain groundwater entering from adjacent uplands; the direction of water flow can be ascertained by piezometric head measurements and verified by stable isotopic analysis of water from the piezometers and the open water of the lake (lake waters will show evaporative concentration of isotopes relative to groundwaters: Krabbenhoft et al. 1994). Wells, springs and piezometers will initially be sampled bimonthly; sampling frequency may be reduced in later years if there is little temporal variability (Table 2.15).

We will also sample the lakes, streams, and wetlands in the study area at bimonthly intervals (Fig. 2.14). Lakes stratify thermally during the summer and under ice and hence will be sampled at several depths to reveal any chemical heterogeneity. Streams will serve as integrated indicators of the overall runoff from the area, and during low-flow periods the stream discharge is almost entirely supported by groundwater inflows. Wetlands, which include permanently wet depressions and riparian areas as well as ephemeral vernal pools, will be sampled as part of a separate NSF-supported project at KBS (S. Hamilton) that seeks to understand how hydrological factors determine the biogeochemistry and ecology of local wetland ecosystems.

A comprehensive understanding of the hydrochemical evolution of water as it passes through the landscape requires measurement of a large suite of variables in addition to the forms of N and P that are biologically available. We plan to measure several variables in all water samples that we collect: conductance, total alkalinity (by Gran titration), pH, Ca^{2+} , Mg^{2+} , Na^+ , K^+ , Cl^- , SO_4^{2-} , SiO_2 , dissolved inorganic carbon, dissolved organic carbon, NO_3^- , NH_4^+ , PO_4^{3-} , total dissolved phosphorus, Fe(II) and total Fe. Additional measurements to be made in surface waters include dissolved O_2 and temperature (vertical profiles in lentic environments), total particulates, total particulate phosphorus, chlorophyll-a, and transparency (lakes).

After characterizing the seasonal and interannual variability of the fluxes of nutrients from upland areas

to local water bodies, we will incorporate this information into models of groundwater and overland flow to produce a spatially explicit description of the hydrochemical evolution of groundwater and the hydrologic transport of nutrients. The distribution of land-use types in the study area will be combined with the lysimeter data to estimate the contribution of solutes from the land surface to underlying groundwater. A 3-dimensional groundwater flow model such as MODFLOW will be used in conjunction with information on the slope of the water table and the hydraulic conductivity of the glacial-drift aquifers to describe subsurface flow across the landscape to surface waters.

After the models are formulated to represent the present situation, we will generate scenarios of land-use change to investigate how the conversion of increasing amounts of land from rural/agricultural to residential use will alter the fluxes of water and nutrients from upland areas to surface and ground waters. Using existing local zoning as well as potential changes, we can evaluate various "build-out" scenarios for their effects on water quality. Our findings should prove valuable not only to the local government agencies interested in land-use planning, but also to other areas throughout the upper Midwest that are attempting to reconcile their rapid growth and suburban sprawl with the desire to maintain environmental integrity.

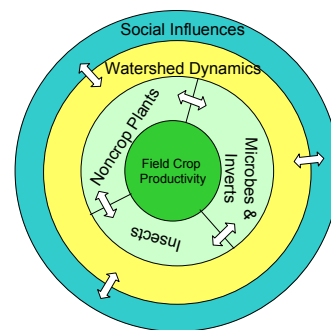
The database on hydrochemistry will stimulate more in-depth research that could be carried out with support from additional funding sources. Possibilities that are of particular interest to the current LTER investigators include a study of groundwater ages at the various sampling points using a combination of tracers such as CFC's and stable isotopes (e.g. Bolke and Denver 1995), investigation of the fate of agricultural N as it passes through groundwater flow paths, and consideration of the effects of increasing nitrogen loading via groundwater on recipient aquatic ecosystems (Morris 1991).

In the longer term, continued monitoring of the hydrochemistry of precipitation, ground waters, streams and lakes in the study area will reveal trends associated with changing land use or with hydrologic alterations caused by climate change. The nutrient flux model will serve to verify whether we understand the controls on nutrient transport to surface waters, and will be refined as necessary. This work on land-water linkages will complement the long-term monitoring of terrestrial ecosystems that has already been established as an integral part of the KBS LTER project, while taking advantage of the rich existing knowledge on local aquatic ecosystems.

2.6 Human Social Influences in Agronomic Landscapes

An integrated model of agricultural and natural resource ecosystems requires a multidisciplinary approach that allows the study of points of interaction between natural and social systems (Kohler 1997, Vanderpool et al. 1994). Key points of integration within natural and social ecosystems include chemical, biological, geomorphological and social dimensions. We feel it is now necessary to incorporate an examination of the social dimensions of our work into the project to better understand the factors that influence the adoption and incorporation of different management practices and how human populations evaluate these changes in relation to the environmental impact of agriculture on rural resources.

Social dimensions are characterized by basic components of a social system: a) demographic --- population size, distribution, growth, migration, etc.; b) economic --- composition of markets, patterns of economic activity, shifts in labor market, changing bases of capital, etc.; c) cultural --- norms, values, attitudes, knowledge and information which define the "lens" through which people view ecosystems; and d) social structure and relations --- patterns of social interaction and relationships, social organizational networks, institutional structure (interrelationship of political, economic, legal, and social institutions), patterns of ownership, power structures, and intersections of inequality (Vanderpool 1987). Both natural and social systems have histories, and the essence of LTER is to mark changes in agricultural and natural ecosystems.



The hypotheses outlined below seek to capture some of the important shifts in these social dimensions that have long term impacts on agricultural and natural resource ecosystems, especially at the KBS LTER site.

Farmer acceptance of ecological technology

Our first hypothesis is that farmers' understandings of ecological processes operating within their fields significantly affect their land management practices. At the micro-level, the interface between the social system and the agroecosystem is the farmer (Harris 1988). The farmer embodies 1) the imperatives of culture of the local community (Salamon 1980), 2) the incentive structure established by agricultural institutions (Ostrom et al. 1992), and 3) the constraints imposed by the social organization of agriculture (Browne et al. 1993). These factors form levels of the social system above the farm and impact the agroecosystem through the farm operator's decision-making about the farm (Gladwin 1989, Barlett 1986). While some decisions concern the farm as a whole (Norman 1994), the object of much of a grower's decision-making is the field (Altieri 1993). Although recent developments in precision agriculture take decision-making to a finer grain below the level of the field (Pierce 1997), these decisions are usually minor variations on the agronomic theme of the field as a whole. It is the field that is planted to a particular crop, irrigated, tilled in a particular way, and treated in certain ways for fertility and pest management.

These considerations imply that to understand the interaction between agroecosystems and social systems one must understand how farm operators make decisions about the management of their land. A grower's decision-making calculus takes into account three types of factors: knowledge and beliefs about soil and agronomy (Bohannon and Harris 1997), values and attitudes about farming and the environment (Harris and Shepard 1992), and aspirations and intentions for the future of the enterprise (Harris 1982). While fairly good understanding is available concerning the influence of the latter two factors (Allbrecht 1998), considerably less is known about the effects of farmers' knowledge and beliefs on soil management practices. While some authors make a distinction between knowledge and beliefs, we treat them as part and parcel of the same type of mental construct: things that one believes to be true. One may recognize different degrees of certainty about those things, and one may recognize various bases for one's certainty about those things, but those things are perceived to be accurate characterizations of the world. (In contrast, attitudes and values are perceived to be right rather than true.)

In general, research in the literature has addressed two questions concerning farmers' knowledge and beliefs about soil management (Napa 1993):

- What are different systems of knowledge and beliefs about the land (Zima 1997)? and
- What are the factors that facilitate or impede the implementation of knowledge and beliefs in farm management practices (Harris 1988)?

Our immediate focus in this project will be on the first of these two questions. In general, most researchers (e.g. Dewlap 1990, Kloppenburg 1992) have distinguished between scientific (also called *etic*) models of soil structure and process as expressed by practitioners of Western biophysical science, as opposed to folk (also called *emic*) understandings of the land, its potential uses and its behavior, as expressed by farmers. Three types of differences between folk and scientific understandings are typically emphasized. First, some studies show that while farmers and scientists use the same or homologous conceptualizations in thinking about soil management, members of the two groups disagree about certain details concerning variables or relationships between variables. Second, some studies (e.g. Warren et al. 1989) have shown that while farmers and scientists appear to use different conceptualizations in thinking about soil, the different conceptual schemes are in fact direct analogues of each other differing only in terminology. Third, some studies find that farmers and scientists use essentially different conceptualizations in their thinking about land.

As the row crop agriculture in the area surrounding the KBS LTER is heavily influenced by land grant university scientists and information disseminated by MSU Extension, we would expect that the growers' and

scientists' conceptualizations of soil would be fairly similar, but we will begin by investigating this question. Interviews will be conducted with a sample of 50 farmers in the region immediately surrounding the KBS LTER to identify their knowledge and beliefs about the soil of their farms. The interviews will also explore how the farmers' knowledge and beliefs enter into their decision-making about soil management, especially with regard to decisions about crop and variety, tillage, fertilization, irrigation, and pest management.

A corollary to this hypothesis is that information from LTER projects can affect farmers' understandings of ecological processes in agricultural systems and thus their farm practices and management of the land. Dissemination of KBS LTER research results to the farming public has been limited to presentations to specific tour groups and field days. There is some informal evidence that these tours and field day expositions have not had substantial impact on farmers and their practices. Results of research from the KBS LTER have been primarily presented in scientific research publications. Until very recently (January 1998, see Section 6; Cavigelli et al. 1998) there have been no presentations of research results in the form of extension bulletins targeted to farmers. Such bulletins provide more accessible knowledge to farmers than formal scientific research papers. This hypothesis seeks to determine the potential impact of LTER on farmers' understandings of ecological processes in agricultural systems and on their land management practices.

To address this corollary we will utilize the MSU Extension Bulletin on Michigan Field Crop Ecology (Cavigelli et al. 1998) and develop complementary extension bulletins of LTER research results, and distribute them to two types of growers: farmers in the KBS area and farmers outside of the area. This division is necessary to determine if proximity to KBS, in itself, influences farmers. Within each type, there will be a treatment group that will receive extension bulletins and a control group that will not.

The extension bulletins will be developed in the first year of the renewal. A small pilot sample of farmers will be asked to critically review the bulletins as to their readability and their ease for accessing research results. Moreover, a baseline study of understandings of ecological processes and farm practices of farmers in and outside of the KBS area will be conducted. This will provide necessary pre-treatment information of farming and land management perspectives. At the beginning of the second and third year, treatment groups will receive LTER research bulletins. In the fourth year, farmers in the treatment and control groups will be surveyed again. Comparisons between these groups as to their understanding of critical ecological processes that influence the sustainability of row-crop agriculture will be determined to provide an estimation of the degree to which LTER results can affect farmers' understandings and practices and whether or not proximity to KBS has an independent effect.

Impacts of social system changes on rural resources

Our second social dimension hypothesis is that changes in the social system in the area of the KBS LTER have had long-term impacts on soil, land, water, and fisheries and wildlife management. The history of Michigan's agricultural and natural resources has involved complex interactions between demographic, economic, socio-cultural, and legal changes, and the environment (Heller and Houdek 1996, Gray 1996). It's early period, at the beginning in the nineteenth century, was marked by a combination of absolute property rights, a view of resources that were unlimited, and a very short-term economic logic which had many adverse impacts on the ecosystem (Heller and Houdek 1996). Towards the end of that century, a conservation ethic began to take hold supported by pro-conservation interests that followed a longer term economic logic, which asserted the right of the whole community to take responsibility for what was happening to Michigan's environment. Today, there are increasing conflicts and debates over public or private control over the environment, its resources, and their development and management. Throughout Michigan's history, these shifting social trends interacted with each other and with changes in landscape and land use, water quality, and fisheries and wildlife issues. These complex interactions continue to define Michigan's environment today and are quite evident at the KBS LTER site.

Since WWII, there have been considerable changes to the social system in the regions surrounding the

KBS LTER site. Some of the most significant include increasing population size, density and heterogeneity; a shift to a mixed economy from agricultural based production with an accompanying diversification of markets; growth of transportation; increased ex-urbanite population; and changing regulatory and legal statutes. In this study, we will seek information on the extent and patterns of these changes and the way they have affected the agricultural and natural resource ecosystem in the KBS area. These include changes in land use and patterns of ownership, shifts in agricultural practices, changing conceptions of the viability of rural life based on agriculture, and increased intensive use of Gull Lake for recreation and as a residential site.

We will address this hypothesis using 1950 as a baseline, with demographic, economic, cultural, and social structural data gathered and compared across decades to the present. The data will be organized from a rural capital perspective (Natural Rural Studies Committee, 1997). Capital is seen as durable assets that have a capacity for increasing the productive capacity and well being of the natural and social system. It exists in four forms: 1) *Natural* capital of the agricultural and natural resource base and alterations to it; 2) *Physical* and monetary capital largely generated from surpluses and savings; 3) *Human* capital derived from increased skill acquisition by people, e.g., education, technical training, knowledge of information technology, etc.; and 4) *Social* capital based on the network of social relationships which facilitate the actions of individuals and groups. Social capital theory is a relatively new perspective on capital formation and has become a central focus of contemporary research in general sociological theory and rural sociology (Coleman 1990, Portes and Zhou 1996).

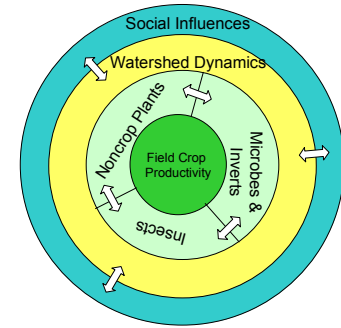
Particular emphasis will be placed on the increasing rural-urban interface. The movement of ex-urbanites, the types of services they demand, and the residences that they live-in are major factors in the transformation of rural America. The meaning of rurality is being challenged and the distinction between the rural and urban systems is increasingly blurred (Brown and Rowley 1997, Castle 1995, Swanson and Brown 1993). Even though these changes are national and regional in scale, local factors have pronounced effects on land tenure changes and natural resource policy (Curry-Roper and Bowles 1991, Curry-Roper and McGuire 1993, Holland et al. 1996). Land use history is particularly important for understanding changes in agriculture and natural resources systems. Moreover, these transformations have important consequences for agricultural experiments, e.g. public concerns about herbicide resistant plants (Comstock and Dekker 1992).

We will also explore patterns of institutional and economic change that have affected the development of the KBS area (Kraybill and Weber 1995), including the types of governance that change and regulate land use. Of particular use are the types of contested property issues that are attendant in the transition to a post-agricultural community (Salamon and Tonatore 1994). The experiences and expectations of farmers for continuing in agriculture and the impacts of social change on rural farm families will be explored as major factors affecting the adoption of sustainable farming system practices (Salamon et al. 1997).

A corollary hypothesis to this work is that changes in the social dimensions and agricultural and natural resource ecosystem of the KBS LTER site are affected by North Central regional transformation processes. Building on the ongoing work of regional productivity (described in the following section) and on determinants of landscape scale biogeochemistry (preceeding section), we will evaluate how social dimensions can influence regional level ecosystem changes. Where possible, comparable regional data to that gathered for the KBS LTER area will be gathered and analyzed. In addition, significant regional level data on changes in agricultural and natural resource markets, recreation and tourism, industrial production, and transportation systems will be examined. The critical issue is the linkage of regional and local changes and their impacts on environmental diversity and patterns.

2.7 Regional application of KBS LTER knowledge

The KBS LTER investigations have so far focused largely on factors that affect row crop production at the field scale (e.g. soil nutrients, trophic interactions), while simultaneously studying nearby unmanaged ecosystems (principally fields and forests). The research proposed in the previous pages includes further expansion of our studies to the landscape scale, as exemplified by the sections on landscape biogeochemistry and social dimensions. In addition to this work, we intend to pursue research that will better define the regional applicability of our knowledge base.



We have learned a great deal about the ecology of the three key row crop systems important in southern Michigan -- corn, soybean, and wheat. These crops are also important throughout the corn-belt states of Ohio, Indiana, Michigan, Minnesota, Missouri, Illinois, Wisconsin, Iowa, Kansas, Nebraska, North Dakota and South Dakota (Fig. 2.16). Thus, from a purely agricultural perspective we can define those states as the region that our LTER site represents. Yet this region is ecologically heterogeneous, in part due to natural gradients in climate and soils, and the productivity of cropping systems varies widely across the region. Areas where crop productivity is lower as a result of natural limitations are subject to more intensive technological interventions such as irrigation and use of soil amendments to maintain yields. Impending changes in climate, as they occur, are likely to shift the geographic distribution of crop productivity, with complex and continuously changing socioeconomic and ecological consequences. Scientific information that enhances our ability to predict these changes can help to anticipate these changes.

Climate dictates many ecosystem characteristics at regional scales (Burke et al. 1991, Bailey 1996). Regional crop productivity patterns are influenced largely by weather, water availability, "negative" biological factors, and nutrients (Olson 1982, Tivy 1990). The two most important limiting factors are temperature and water availability (determined by precipitation, temperature, and soil water holding capacity). Models to predict yield for corn, wheat, and soybean incorporate information on weather data and soil parameters related to water availability (Ritchie et al. 1986, Jones et al. 1989). Optionally they include data on nutrients (nitrogen) but do not include information on pests, weeds, or pathogens. These models often require site-specific information on soils and pests that is not available at regional scales, although such detailed information may not be necessary at larger scales to link broad patterns in productivity to ecosystem characteristics. To gain the sufficient generality necessary to explain crop productivity at regional scales it will be necessary to reduce the information that has no meaning at those scales (reduce data resolution; Table 2.17; Allen and Starr 1982).

We have recently started to synthesize knowledge from the literature about optimal and sub-optimal thermal, water, and soil conditions for crop productivity, and to apply this knowledge at the regional scale using a system approach. The climatic variables that predict crop yield will form the basis of an initial model to construct regional crop productivity units. We then plan to compare model output to statistical analyses of crop productivity, weather and soil characteristics of the region. We will evaluate how spatial patterns of crop production in the region have varied under the historical variability of weather, using drought years as an analog of the drier growing season expected for much of the region as the climate warms. A final phase is to link optimal and sub-optimal crop productivity to ecosystem characteristics of the region. These will include spatial matching of crop productivity with ecosystem units developed by Bailey (1996) and Omernik (1987) (Figure 2.18). We will then determine, using a variety of analytical spatial technologies, how this systems perspective matches with real world production based on crop, climate and soils databases developed by the NC94 Regional Research Committee (Gage et al. 1995). This work will take us in the direction of one of the ultimate goals of the LTER research – to be able to apply the knowledge developed from years of study of representative sites to the broader regions that they represent.

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