

Ecological Variability in Space and Time: Insights Gained from the US LTER Program

TIMOTHY K. KRATZ, LINDA A. DEEGAN, MARK E. HARMON, AND WILLIAM K. LAUENROTH

Long-term observations of comprehensive sets of ecological variables have resulted in a richer understanding of long-term ecological dynamics. In this article, we present a series of examples of research from the Long Term Ecological Research (LTER) Network that show how observation and analysis of temporal and spatial variability of ecological parameters and processes have allowed us to answer questions not previously possible and have increased our understanding of ecological phenomena. The examples offered range in spatial scale from observations at individual locations at a single LTER site, to observations from multiple locations within an LTER site, to comparisons across multiple LTER sites. Collectively these examples and the LTER experience demonstrate that long-term observations are often necessary to discover important ecological relationships.

Keywords: LTER, spatial variability, temporal variability, long-term regional ecology

It has become clear over the past two decades that a rich understanding of ecological systems requires studying them over time periods that range from days to decades and over distances that span millimeters to kilometers (Magnuson 1990, Swanson and Sparks 1990). We now know that the environmental conditions that influence ecosystems, and the ways that components of ecosystems respond to those conditions, are expressed differently depending on the time and distance over which we observe the phenomena. A key feature of the Long Term Ecological Research (LTER) program is that it provides unprecedented opportunities to understand ecological phenomena at multiple time and space scales and emphasizes the importance of understanding ecological interactions as they are expressed over decades and centuries (Hobbie et al. 2003).

Understanding long-term ecological interactions at multiple spatial and temporal scales is difficult or, in some cases, impossible without a foundation of long-term observations. Long-term observations and experiments such as those made at LTER sites are important for at least four reasons. First, observations across many years can define the range of natural variability of ecological systems and provide a baseline from which to determine if a system has changed significantly. Second, long-term observations on a comprehensive set of interacting physical, chemical, biological, and social variables allow us to assess relationships among components of ecological systems. Third, experiments that are maintained for many years allow us to detect cause–effect relationships

among slowly changing variables. Fourth, comparisons of long-term observations or experiments across multiple sites can lead to a more generalized understanding than that gained from individual sites alone.

This article provides five examples drawn from over 20 years of research at LTER sites that illustrate what we have learned from long-term observations of ecological systems and comparisons among different types of ecosystems. The examples are a small subset of results generated by the LTER program and were chosen to span a range of scales and perspectives from individual locations to landscapes to multiple sites across North America and from long-term observations to long-term experiments. Several of the examples clearly illustrate the importance of understanding the interplay among spatial and temporal processes in ecological systems. Each of the examples shows how the LTER program has allowed us to address ecological questions that could not previously be addressed.

Timothy K. Kratz (e-mail: tkkratz@facstaff.wisc.edu) is the director of the Trout Lake Station, Center for Limnology, University of Wisconsin–Madison, 10810 County Highway, N. Boulder Junction, WI 54512. Linda A. Deegan is an associate scientist at the Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543. Mark E. Harmon is Richardson Chair and Professor, Department of Forest Science, Oregon State University, Corvallis, OR 97331-5752. William K. Lauenroth is a professor in the Department of Forest, Rangeland and Watershed Stewardship at Colorado State University, Fort Collins, CO 80523. © 2003 American Institute of Biological Sciences.

Perspectives from long-term observations at individual sites

The Arctic streams in the foothills region of the North Slope of Alaska are strongly shaped by the physical setting and the cold climate. The Arctic climate greatly shortens the flowing water season and maintains a layer of virtually continuous permafrost beneath the land. Arctic tundra streams characteristically have low nutrients, high environmental variability, and low productivity at all levels in the food web. Variability in stream environmental conditions is controlled by river discharge, which is determined by winter snow accumulation as well as summer storms (McNamara et al. 1998). The snow accumulates during the long winter, melts, and runs off abruptly during May and early June, often while the streambed is still encased in ice. In some years, summer storm discharge may exceed snowmelt discharge, while in other years there are few summer rains large enough to affect stream discharge (figure 1). To survive, the stream biota must adapt to the low nutrient levels, the high variability in environmental characteristics, and the winter freeze. For insects, these special adaptations include a tolerance for below-zero temperatures; for fish, they include the ability to migrate to lakes where they can find nonfrozen water during winter. Observations and experiments on the biota in rivers during the summer have provided insight into the long-term controls on population dynamics.

To test the hypothesis that the low productivity of Arctic streams was due to a lack of nutrients rather than to harsh environmental conditions, an experimental nutrient enrichment study of the Kuparuk River was started in 1983, and in 1991 a second experimental stream, Oksrukuyik Creek, was added. These rivers are clear-water, low-nutrient (approximately 0.05 micromolar phosphorus [$\mu\text{M P}$]) tundra streams and are part of the Arctic LTER site located on the north slope of the Brooks Mountain Range, Alaska (68°38' N, 149°38' W). The Kuparuk River (a fourth-order stream) and Oksrukuyik Creek (a third-order stream) flow freely from May to late September and are frozen from October to early May. The nutrient enrichment increased phosphorus concentration from the ambient concentration by approximately a factor of 10. The arctic grayling is the only fish species in these rivers and in most tundra rivers that have fish populations. Because juvenile age classes (1- to 5-year-old fish) use smaller tributaries, age 0 and adult grayling (6- to 18-year-old fish) are the dominant age classes in the main stem of these rivers. Grayling make an annual migration to deep-water habitats, driven by the fall freeze-up of tundra streams. In late May they reenter the river, spawn, and then establish summer territories that they defend against other grayling. In 3 to 4 short months, they must obtain enough energy by feeding on stream insects to grow, migrate, survive the winter, and spawn the following spring.

Even in the first summer of the fertilization, it was apparent that phosphorus addition stimulated biotic activity at all trophic levels in these rivers (Peterson and Hobbie 1985, Peterson et al. 1993, Harvey et al. 1998). Nutrient addition and

the stimulation of the underlying food web enhanced growth of both adult and age 0 grayling, significantly increasing growth more than twofold over reference habitats in some years (figure 2; Deegan and Peterson 1992, Deegan et al. 1997, Golden and Deegan 1998). However, nutrient level alone did not fully explain the interannual differences we observed. The influence of hydrology on biological processes is evident in the 12-year record of arctic grayling summer growth from these rivers.

The year-to-year variation in the growth of grayling often exceeded the differences caused by nutrient enrichment. There is a significant correlation between discharge and growth for both adult and age 0 fish (Deegan et al. 1999) that

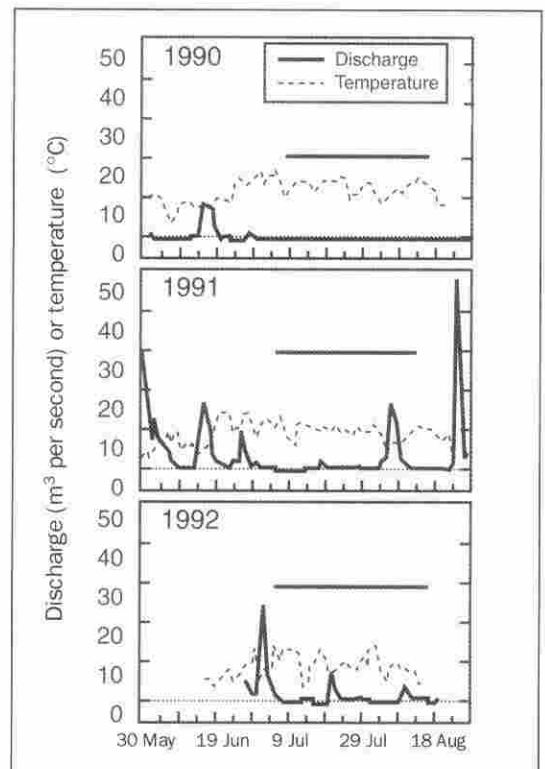


Figure 1. Stream discharge and temperature of the Kuparuk River, Alaska, from 1990 to 1992. Interannual variability of stream discharge and temperature is high in tundra streams. This variability is related to the amount of winter snow accumulation as well as summer storms. These data represent 3 sequential years of discharge for the Kuparuk River, a fourth-order tundra stream in the Arctic. Mean summer discharge (June, July, and August 1985–1996) was $2.41 (\pm 0.35)$ cubic meters (m^3) per second and ranged from 0.3 to 4.4 m^3 per second (Deegan et al. 1999). Variability in discharge is also reflected in the number of days (0 to 20) in the summer when flow exceeded the 10-year 75th percentile discharge, and in the number of days (0 to 29) the discharge was below the 25th percentile. The solid horizontal line in each graph represents the period of added nutrients.

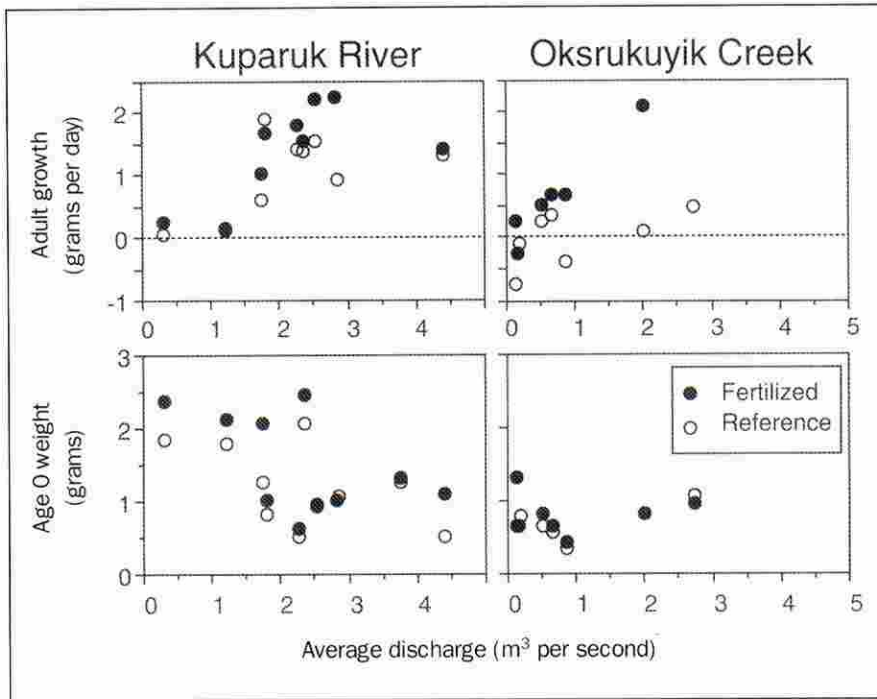


Figure 2. Interannual variability of adult and age 0 arctic grayling is related to river discharge and nutrient availability.

was observable only after many years of study, because of the high among-year variability in each of the river systems (figure 2). Fifty-six percent of the variance in adult grayling growth rate in both rivers was associated with nutrient level and mean summer discharge ($p < .05$), while 60% of the variance in age 0 grayling growth was associated with nutrient level, mean summer discharge, mean summer temperature, and the particular river ($p < .01$). These correlations indicate that adult fish grow better when discharge is high and temperatures are low and that young fish grow better when discharge is low and temperatures are high. The increased growth attributable to altering the nutrient regime of the river was superimposed on the fundamental relationship between grayling growth and discharge.

Fluctuations in river discharge and temperature may influence grayling growth by altering food availability and energetic demands. Higher discharge can make food more available by sweeping benthic invertebrates into the drift, making them more accessible as food for drift-feeding fishes (Poff and Ward 1991). Adult grayling are efficient swimmers and at low current velocities grayling expend more energy swimming than at moderate velocities (Stolbov and Alikin 1978). Thus, up to a point, energy demands for swimming decrease with increasing discharge. At high discharges, however, age 0 fish are unable to maintain the swimming speeds necessary to catch drifting invertebrates, and, like the closely related European grayling and other salmonids, they seek refuge in microhabitats with low-flow velocities (Heggenes and Traaen 1988, Valentin et al. 1994, Northcote 1995). These habitats provide shelter from fast flows for young fish but do not provide sufficient food.

Discharge-related changes in stream habitat might also influence grayling growth by affecting fish density. As water depth and pool area decrease with declining discharge, the density of fish per square meter (m^2) of habitat increases. Experimental manipulations that increased the density of adult grayling tenfold showed that growth was severely affected at high densities, declining from a mean weight gain of 5 grams (g) at ambient level to a loss of 10 g per fish at high density, a result of both lower food availability per capita and aggressive behavior (Deegan et al. 1997). Aggressive behavior increases with increasing fish density, which suggests that changes in social interactions that are associated with density can be an important determinant of growth (Nielsen 1992). If density of fish increases because of shrinking habitat availability that is due to low discharge, the energy costs of aggressive behavior may become significant. Optimal conditions for growth, therefore, might include a

combination of beneficial temperature and discharge regimes, superimposed on basic levels of stream productivity set by nutrient input.

In these Arctic tundra streams, interannual sequences of environmental conditions can influence population structure because of the inverse response of adult and young grayling to the same environmental conditions. Recruitment may be maximized when environmental conditions in sequential years first favor adult (high flow, low temperature) then young (low flow, high temperature) fish. Adults would grow well in the high-flow year, resulting in high egg production the following year; low discharge the following year would lead to high growth and survivorship of age 0 grayling, resulting in a strong year class. Conversely, consecutive years of high discharge, while producing a healthy adult population, could result in little to no recruitment because of poor age 0 growth and survivorship. In response to the variability of the Arctic environment, grayling appear to have evolved a life history that includes a relatively long life span, annual reproduction, and relatively few offspring per spawning event, which increases the likelihood that some offspring will encounter exceptionally good conditions in some years.

Perspectives from landscape-level observations

Predicting ecological change for individual systems is challenging, because seemingly similar ecosystems can respond differently to identical changes in system drivers, depending on their prior history and spatial location within the landscape. For this reason most LTER programs have chosen to study the long-term dynamics of a suite of locations within their study areas. Developing a long-term understanding of a set of lo-

cations is central for forecasting responses to change and extends our understanding of ecological processes across both temporal and spatial scales. In the following examples, we show how long-term observations of spatial and temporal variability in suites of lakes can be used to better understand long-term change at landscape scales.

In north temperate regions that were subject to past glaciation, lakes are often dominant features of the landscape. In many areas, such as the Northern Highland Lake District in northern Wisconsin, lakes occur in high density. Lakes within these lake districts have similar short-term weather and long-term climate, process of origin, geological setting, regional species pools, and human influences. Yet, despite these shared characteristics, individual lakes within lake districts can be remarkably different from each other, varying up to several orders of magnitude in surface area, concentrations of nutrients, major ions, and acidity, and varying several-fold in species richness (Kratz et al. 1997). Moreover, lakes also differ in their responses to external influences such as drought (Webster et al. 1996). Thus, long-term observations from multiple locations within a landscape can provide important clues to understanding this variability.

There is often a spatial pattern in the distribution of lakes with various characteristics, which suggests that a landscape perspective is useful in understanding why lakes differ. Even in lake districts with relatively little relief, small elevation differences among lakes can lead to large differences in lake characteristics. Lakes that are relatively high in elevation tend to receive most of their water directly from precipitation, whereas lakes lower in the regional hydrologic flow system receive additional water from surface water, groundwater, or both. Because precipitation differs in chemistry from surface water and groundwater, the relative importance of various water sources to lakes might help explain differences among lakes. Analyses of lake data collected by the North Temperate Lakes LTER program in northern Wisconsin have shown that lakes higher in the landscape tend to be smaller, more dilute chemically, and clearer; they also have fewer fish species and are less used by humans than lakes lower in the landscape (figure 3; Riera et al. 2000). Similar results have been found from lake districts throughout the Northern Hemisphere (Soranno et al. 1999, Kling et al. 2000), suggesting that spatial positioning of a lake within the larger landscape is an important determinant of a lake's general limnological characteristics.

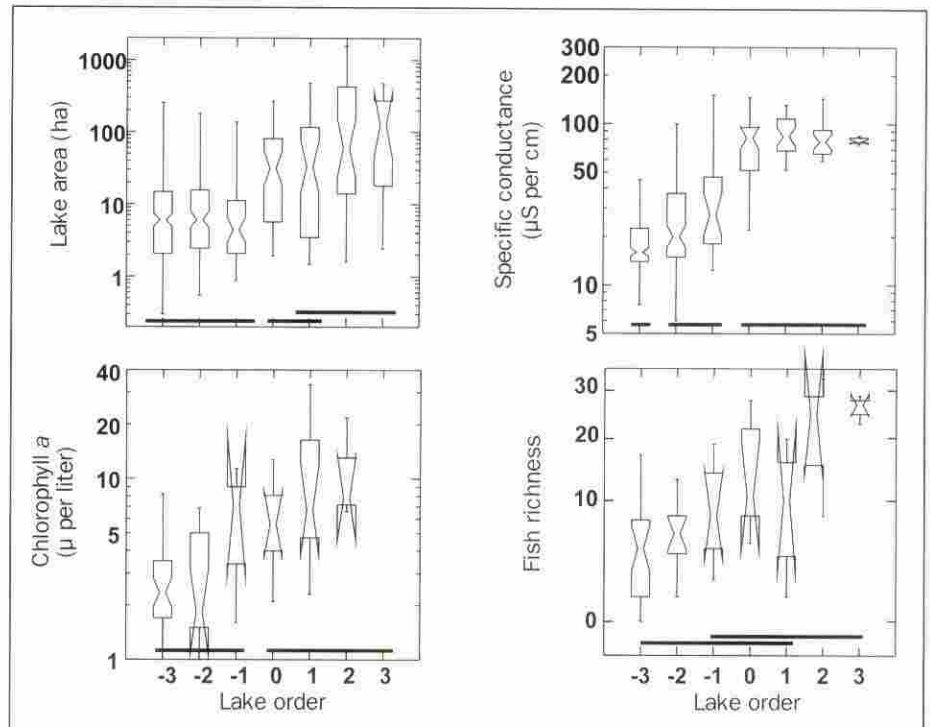


Figure 3. Characteristics of north temperate lakes as a function of landscape position. Negative lake order indicates seepage lakes; positive lake order indicates lakes with inlets and outlets (see text). The bars at the bottom of the graphs represent lake orders that are not significantly different. Adapted from Riera and colleagues (2000) with permission. Symbols: micrograms per liter, $\mu\text{g per L}$; hectare, ha; microsiemens per centimeter, $\mu\text{S per cm}$.

Moreover, several decades of observation have shown that aspects of a lake's long-term dynamics are also related to the lake's position in the landscape. Northern Wisconsin lakes sharing similar positions in the landscape tended to have among-year variation in calcium concentration that was more synchronous than lake pairs that differed widely in landscape position (figure 4; Baines et al. 2000). Similarly, at the Arctic Tundra LTER site in northern Alaska, lakes that were closer together in a series of connected lakes showed more synchronous variation across years than lakes that were far apart in the chain (Kling et al. 2000). Thus, landscape position is an important determinant of the extent to which lakes vary similarly over years.

The position of lakes within the landscape also influences how they respond to large-scale environmental change. Webster and colleagues (1996, 2000) showed that the way water chemistry of lakes in the Midwest was affected by drought depended on the spatial position of the lake within the landscape. Crystal Lake, located high in the landscape in northern Wisconsin, received up to 10% of its water inputs from groundwater during wet periods but became isolated from groundwater inputs during drought. Lakes lower in the landscape, however, continued to receive groundwater, because their groundwater inputs were dominated by regional-scale flows that were less influenced by drought.

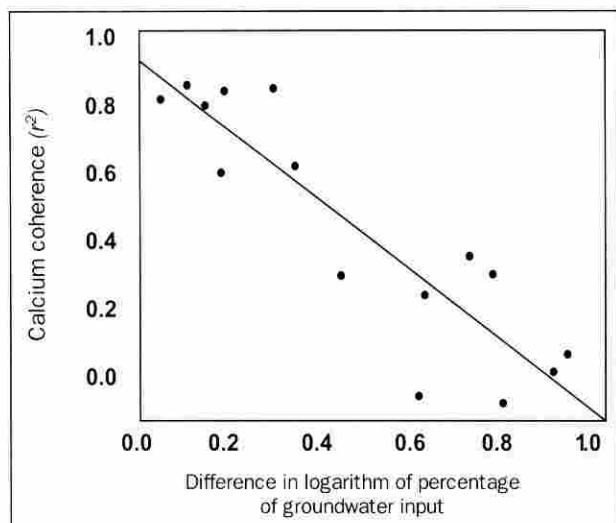


Figure 4. Synchrony of among-year variation of calcium concentration of lakes is a function of the lakes' similarity in groundwater inputs. Each point represents a lake pair. Adapted from Baines and colleagues (2000) with permission.

These variations in groundwater inputs have important implications for lake chemistry and biological communities. In this region, groundwater is the major source of ions that support aquatic life, such as calcium that is needed by snails to build shells. Moreover, groundwater inputs provide ions that buffer lakes from acid rain. Long-term data on lake chemistry demonstrates that lakes moderately high in the landscape, where reversals in groundwater inflow are likely, lose cations during drought (Webster et al. 1996). Lakes lower in the landscape, however, accumulate cations during drought. The switch to warmer and drier conditions predicted by climate change models over the next century or two could differentially affect lakes depending on their position in the landscape, with the concentration of biologically important cations and acid-neutralizing substances declining in lakes that are higher in the landscape (Kratz et al. 1997).

From the temperate Midwest to the cold Arctic, these results suggest that material processing in lakes differs and that apparently similar lakes can respond differently to the same changes in environmental factors, depending on where in the landscape the lakes are located. Developing a landscape awareness of ecosystems is central to forecasting how lakes are likely to respond to change in important external drivers such as climate change.

Perspectives from multisite, long-term experiments

Because the LTER Network consists of 24 individual sites, there is an opportunity for coordinated research on topics that are difficult to address at single sites. One example involves better understanding of the factors controlling the long-term dynamics of carbon and nitrogen in decomposing leaf and fine root litter. The degree to which substrate quality and climate affect long-term decomposition dynamics has rarely been

explored—the majority of studies examine the first year of these dynamics only. The Long-Term Intersite Decomposition Experiment Team (LIDET) designed and conducted a 10-year, multisite experiment to explore how these factors control the formation of stable organic matter and nitrogen after extensive decomposition. When this experiment was conceived, a few long-term, site- and species-specific studies indicated, for example, that a constant fraction of “stable” litter remained after extensive decomposition regardless of species or site. The best way to test the generality of this hypothesis was to coordinate efforts at many sites. Twenty-six sites (17 from the LTER Network) participated, representing a wide array of vegetation type, moisture, and temperature conditions (figure 5).

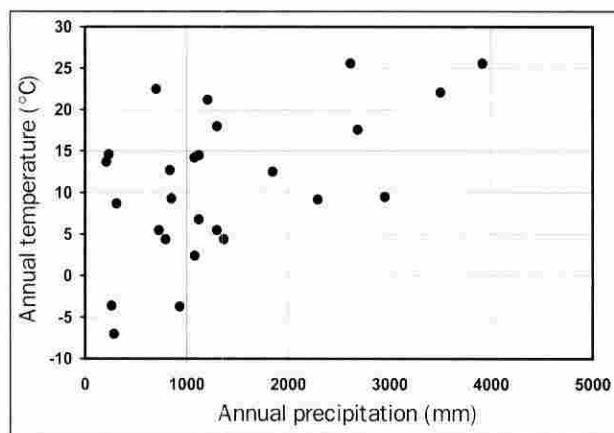


Figure 5. Climatic conditions for the sites used in the LIDET project.

Preliminary analysis of the data gathered by LIDET researchers revealed that our understanding of decomposition was correct in some regards and wrong in others. Decomposition during the first 5 years was a function of both substrate quality and climate (Gholz et al. 2000). This was similar to results found by Meentemeyer (1978), but given that the LIDET research spanned a wider range of climates, the latter results are probably more robust. For example, in terms of actual evapotranspiration data, the LIDET research spanned almost three times the range of the data analyzed by Meentemeyer (343 to 797 millimeters [mm] versus 300 to 2000 mm). Extrapolation of the original Meentemeyer results, something that has been done repeatedly to estimate global level rates, appears to overestimate decomposition rates for lower-quality litters (Gholz et al. 2000). The range of decomposition rates observed in the first 5 years of LIDET research spanned two orders of magnitude, from 0.03 to 3.73 per year, with species containing high nitrogen and low lignin concentrations decomposing the fastest (figure 6). There was also evidence that there were local biological effects, with hardwood leaves decomposing faster at hardwood sites than at conifer sites with similar climates (Gholz et al. 2000). This indicates that simple substrate quality–climate models of decomposition may predict general trends but fail to predict vari-

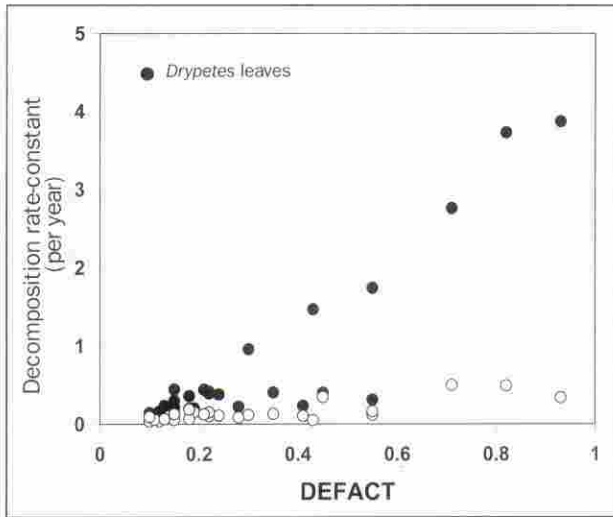


Figure 6. Relationship of decomposition rate during the first 5 years of high- (*Drypetes*) and low-quality (pine) litter to DEFACT, an index of decomposition favorability based on temperature and moisture (Parton et al. 1994).

ation introduced by ecosystem-specific factors such as the decomposer community.

The decomposition process can be separated into two phases: a relatively fast phase in which labile materials decompose, followed by a slow or stable phase in which more recalcitrant material decomposes. A relatively limited number of long-term decomposition studies in the eastern United States suggested that the fraction of the litter decomposing in the slow or stable phase is about 20% (Aber et al. 1990). Long-term data from LIDET sites spanning a much broader range of environments indicate a more complex situation in which the fraction of litter remaining after the fast phase is highly variable (equivalent to 3% to 40% of the initial mass) and is dependent on both the species and environment (Gholz et al. 2000). Data from the Luquillo Experimental Forest, a tropical LTER site in Puerto Rico, indicate that the amount of stable material is a function of the initial lignin content, although the exact chemical constituents of this material have yet to be determined. The fraction of stable material also appears to decrease as the climate becomes more favorable for decomposition. Although the material left after the fast phase is thought to be stable, a preliminary analysis of mass loss of this material at temperate and tropical sites indicates decomposition rates in excess of 5% and 30% per year, respectively. We may need to rethink how stable this material actually is, as these rates of decomposition are several orders of magnitude higher than what is thought to occur in soil organic matter. Comparison of average decomposition rates during a decade of decomposition indicates that these rates are one-third to one-half that observed during the first year. This is a significant finding because current global carbon stores of fine litter have been estimated from litterfall values and short-term decomposition rates. LIDET results indicate

these calculations could have underestimated litter stores by a factor of two to three.

There have been numerous benefits from the LIDET project, some of which go beyond testing the original hypotheses. First, the project demonstrated that large, intersite experiments were possible to conduct and could serve as models for other experiments. Second, the methodology employed in LIDET led to an increased standardization of methods to examine litter decomposition processes (Harmon et al. 1999) and changes in litter chemistry, as this process unfolds (Harmon and Lajtha 1999). Methodological standardization can be a mixed blessing, however, and should always be balanced against the specific objectives of a study. For experiments similar to LIDET's, this has largely had a positive effect (Bryant et al. 1998). Third, LIDET experimental data have been used by other studies for comparison (Bolster et al. 1996, O'Lear et al. 1996). This includes the parameterization (Parton et al. 1994) and corroboration (Moorhead et al. 1999) of models. Moorhead and colleagues (1999) compared four models against mass loss data for the first 2 years of decomposition. Although the general correspondence of the models to the data was good, the models tended to underestimate mass losses in the tropics and overestimate rates in the desert and tundra. A similar result was observed for nitrogen dynamics, with models underestimating losses from poor-quality litter and overestimating them for high-quality litter. Both sets of mismatches between the observed data and model predictions probably stem from the fact that the models have been developed for a narrower set of environmental and substrate conditions than those that are used in the LIDET project. This theme, that hypotheses, empirical relationships, and simulation models developed at a local level for a narrow set of conditions cannot be directly extrapolated to general conditions, seems to be a major lesson from LIDET.

Comparison of spatial and temporal patterns

Space-for-time substitution is a widely accepted technique in ecology that has been used most in studies of systems with long-term and strongly directional dynamics. The most widely recognized application is in the study of succession (Pickett 1989). In studies of secondary succession, a chronosequence of sites is identified and studied, and from the results, a temporal sequence of events during succession is inferred. The underlying assumption of the space-for-time approach is that there is a similarity between spatial and temporal sequences (Drury and Nisbet 1973, Delcourt and Delcourt 1991). This approach is so widely used in studies of secondary succession that it is rarely discussed as a potential source of errors in the resulting temporal sequence.

Recently, with the increased level of interest in understanding and predicting the effects of climate change on ecosystems, space-for-time substitutions have found their way into the simulation models that are used for many of these analyses (Parton et al. 1987, Coffin and Lauenroth 1989, Aber and Federer 1992). The use of spatial data sets in time-dynamic simulation models has the same origin as their use

in secondary succession—the very limited availability of long-term data for critical processes. How good is the assumption that there is a similarity between spatial and temporal sequences for ecosystem processes? What are the consequences of using such relationships to predict future effects of climate change? These are unanswered questions and in many cases remain unanswerable in the absence of long-term data sets.

A relationship that is often used in grassland simulation models is a straight-line regression that links annual net primary production to annual precipitation (Coffin and Lauenroth 1989). This relationship is best defined between the variables mean annual net primary production and mean annual precipitation, measured across sites varying in precipitation (Walter 1971, Lauenroth 1979, Sala et al. 1988, Epstein et al. 1997, Lauenroth et al. 1999). How good is the assumption that there is a similarity between spatial and temporal sequences for net primary production in grasslands? Data are available to provide an answer to this question, and this section will focus on describing the relationship between spatial and temporal patterns of precipitation and net primary production in North American grasslands.

Water availability is a key control on net primary production in grasslands. Researchers at the Shortgrass Steppe (SGS) LTER site compared spatial and temporal patterns by asking whether the slopes of regressions between annual aboveground net primary production (ANPP) and precipitation are similar for spatial and temporal data sets. Lauenroth and Sala (1992) summarized 52 years of ANPP data for the SGS LTER site and developed a regression between ANPP and annual precipitation:

$$\text{ANPP}_i = 56 + 0.131 \times \text{APPT}_i$$

where ANPP_i is annual aboveground net primary production in year i (g per m^2) and APPT_i is annual precipitation in year i (mm). They then compared this temporal model with a spatial model developed for the entire grassland region by Sala and colleagues (1988):

$$\text{ANPP}_m = -34 + 0.60 \text{APPT}_m$$

where ANPP_m is mean annual aboveground net primary production (g per m^2) and APPT_m is mean annual precipitation (mm) at a site.

It is clear from this comparison that the temporal relationship between water inputs (precipitation) and ANPP is different from the spatial relationship (figure 7). The source of the differences is that in the temporal case the relationship is between ANPP in a specific year and the amount of precipitation received in that year, whereas in the spatial case the relationship is between mean annual ANPP and mean annual precipitation across a number of sites. The temporal model reflects the ability of the vegetation to capitalize on the amount of precipitation and nitrogen made available as a result of the amount and timing of water inputs in a specific year. One should expect that either the vegetation, the biogeochemical processes, or both constrain the response to an amount of water input that is greater than or less than the

long-term average. In dry years ($\text{APPT}_i < \text{APPT}_m$), the vegetation (the number of individual plants, their identity, and their size) and the biogeochemistry (the size and turnover rate of organic matter pools) will reflect the average conditions of the site (wetter), and ANPP will likely exceed the value one would expect for a site in which APPT_i equals APPT_m . In a wet year ($\text{APPT}_i > \text{APPT}_m$), the vegetation and biogeochemical processes will reflect drier conditions and will not be able to capitalize on the extra water available, so ANPP_i will be lower than what the spatial model would predict for a site in which APPT_i is equal to APPT_m . Knapp and colleagues (1998) conducted a similar analysis for the Konza Prairie LTER site and also reported that the slope of the temporal relationship was less than the slope of the spatial relationship.

Paruelo and colleagues (1999) evaluated relationships between spatial and temporal models for the entire precipitation gradient (200 to 1200 mm per year) across the central North American grassland region. They found that temporal precipitation use efficiency (PUE_p , the slope of the relationship between ANPP_i and APPT_i) was lower than the spatial precipitation use efficiency (PUE_s , the slope of the relationship between ANPP_m and APPT_m) at both the dry (shortgrass steppe) and wet (tallgrass prairie) ends of the gradient (figure 8; Paruelo et al. 1999). This is consistent with the results of Lauenroth and Sala (1992) and Knapp and colleagues (1998). Paruelo and colleagues (1999) interpreted this to mean that at the dry end of the precipitation gradient (e.g., at the SGS LTER site) vegetational constraints were the dominant influence and at the wet end (e.g., at the Konza LTER site) biogeochemical constraints dominated. This suggests that the reason that PUE_i in Lauenroth and Sala's (1992) data is less than PUE_s is the result of the low productive potential of the dominant shortgrass species (*Bouteloua gracilis* and *Buchloë dactyloides*).

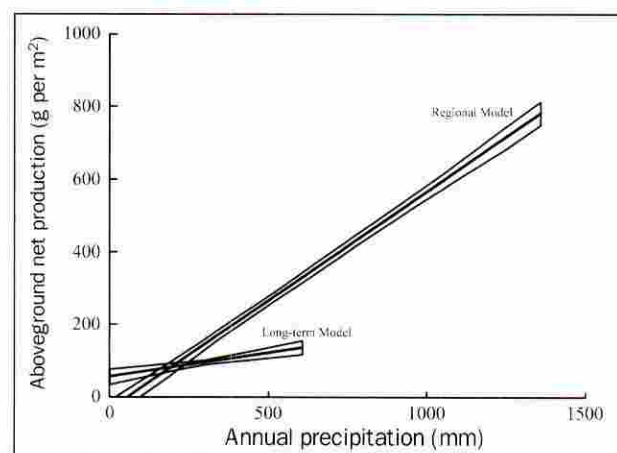


Figure 7. Relationship between spatial and temporal models for aboveground net primary production. The spatial model (regional model) is from Sala and colleagues (1988) and the temporal model (long-term model) is from Lauenroth and Sala (1992). The bounded areas represent 95% confidence intervals. Reprinted from Lauenroth and Sala (1992) with permission.

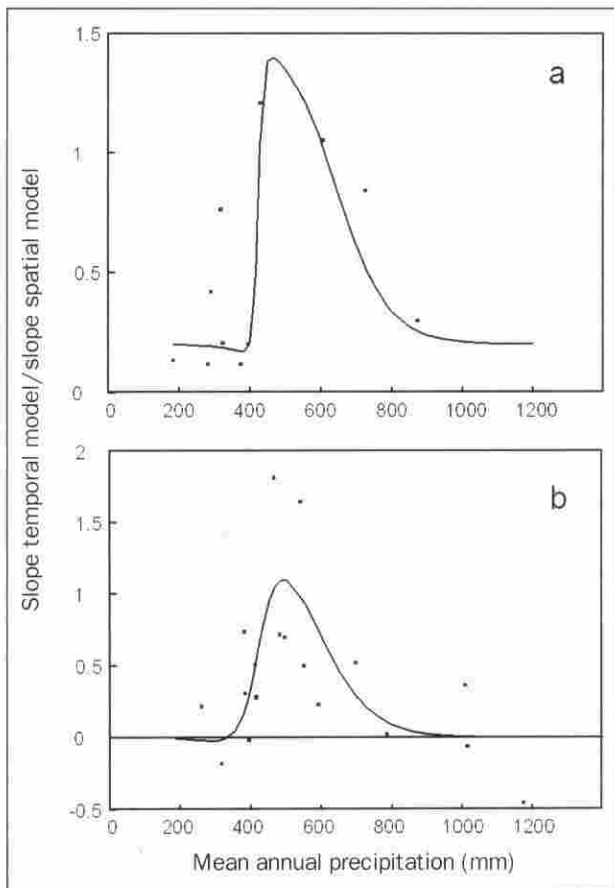


Figure 8. (a) Ratios of the slopes of the temporal models and spatial models for each site, based on field data over the range of mean annual precipitation for the North American grassland region. (b) Ratios of the slopes of the temporal models and spatial models for each site based on remotely sensed data over the range of mean annual precipitation for the North American grassland region. Reprinted from Paruelo and colleagues (1999) with permission.

On the basis of data from two LTER sites and a number of other sites in the central North American grassland region, we can conclude that there are some important differences between temporal and spatial sequences of data for net primary production. Space-for-time substitution, in this case, will lead to serious overestimation of annual aboveground net primary production. How might such substitutions affect other relationships? Few data exist that allow us to answer this question, but Hooper and Johnson (1999) evaluated the effect of nitrogen supply on temporal and spatial relationships between precipitation and annual aboveground net primary production. They reported that nitrogen addition reversed the relationship between PUE_t and PUE_s . Temporal variation in precipitation had a greater effect on $ANPP_t$ than geographic variation in precipitation had on $ANPP_m$. Analyses of differences between spatial and temporal models for ecosystem processes have the potential to lead to important hypotheses about the operation of those processes. To date, very limited

data are available, but as LTER sites accumulate long-term data sets on critical ecological processes, we can expect increased opportunities for such analyses. On the basis of the extant results, space-for-time substitutions for ecosystem processes should be made with extreme care.

Perspectives from comparing diverse systems

In our final set of examples, we examine how long-term research at diverse sites can lead to insights into general ecological features such as the nature of spatial and temporal variability of ecological phenomena and processes. One strength of the LTER Network is that a diverse set of sites, representing many biomes, are studied from a long-term and spatially extensive perspective. Most of the individual LTER programs have established long-term study sites at multiple locations within their study areas. Often these locations are arrayed along one or more environmental gradients to capture the range of natural variability present. Scientists have taken advantage of this opportunity to compare general features of these diverse systems. In particular, LTER scientists have asked two questions: What are the relative magnitudes of among-year and among-location variability of a broad suite of ecological variables within LTER sites, and what factors are related to variability in large-scale landscape heterogeneity across LTER sites?

Broad patterns of spatial and temporal variability of ecological properties were assessed using data from 12 LTER sites (Kratz et al. 1995). Within each of the LTER sites, data from 2 to 18 locations were used to assess spatial variation, and data from 3 to 17 years were used to assess among-year variation. A broad suite of climatic, edaphic, and biological variables was considered, including such measurements as air and water temperature; soil moisture; nutrient concentrations; major ions; and abundance, diversity, and productivity of organisms. For each of these variables at each LTER site, a two-way analysis of variance framework was used to compute the variance associated with year, location within the LTER site, and a combination of year-by-location interaction and error. In all, 448 variable-by-site combinations were analyzed.

Two clear patterns emerged from this analysis. First, variability among locations within a single LTER site for a given year greatly exceeded variability among years (Kratz et al. 1995), and variability associated with year-by-location interaction was substantial. This result is significant because it demonstrates that multiple locations within a single study area must be studied to understand the full range of dynamics across a landscape. The large year-by-location interaction variability demonstrates that different locations in landscapes differ substantially in their long-term dynamics (Kratz et al. 1991). Therefore, long-term research needs to deal explicitly with spatial heterogeneity of ecosystems. Focusing long-term studies on single sites within a landscape is likely to be insufficient to understand the causes and consequences of long-term dynamics of ecological systems.

Second, there were clear patterns in the variability of broad classes of ecological variables. Climatic variables showed the

least temporal and spatial variability, edaphic variables such as those associated with nutrient dynamics showed intermediate variability, and biological variables exhibited the largest spatial and temporal variance (Kratz et al. 1995). This result is consistent with the idea that small spatial or temporal variability in such driving factors as climate or nutrient availability can lead to large variability in biological response.

These assessments of variability led to a careful analysis of factors related to landscape heterogeneity at the scale of full Landsat scenes (circa 34,000 square kilometers [km²]) at 13 North American landscapes, which included 12 LTER sites (Riera et al. 1998). Landscape heterogeneity was measured as the standard deviation of the Normalized Difference Vegetation Index for each of these scenes. Landscape heterogeneity was related both to the degree of topographic relief and to land-use characteristics (figure 9), and it tended to increase with the magnitude of topographic complexity (as measured by the standard deviation of elevation within each scene) for those sites with little agricultural land. In landscapes with low topographic complexity, landscape heterogeneity was positively correlated with the percentage of agricultural land use. These results suggest that, even at the large spatial extent of full Landsat Thematic Mapper™ scenes, heterogeneity in vegetation is related to complex interactions of geophysical templates and anthropogenic effects.

Summary

In the past 20 years, the LTER program has uncovered myriad examples of long-term interactions at a variety of spatial scales and conceptual levels. The examples described above were chosen to depict a set of particular cases that together span a variety of ecological systems, spatial scales, and conceptual approaches. There are at least two important lessons gained from the LTER program's experience with developing long-term understanding of temporal and spatial variability of ecological systems.

First, discoveries of important ecological relationships often require long-term observations. Long-term observations on comprehensive sets of variables across multiple biomes are a foundation upon which long-term ecological understanding and the ability to forecast ecological change can be built. As the examples presented above indicate, whether the focus is on a specific location within an LTER site or across multiple LTER sites, whether the approach is comparative or experimental, a long-term perspective has been critical to developing our understanding of a broad suite of ecological phenomena and processes. LTER sites are replete with examples of how conclusions that might have been made after a few years of observation are different from those made in the light of longer-term observation.

Second, forecasting ecological change requires understanding interactions of spatial and temporal dynamics of ecological systems. To gain this understanding, it is important to study long-term ecological dynamics at multiple spatial scales, which the LTER Network is uniquely positioned to do. One of the strengths of the LTER Network is that long-term dy-

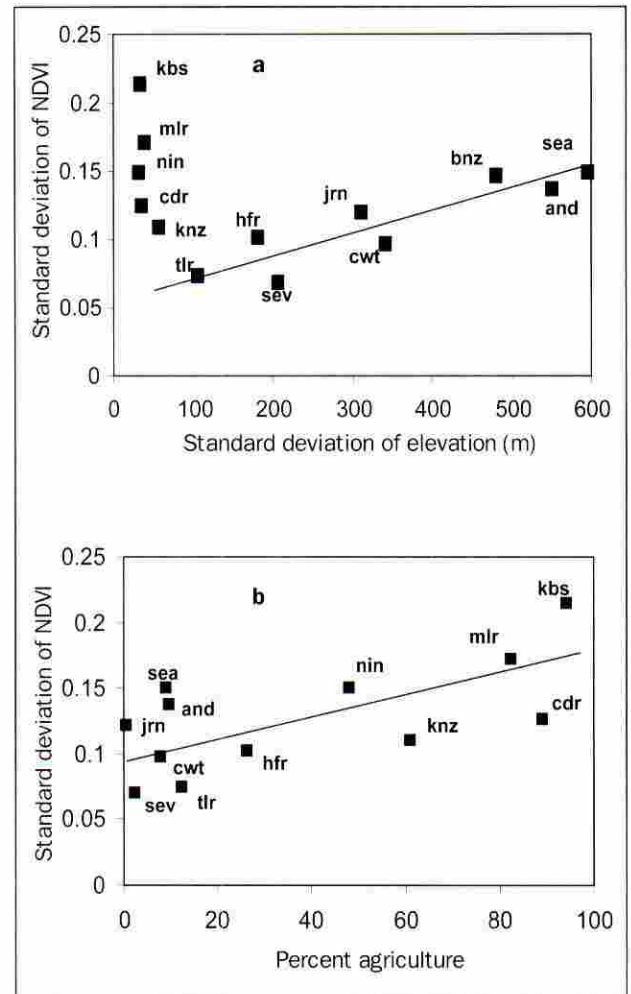


Figure 9. Variation in normalized difference vegetation indices (NDVI) of Landsat scenes from LTER sites as function of (a) variation in elevation (regression line shown for landscapes with less than 40% agricultural land, $r^2 = 0.82$, $p < 0.05$) and (b) percent agriculture (regression line applies to all landscapes, $r^2 = 0.38$, $p < 0.05$). Land-use data were not available for Bonanza Creek. Site codes: and = H. J. Andrews Experimental Forest; bnz = Bonanza Creek Experimental Forest; cdr = Cedar Creek Natural History Area; cwt = Coweeta Hydrologic Laboratory; hfr = Harvard Forest; jrn = Jornada; kbs = W. K. Kellogg Biological Station; knz = Konza Prairie; mlr = Madison Lake Region, North Temperate Lakes; nin = North Inlet Marsh; sea = Seattle area; sev = Sevilleta National Wildlife Refuge; tlr = Trout Lake Region, North Temperate Lakes. Adapted from Riera and colleagues (1998) with permission.

namics are studied at spatial scales ranging from individual locations to cross-biome comparisons. The resulting data, for example, will be especially useful in examining potential problems with space-for-time substitutions. In studies ranging from understanding the ecological organization of lake districts at landscape levels to understanding the continen-

tal scale controls of leaf litter decomposition to understanding factors associated with broad-scale landscape heterogeneity, scientists have taken advantage of the LTER Network to ask and answer questions previously beyond reach.

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