Long-Term Ecological Research and the Invisible Place

The local to global spatial scales of the Long-Term Ecological Research Program

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The distinctive feature of the National Science Foundation's Long-Term Ecological Research (LTER) Program has been the opportunity to examine ecosystem behavior on longer time scales than traditionally emphasized in ecological research (Callahan 1984, Franklin et al. page 509 this issue, Magnuson page 495 this issue, Magnuson et. al. in press, Swanson and Franklin 1988). As Magnuson has argued, lack of historical perspective can place short-term studies in the "invisible present," where a lack of temporal perspective can produce misleading conclusions. Similarly, the broad significance of research results from a particular site is difficult to interpret if the site's context in space (e.g., location within region-scale variation in disturbance regime and temperature-moisture conditions) is not understood. In this sense, an isolated research site may reside in an "invisible place" where the significance of results is unclear.

Significance of research results is difficult to interpret if a site's context in space is not understood

As LTER research addresses longer time scales, it has been natural to also confront greater spatial scales (Delcourt et al. 1983). For example, vegetation change at a site over a few years involves processes such as competition among neighboring individual plants. Vegetation change at the same site, but on time scales of centuries and millennia, also involves species migration on broader spatial scales.

Consideration of broader spatial scales in LTER research is fostered by: emergence of critical, large-scale questions concerning ecological effects of global climate change and land use at landscape and regional scales; opportunity to compare ecosystem properties across the continent-spanning LTER system of sites; and development of regional-scale databases and modeling efforts using LTER sites as focal points (Gosz and Sharpe 1989). These factors have resulted in studies within the LTER network at a series of spatial scales. The intent of such multiscale research is to use knowledge of coarser scales of resolution to provide context for interpretation of fine-scale system behavior and to use knowledge of finer-scale processes to explain mechanistically the patterns observed at coarser scales (O'Neill et al. 1986).

In this article, we describe examples of LTER research activities at a series of spatial scales; present an example of multiscale, intersite comparison of ecosystem behavior; and describe multiscale research at one LTER site. The LTER program has substantially encouraged comparative analysis across diverse ecosystems. Such intersite research is facilitated through mechanisms such as workshops, scientist exchanges during sabbaticals, and LTER funds used for pilot projects leading to larger intersite studies with separate funding. However, we emphasize that LTER sites were not selected and LTER science was not designed around testing major hypotheses at the intersite level. Further, many of the studies described here are not unique to LTER.

Scales of LTER Research

Research in the LTER Program occurs at a series of spatial scales: plot/patch, landscape, region, continent, and globe, but the research focuses primarily on the plot/patch and landscape scales (Figure 1). Past ecological research has tended to focus on the spatial scales at the finer end of the spectrum, whereas global-change programs emphasize very-large-scale phenomena. LTER can help bridge this disparity of scales of study.

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Plot/patch scale. Distinctions among plots, patches, and landscapes as identified here are not necessarily based on absolute size, but, instead, represent the degree of contrast and extent of interaction with neighboring areas. A plot or patch is an ecological or geomorphic unit that can be treated as homogeneous for a particular purpose. Plots generally reside within larger areas of similar make-up—a patch. Patches have edges that border adjacent areas with differing system properties, and patches can be defined within or between systems as diverse as forests, streams, and lakes. Questions concerning edge effects may be included in the study of patches, but plots are usually designed to avoid edge effects.

Much LTER research is designed and implemented at the plot scale, employing experimental manipulations and long-term observations of change in natural systems. The size of these plots ranges from less than one square meter to experimental watersheds of more than 100 ha. Manipulations of plots and patches have targeted nutrient and water availability (e.g., at the Cedar Creek [Minnesota] site) and disturbance, including fire (Konza [Kansas] and Cedar Creek sites), erosion/deposition (Andrews [Oregon] site), clearcut logging (Hubbard Brook [New Hampshire], Coweeta [North Carolina], and Andrews sites), grazing by large mammals (Konza site), cattle fecal pats (Central Plains Experimental Range [Colorado] site), and invasion by exotic organisms (North Temperate Lakes [Wisconsin] and Central Plains Experimental Range sites) (Franklin et al. page 509 this issue).

Landscape scale. Landscapes contain multiple patches, and landscape research concerns interactions among patches (Forman and Godron 1986, Turner 1989, Urban et al. 1987). A small watershed may be treated as a plot in terms of overall water and nutrient balances, but it is a landscape in terms of movement of materials among areas within it.

Many aspects of the landscape scale of LTER work focus on flows of materials (water, nutrients, soil, and sediment organisms) and distributions of plants, animals, soil types, and hydrologic conditions along flow paths crossing landscapes. At the North Temperate Lakes and Niwot (Colorado) sites, the hydrological flow paths of interest pass through chains of lakes and interspersed areas of subsurface flow (Swanson et al. 1988). The flow paths of materials considered in landscape research at North Inlet (South Carolina) pass from forest through freshwater stream to salt marsh, estuary, and eventually to the ocean. A landscape perspective is also applied in analysis of flows of sediment through experimental drainage basins at the Niwot and Andrews sites (Caine and Swanson 1989).

A common approach to analysis of landscapes is to scale up to landscapes from plot-level observations sampled along gravitationally determined flow

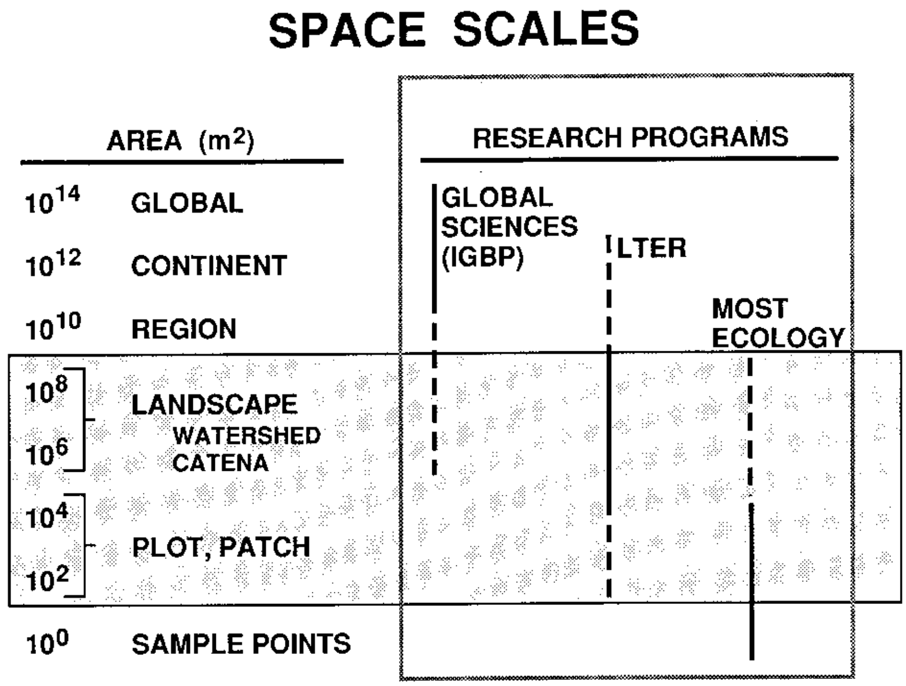

Figure 1. Spatial scales of ecology research. Shading shows scales of LTER concentration.

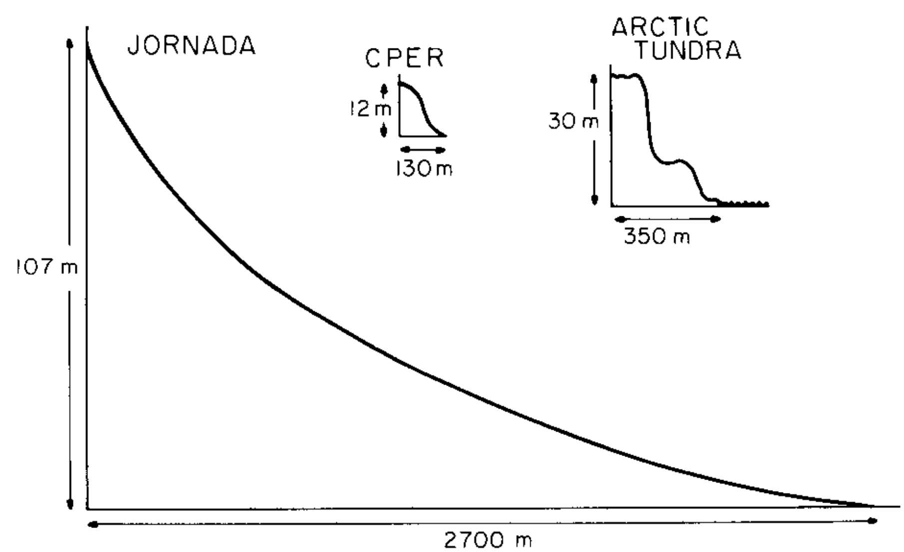

Figure 2. Hillslope cross sections showing topographic profile of sites of soil catena/connected ecosystem studies at three LTER sites. The length of 1 m on the vertical axis is 15 times that on the corresponding horizontal axes. CPER: Central Plains Experimental Range.

paths passing downslope from ridge top to valley floor through a sequence of soil and vegetation patches. This approach is employed in nutrient cycling, vegetation, and soil catena studies, for example, at Central Plains Experimental Range, Jornada (New Mexico), and Arctic Tundra (Alaska) (Figure 2). The types and degrees of control of landscape position on ecosystem properties varies significantly among these sites.

In the arid Jornada environment, for example, productivity of a site is controlled in part by water availability; therefore, patterns of surface water runon/runoff in response to downslope variation in soil hydrologic properties are critical (Whitford et al. 1987, Wondzell et al. 1987). The brief, infrequent runoff events characteristic of the Jornada landscape create patterns of net removal or accumulation of organic matter and nutrients along a topographic sequence—patterns controlled by physical processes.

In contrast, at the Arctic Tundra site, subsurface water flow in a thin (20–100-centimeters-thick) layer above the permafrost transports nutrients downslope during a three-month thaw period each year. Because this flow is subsurface and persists through the growing season, biotic processes—for example, nutrient uptake by plants—control net nutrient retention or loss in sites distributed along the slope (Shaver et al. in press). In both the desert and tundra examples, the interactions of topography, soil properties, and downslope transport processes control patterns of vegetation and rates of biogeochemical processes, although the primary controlling factors differ substantially between systems.

In addition to this approach of viewing landscapes as linear sequences of system elements, it is important to recognize the three-dimensional structure of landscapes. This structure is conspicuous in analysis of landform effects on disturbances. Retrospective studies of the pattern of disturbance across landscapes at LTER sites and elsewhere consider the roles of landforms in constraining disturbance by hurricanes (Harvard Forest [Massachusetts] and Luquillo [Puerto Rico] sites), landslides (Luquillo and Andrews sites), wildfire (Andrews site), and river channel change (Andrews and Bonanza Creek [Alaska] sites). A common theme in many of these studies is that spatial patterns of disturbances are strongly controlled by landforms; for example, particular topographic settings experience highest hurricane damage (Foster 1988), slopes of 32–38° steepness experience greatest landslide occurrence (Guariguata 1989, Swanson and Dyrness 1975), and areas of wide valley floor have most extensive channel change.

Regional scale. LTER programs are synthesizing regional data sets collected by remote sensing or by field observation at plots. These programs are hubs of region and biome scale studies, including work on the effects of broad-scale disturbances, such as drought and air pollution.

The regional modeling effort of the Central Plains Experimental Range LTER, for example, draws on data from more than 6000 field plots scattered across the central US grasslands from Canada to Mexico, including two other LTER sites (Parton et al. 1987). In another regional study, the Andrews LTER and allied programs have established a network of 0.25- to one-hectare reference stands and other permanent sample plots in the coniferous forests of western North America. Some plots date from as early as 1915, although most began in the 1970s. Long-term records from these plots, which are located within forests ranging from 10 to 1000 years since originating disturbance, are used in studies of forest succession and demography and in modeling effects of land use and climate change on forests of the region (e.g., Franklin and DeBell 1988, Harmon et al. 1990).[1]

Dynamics of boundaries (ecotones) between biomes are another aspect of region-scale ecosystem research. The Sevilleta (New Mexico) LTER site, for example, contains transitions among four biomes, providing an opportunity to examine the effects of climate change on the spatial distribution of ecosystems at various temporal scales, for example, El Niño and potential climate change during the next century (Gosz and Sharpe 1989). Scientists at other sites are studying the dynamics of snow-tundra (Arctic Tundra and Niwot sites), forest-tundra (Niwot site), and marine-terrestrial (North Inlet site) interfaces. Sampling approaches include long-term observations of the physical environment (e.g., seasonal snow duration), soil properties, vegetation, and small-mammal populations along belt transects and series of plots crossing ecotones. It is hypothesized that these ecotonal sites will be among the first to display biogeographic aspects of ecosystem response to climate and land-use change.

Continental scale. Continent-spanning comparative research is greatly facilitated by the network of LTER sites extending over 11 biomes—from the north slope of Alaska south to Puerto Rico and from Oregon east to New England. Currently, subsets of LTER sites are undertaking comparative and cooperative field studies on subjects such as effects of resource limitations on productivity and plant succession, processes and rates of wood decomposition, and invading species and their ecological effects. Sites for some studies, such as the resource limitations project, are selected to represent points along a physiognomic gradient from shortgrass to forests.

The most extensive example of intersite research is a 21-site (all the LTER sites plus four additional sites) study of leaf litter decomposition. This study offers a first-of-its-kind opportunity to distinguish effects of litter chemistry and climate on decomposition rates across such a broad range of environments. Also at the continental scale, some LTER sites and research groups are contributing to research programs addressing the effects of climate change and broad-scale air pollution on forest and freshwater ecosystems of North America (e.g., Hubbard Brook, North Temperate Lakes, and Harvard Forest).

Global scale. LTER involvement in global-scale issues is in its initial stages. LTER is providing field observations and experimentation for verification of remote sensing and model-

[1]F. J. Swanson, S. Wondzell, and G. E. Grant, 1990, manuscript submitted.

[2]V. H. Dale and J. F. Franklin, 1990, manuscript submitted.

ing efforts that are part of the National Science Foundation's Global Geoscience Programs. To global change research programs, LTER brings experienced, interdisciplinary teams of ecosystem scientists, long-term data sets on environmental and biological conditions, and facilities and logistical support for field studies. The First ISLSCP (International Landsurface Climatology Project) Field Experiment (FIFE) project at the Konza LTER site is a prime example of an effort to couple ground-based and remotely sensed information sampled at a series of spatial scales of resolution (see Franklin et al. 1990 for a brief description).

Current interactions with scientific groups in other countries, notably in Europe, China, and South America, are an early step in expanding large-scale research to an international network of cooperating research sites and programs. This research has been facilitated in part by links among biosphere reserves in UNESCO's Man and the Biosphere Program, of which several LTER sites are a part.

Intersite comparison

Intersite comparisons reveal the importance of conducting multiscale analysis of ecosystems and of distinguishing system features controlled by absolute and relative (within-site) scales. The variable size and the network structure of riverine systems provide useful examples for multiscale comparison. Unfortunately, no LTER site contains the full continuum from small streams to large rivers, so we cannot deal comprehensively with the issue of scaling up through a drainage network. However, we can compare two study areas in different locations within their respective river networks and identify similarities and differences in system properties. The role of LTER within this analysis is to foster such comparisons; LTER sites were not selected originally to test these ideas.

Considering interactions of rivers and their riparian forests, we see important effects of scale in comparing large, floodplain rivers (LTER-funded research from 1982 to 1989 in the Illinois-Mississippi Rivers [Illinois] site) and small, mountain streams (Andrews site) (Figures 3 and 4).

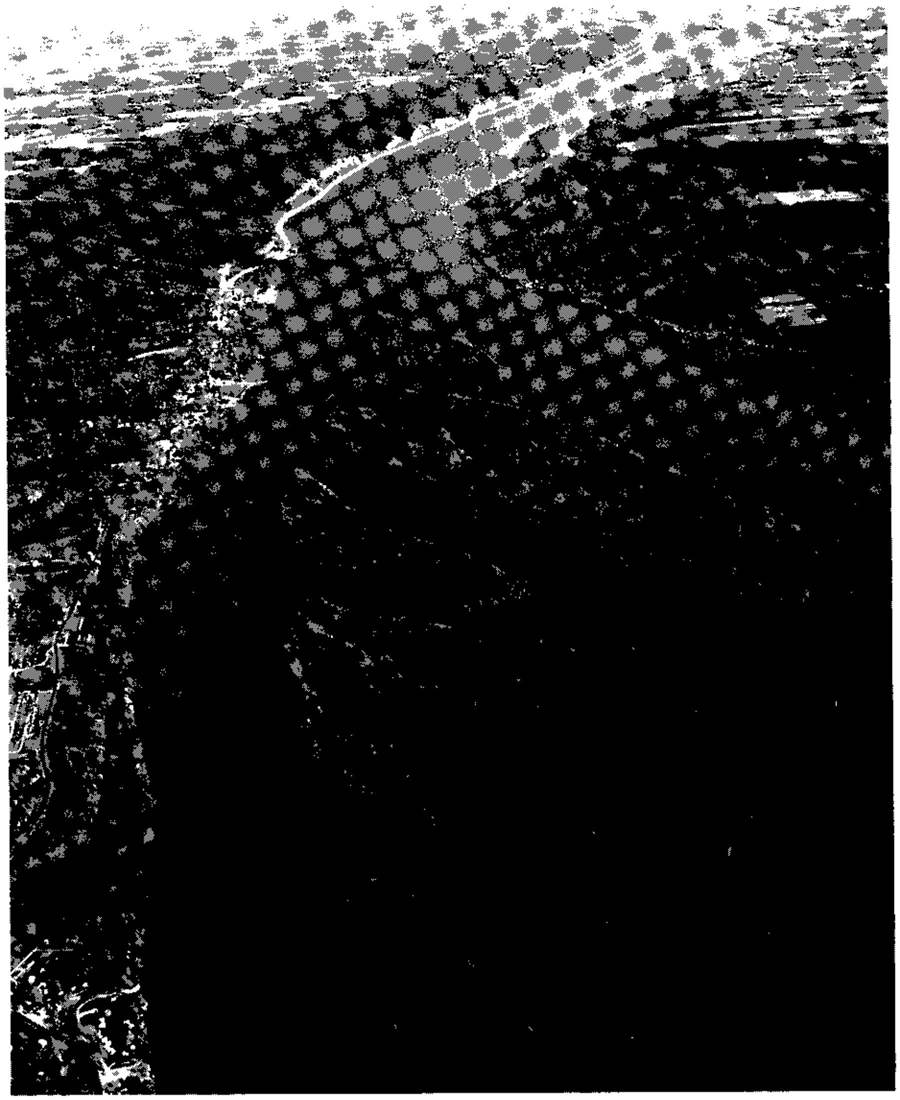

Figure 3. Confluence of the Mississippi and Illinois Rivers 64 km upstream of St. Louis, Missouri, showing the floodplain forest, side channels, and backwaters typical of both channels.

These systems have striking similarities in ecosystem function. In both systems, streamside forests regulate riverine habitat structure (downed logs at any flow stage and standing trees during floods) and nutrient availability (input of litter and nutrients dissolved in groundwater to the aquatic system; Grubaugh and Anderson 1989, Sedell et al. 1989). These two systems differ greatly in absolute scales of channel and floodplain width, channel gradient, average annual and peak flows, and duration, predictability, and areal extent of inundation of floodplain forest (Table 1). The physical differences between sites result in substantial differences in the location and timing of river-forest interactions and in the resulting conceptual models of system behavior.

A key to contrasting these two fluvial systems is the flood regime. Floods in large, temperate, lowland rivers tend to be predictable in seasonality. Large drainage areas, low gradient of the main channel, and low water velocity through forest vegetation and complex channels result in slow passage of large-volume floods, so that extensive areas of floodplain forests may be inundated many months each year where landforms permit. Consequently, many organisms, including fish, have adapted to using the flooded floodplain environment in various life-history stages. Overall, aquatic productivity is high where river systems exchange nutrients with highly productive terrestrial systems on periodically flooded floodplain areas.

In steep, mountain channels, on the other hand, flooding by rainfall and rain-on-snow events is likely to be less

Figure 4. Mountain streams in the Lookout Creek basin (Andrews [Oregon] site) with narrow floodplain and abundant woody debris from streamside forest.

predictable in timing and inundates much less floodplain area for shorter periods of time (Table 1). Basins with a seasonal snowmelt hydrograph, however, may be quite predictable in timing of high flows (Resh et al. 1988). The steep channels and small drainage area facilitate rapid passage of flood flows, which have smaller total volumes than floods produced in much larger basins. Furthermore, in nonglaciated areas, valley floors and their floodplains tend to be narrow, because of constraints such as bedrock outcrops and landslides from adjacent hillslopes. Aquatic organisms in these systems possess few, if any, adaptations to the flooded floodplain environment. Aquatic productivity appears to be regulated by upstream processes that control the quantity and quality of nutrients and water delivered to a downstream site and by effects of adjacent forest on the channel environment (e.g., shading and input of coarse, woody debris).

A major difference between the two systems, therefore, is that river-forest interactions are played out predominantly in the flooded floodplain environment of the large, lowland river and in the channel of the steep, mountain river. Actually, both of these study sites and much of the world's river systems contain a mixture of these two contrasting cases. Geologic and human-constructed constraints on water flow and valley floor geomorphology cause great along-stream variation in the degree and type of river-forest interaction.

We recognize this variation as we shift our view from the valley floor cross-section (plot scale) up to a scale that includes longitudinal variation in valley floor structure and its role in regulating river-forest interaction (landscape scale). In the case of the small mountain river at the Andrews site, landslides, bedrock, and alluvial fans locally constrain floodplain width and, therefore, the opportunity for river-forest interaction. Areas upstream of constrained valley-floor segments tend to have extensive river-forest interaction (Figure 5).

In the Illinois-Mississippi River systems, navigation dams and levees for flood protection (Figure 5) are major constraints on valley floor processes. Areas upstream of the dams are inundated on a continuous basis, and levee districts are isolated from all but the major floods (occurring every 25–50 years), thereby eliminating the flood pulse effect (periodic inundation of floodplain areas). After many decades, the impounded areas will accumulate sufficient sediment that emergent bars and islands form and become forested (Bhowmik et al. 1986), so the flood pulse phenomenon is reestablished.

A common theme at these two sites is that aquatic productivity is highest where river-forest interaction is greatest. Aquatic productivity at a site reflects a tangled web of interactions among physical and biological processes at several absolute and relative spatial scales and at several time scales. Processes related to differences in absolute spatial scales between the two sites contribute to longer-duration flooding in the larger basin. Both systems provide examples of landform (including dams) constraints on the extent of river-forest interaction. Important temporal dimensions of river-forest interactions include seasonal patterns of hydrology and production/decomposition of organic detritus and the decades-to-millennia scale of geomorphic change.

The types of contrasts represented by these mountain stream and big, lowland river examples have resulted

Table 1. Characteristics of a big, floodplain river (Illinois-Mississippi River LTER Site) and a small, mountain stream (Lookout Creek, Andrews [Oregon] LTER Site).

Hydrologic and average characteristics	Mississippi River near Burlington, IA	Lookout Creek, OR
Channel width (m)	600*	10–12
Floodplain width (m)	3400*	6–8
Channel gradient (m/m)	0.0007†	0.022
Discharge (m^3/s)		
Average annual flow	1815*	3.6
Peak flow	5044‡	49
Flood (inundation of floodplain forest) duration (days/yr)	22	2

*Grubaugh and Anderson (1988).
†Fremling et al. (1989).
‡Stahl et al. (1989) at Keokuk, IA, 1878–1988.

in a pair of theories of riverine ecosystems behavior. These theories differ in the scale and processes emphasized. The flood pulse concept of river-forest interaction (Junk et al. 1989, Welcomme 1979) states that seasonal flood-flows onto floodplains strongly and positively influence the productivity of the fluvial system. This conceptual model derives from analysis of large, lowland rivers at the scale of a valley floor cross-section or individual reach of river. The river continuum concept of river ecosystems (Minshall et al. 1985, Vannote et al. 1980) emphasizes controls of upstream factors, rather than lateral floodplain systems, on properties of stream ecosystems. This concept considers the full length of the drainage system, which typically encompasses a landscape or even an entire region.

Attention to landscape and full-drainage basin scales of variation in system structure and function reveals that a marriage of flood pulse and river continuum concepts is probably required to explain river-forest interactions in most river systems (Sedell et al. 1989). The flood pulse concept accounts for lateral influences within a reach, and the river continuum concept offers a framework for interpretation of links among successive reaches along the stream.

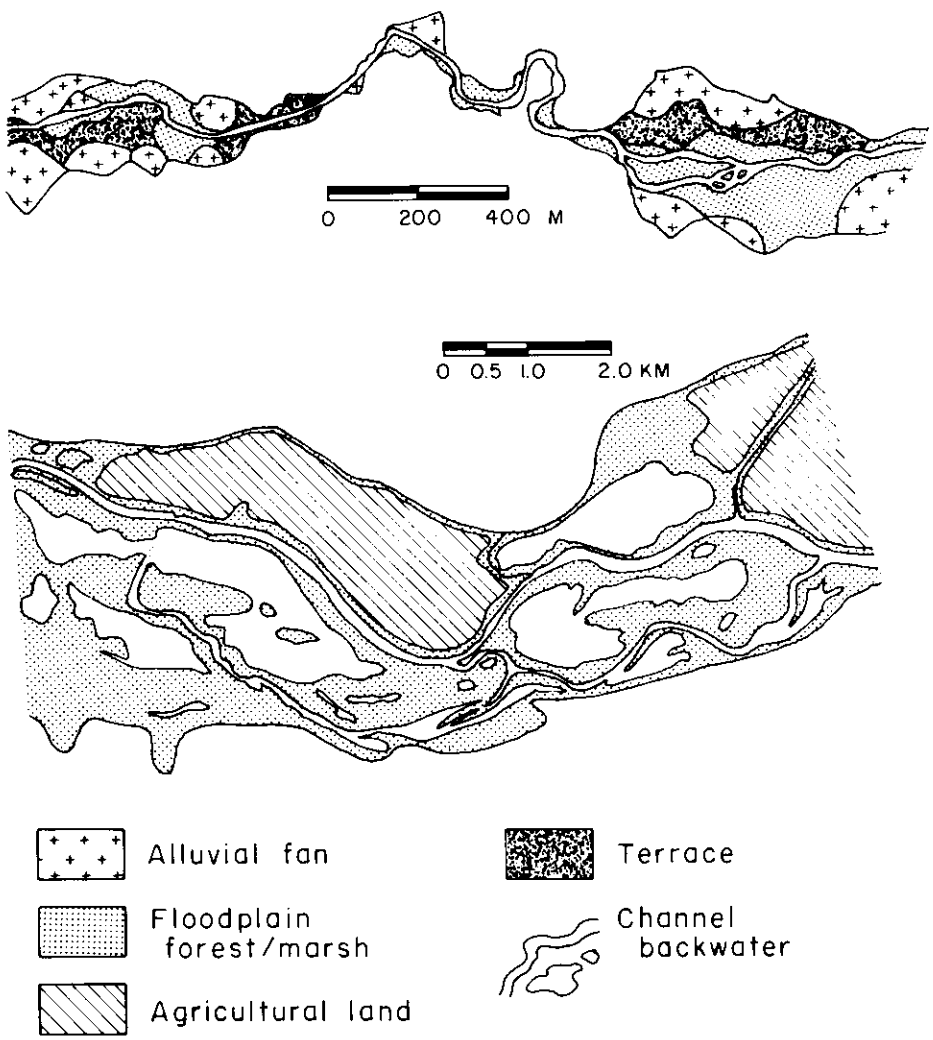

Figure 5. Map of reaches of Lookout Creek (top) and Illinois River (bottom) valley floors. The Lookout Creek site shows substantial variation in the width of its valley floor as a result of geological processes operating on the valley walls. The Illinois River site (160 km upstream of confluence with the Mississippi River) has a more uniform valley floor width. Flow is from right to left.

Multi-scale LTER studies—future work

Research programs at several LTER sites are tackling the important, but difficult, task of working across multiple spatial scales. The Sevilleta LTER group, for example, is using Fourier transform infrared spectroscopy (FTIR) to sample trace gas concentrations over terrestrial and aquatic ecosystems at scales ranging from meters to a kilometer (Gosz et al. 1988). This new technology is being used to measure spatial heterogeneity of biogeochemical processes at a range of scales in both homogeneous vegetation and across ecotones. At fine scales, the spatial patterns of biogeochemical processes are known to be extremely variable (Robertson et al. 1988). The purpose of the multiscale work with FTIR is to better characterize the spatial patterns of variation so that future measurements can be scaled appropriately: observations at finer scales may be directed to interpretation of controls on process rates, whereas coarser-scale observations can average out fine-scale variation to yield useful measures of flux between landscapes and the atmosphere.

Another multiscale project in the desert environment of Sevilleta measures streamflow in a nested set of 20- to 350,000-hectare drainage basins to sense climatic processes at a variety of temporal and spatial scales. Hypotheses concerning scale dependence of the streamflow regime include:

- Small basins with dimensions smaller than single convective storm cells experience several flow events per year.
- Intermediate-sized basins (200 ha) that are larger than the typical precipitation cell diameter experience less frequent, but more destructive, flow events, because unusually large cells or closely spaced cells are needed to produce a discharge event.
- Large basins exhibit spatially intermittent flow; some reaches have perennial flow, and others carry surface flow periodically.
- Long-term gauging records on the Gila (484,000-hectare basin area sampled) and Pecos (49,000-hectare area sampled) rivers indicate that the magnitude of annual flows differs by a factor of 6.0 to 7.4 between El Niño and La Niña

years (Molles and Dahm in press).

As these spatial and temporal patterns of streamflow become better known, they will form an important framework for analysis of geomorphic and ecological change of stream and riparian systems of the Sevilleta.

These analytical approaches are mainly descriptive and exploratory at present. But they set the stage to test scale theory relating to ecosystem processes (O'Neill et al. 1986), to detect effects of climate and other environmental change, and to design better field measurement systems for sampling at appropriate scales.

Conclusions

The importance of tackling ecological questions at their appropriate scales with appropriate tools is widely recognized (Delcourt et al. 1983, Gosz and Sharpe 1989, O'Neill et al. 1986). In many cases, it is important to examine ecosystems at different spatial scales. By extending the breadth of temporal scales considered in a sustained research program, LTER has also made it possible, indeed essential, to examine ecosystem behavior on multiple spatial scales.

Acknowledgments

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References cited

Bhowmik, N. G., J. R. Adams, and R. E. Sparks. 1986. Fate of a navigation pool on the Mississippi River. *Journal of Hydraulic Engineering* 112: 967–970.

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

Callahan, J. T. 1984. Long-term ecological research. *BioScience* 34: 363–367.

Delcourt, H. R., P. A. Delcourt, and T. Webb III. 1983. Dynamic plant ecology: the spectrum of vegetation change in time and space. *Quaternary Science Reviews* 1: 153–175.

Formann, R. T. T., and M. Godron. 1986. *Landscape Ecology*. John Wiley & Sons, New York.

Foster, D. R. 1988. Species and stand response to catastrophic wind in central New England, U.S.A. *J. Ecol.* 76: 135–151.

Franklin, J. F., C. S. Bledsoe, and J. T. Callahan. 1990. Contributions of the Long-Term Ecological Research Program. *BioScience* 40: 509–523.

Franklin, J. F., and D. S. DeBell. 1988. Thirty-six years of tree population change in an old-growth Pseudotsuga-Tsuga forest. *Can. J. For. Res.* 18: 633–639.

Fremling, C. R., J. L. Rasmussen, R. E. Sparks, S. P. Cobb, C. F. Bryan, and T. O. Claflin. 1989. Mississippi River fisheries: a case history. Pages 309–351 in D. P. Dodge, ed. *Proceedings of the International Large River Symposium (LARS)*. Canadian Special Publication in Fisheries and Aquatic Science 106, Ottawa, ON.

Gosz, J. R., C. N. Dahm, and P. G. Risser. 1988. Long-path FTIR measurement of atmospheric trace gas concentrations. *Ecology* 69: 1326–1330.

Gosz, J. R., and P. J. H. Sharpe. 1989. Broad-scale concepts for interaction of climate, topography, and biota at biome transitions. *Landscape Ecology* 3: 229–243.

Grubaugh, J. W., and R. V. Anderson. 1988. Spatial and temporal variability of floodplain habitat: long-term changes at Pool 19, Mississippi River. *Am. Midl. Nat.* 119: 402–411.

______. 1989. Upper Mississippi River: seasonal and floodplain influences on organic matter transport. *Hydrobiologia* 174: 235–244.

Guariguata, M. R. 1989. Landslide natural disturbance and forest regeneration in the Luquillo Mountains of Puerto Rico. Masters dissertation, University of Florida, Gainsville.

Harmon, M. E., W. K. Ferrell, and J. F. Franklin. 1990. Effects of carbon storage of conversion of old-growth forests to young forests. *Science* 247: 699–701.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Pages 110–127 in D. P. Dodge, ed. *Proceedings of the International Large River Symposium (LARS)*. Canadian Special Publication in Fisheries and Aquatic Science 106.

Magnuson, J. J. 1990. Long-term ecological research and the invisible present. *BioScience* 40: 495–501.

Magnuson, J. J., T. K. Kratz, T. M. Frost, C. J. Bowser, B. J. Benson, and R. Nero. In press. Expanding the temporal and spatial scales of ecological research: examples from the LTER program in the United States. In P. G. Risser and J. Melillo, eds. *Long-Term Ecological Research: An International Perspective*. John Wiley & Sons, New York.

Minshall, G. W., K. W. Cummins, R. C. Peterson, C. E. Cushing, D. A. Burns, J. R. Sedell, and R. L. Vannote. 1985. Developments in stream ecosystem theory. *Can. J. Fish. Aquat. Sci.* 42: 1045–1055.

Molles, M. C., and C. N. Dahm. In press. El Niño and La Niña: a global perspective on stream ecology. *J. North Am. Benthol. Soc.*

O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. *A Hierarchial Concept of Ecosystems*. Princeton University Press, Princeton, NJ.

Parton, W. J., J. W. B. Stewart, and C. V. Cole. 1987. Dynamics of C, N, P, and S in grassland soils: a model. *Biogeochemistry* 5: 109–131.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. *J. North Am. Benthol. Soc.* 7: 433–455.

Robertson, G. P., M. A. Huston, F. C. Evans, and J. M. Tiedje. 1988. Spatial variability in a successional plant community: patterns of nitrogen availability. *Ecology* 69: 1517–1524.

Sedell, J. R., J. E. Richey, and F. J. Swanson. 1989. The river continuum concept: a basis for the expected ecosystem behavior of very large rivers? Pages 49–55 in D. P. Dodge, ed. *Proceedings of the International Large River Symposium (LARS)*. Canadian Special Publication in Fisheries Aquatic Science 106.

Shaver, G. R., K. J. Nadelhoffer, and A. E. Giblin. In press. Biogeochemical diversity and element transport in a heterogeneous landscape: the North Slope of *Alaska*. In M. G. Turner and R. H. Gardner, eds. *Quantitative Methods in Landscape Ecology*. Springer-Verlag, New York.

Stahl, R. L., R. H. Coupe, T. E. Richards, and P. D. Hayes. 1989. Water resources data Illinois water year 1988. vol. 1. Illinois except Illinois River Basin. US Geological Survey Water-Data Report IL-88-1, Urbana, IL.

Swanson, F. J., and C. T. Dyrness. 1975. Impact of clear-cutting and road construction on soil erosion by landslides in the western Cascade Range, Oregon. *Geology* 3: 393–396.

Swanson, F. J., and J. F. Franklin. 1988. The Long-Term Ecological Research Program. *EOS: Transactions of the American Geophysical Union* 69(3): 34, 36, 46.

Swanson, F. J., T. K. Kratz, N. Caine, and R. G. Woodmansee. 1988. Landform effects on ecosystem patterns and processes. *BioScience* 38: 92–98.

Turner, M. G. 1989. Landscape ecology: the effect of pattern and process. *Annu. Rev. Ecol. Syst.* 10: 171–197.

Urban, D. L., R. V. O'Neill, and H. H. Shugart Jr. 1987. Landscape ecology. *BioScience* 37: 119–127.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.* 37: 130–137.

Welcomme, R. 1979. *Fisheries Ecology of Floodplain Rivers*. Longman, London.

Whitford, W. G., J. F. Reynolds, and G. L. Cunningham. 1987. How desertification affects nitrogen limitation of primary production on Chihuahuan Desert watersheds. USDA Forest Service General Technical Report RM-150, Fort Collins, CO.

Wondzell, S. M., G. L. Cunningham, and D. Bachelet. 1987. A hierarchical classification of landscapes: some implications for understanding local and regional vegetation dynamics. USDA Forest Service General Technical Report RM-150, Fort Collins, CO.

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