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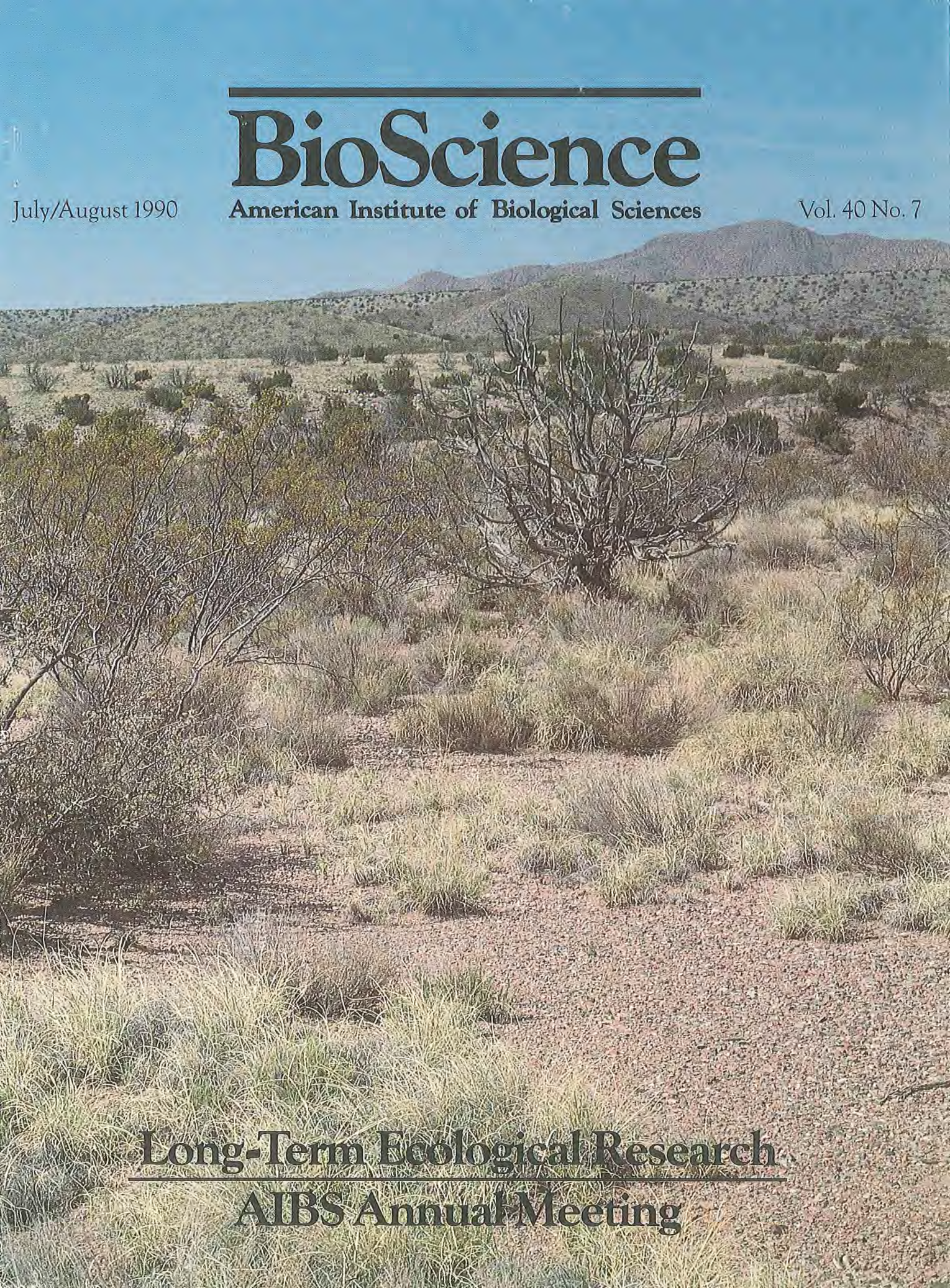

Long-Term Ecological Research

AIBS Annual Meeting

Contributions of the Long-Term Ecological Research Program

An expanded network of scientists, sites, and programs can provide crucial comparative analyses

Jerry F. Franklin, Caroline S. Bledsoe, and James T. Callahan

The importance of long-term phenomena in ecology is well-documented (Likens 1989). Transient responses that extend over decades, or even centuries, are common, such as the gradual changes associated with community succession, soil development, and populations of large vertebrates. Other ecological phenomena are infrequent (rare or episodic) events, including such disturbances as floods, hurricanes, wildfires, or volcanic eruptions, and the reproduction of long-lived plant species. Long-term studies are essential to understand such phenomena, as well as for the formulation and testing of ecological theory (Franklin 1988, 1989, Likens 1989).

Substantial networking efforts are being made among LTER scientists and others involved in long-term ecological studies

Research with an extended time perspective is crucial if one accepts the premise that long-term phenomena have a central role in ecological science. Such studies are uncommon despite this obvious need and repeated evidence of the misleading nature of short-term research (Tilman 1989). Factors contributing to the rarity of long-term studies include difficulties in obtaining sustained financial support and in providing continuing leadership (Strayer et al. 1986).

The National Science Foundation (NSF), responding to this need for support of long-term studies in ecology, initiated a program in Long-Term Ecological Research (LTER) in 1980. This initiative followed an extended planning period involving ecological scientists of varied interests (Callahan 1984). The LTER program now has 17 sites with more than 400 associated scientific personnel.

The preceding two articles addressed the temporal and spatial scales of the LTER program (Figure 1). As described by Magnuson (page 495 this issue), LTER temporal scales, generally much greater than those of other ecological research, are necessary for the correct interpretation of short-term studies. Similarly, Swanson and Sparks (page 502 this issue) described how LTER programs typically address large spatial scales as well as smaller, more traditional scales, such as plot, stand, and small watershed. This final article describes the LTER program, reviews the development of the LTER network, identifies its contributions to ecological science, and considers ways in which LTER efforts can interface with other ecological research programs. The potential for an expanded network of scientists, sites, and programs is emphasized because of the importance of comparative analyses in advancing ecological science.

History of the program

At a series of three workshops beginning in 1977, ecologists considered the potential content and structure of a program of long-term research (NSF 1977, 1978). These efforts became the basis for the first LTER "request for proposals" in 1979. Five core areas were identified and have become the major program theme common to the 17 sites in the current network. These core areas are:

- pattern and control of primary production;

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- spatial and temporal distribution of populations selected to represent trophic structure;
- pattern and control of organic matter accumulation in surface layers and sediments;
- patterns of inorganic inputs and movements of nutrients through soils, groundwater, and surface waters;
- patterns and frequency of site disturbance.

Nineteen research projects have been been funded as a result of four separate NSF competitions, the most recent in 1987. Special panels were created for peer review of each set of proposals. Site selection was based on the quality of the proposals, not on their potential place within a larger network. Awards have usually been for five-year periods, after which sites have been required to submit renewal proposals. Two projects originally funded were not renewed by NSF. Development of the LTER program by NSF has been described in more detail by Callahan (1984) and Swanson and Franklin (1988).

Characteristics of the network

Sites in the LTER system currently extend from Puerto Rico to northern Alaska (Table 1, Figure 2) and represent a broad diversity of environments and ecosystems (Brenneman 1989). Included are grassland, desert, forest, tundra, lake, stream, river, agricultural, and coastal ecosystems. All sites are large enough to incorporate moderate to large landscape mosaics, and the majority include human-manipulated as well as natural ecosystems (Figure 3). Therefore, substantial within-site variability in ecosystems is also present within the network.

The sites are as varied in research design as they are in ecosystem type. Approaches include observation, experimentation, comparative analysis, retrospective study, and modeling. Although most sites incorporate elements of all these approaches, emphases differ among sites. Detailed reports on site programs can be found in numerous site-based articles and in major syntheses (e.g., Bormann and Likens 1979, Dancik 1983, Likens et al. 1977, Likens 1985a, Swank and Crossley 1988, Tilman 1982, 1988, VanCleve et al. 1986). Comprehensive bibliographies are available for many sites (Conley and Conley 1984, Gaskin et al. 1983, Kirchner and Lauenroth 1989, Likens 1989, McKee et al. 1987, Whitney 1989).

Development of comparable data sets and standardization in methods and equipment have been concerns from the beginning of the LTER program. Comparability in databases includes at least two major components—statistical (similar confidence in estimates of parameters) and documentary (written descriptions of the conditions permanently associated with the data sets).

Significant effort has gone into development of a common philosophical and technical basis for the management of data sets; an early LTER-sponsored workshop on this topic resulted in a book (Michener 1986).

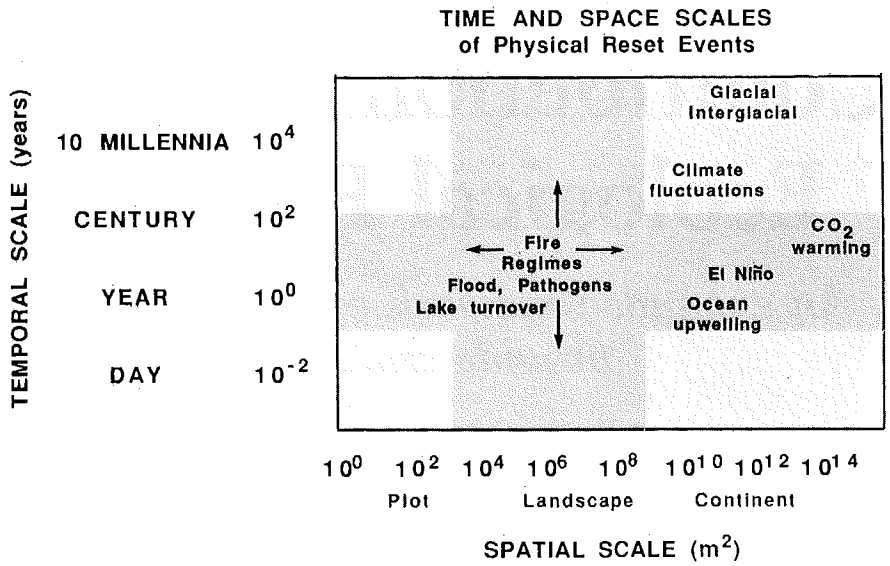


Figure 1. The spatial and temporal scales addressed by the Long-Term Ecological Research Program fall outside of the range that is typically addressed in ecological research programs. Figure: John J. Magnuson.

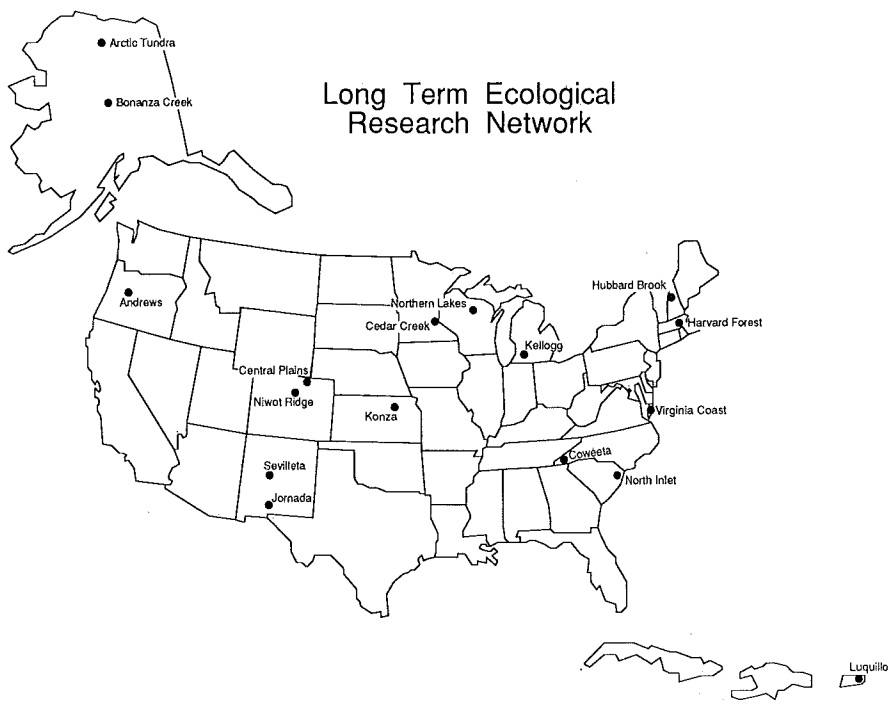


Figure 2. Location of the 17 LTER sites.

The database management activities have been led by researchers at six sites: J. J. Andrews Experimental Forest, North Inlet Marsh-Estuarine System, Hubbard Brook Experimental Forest, Kellogg Biological Station, Konza Prairie, and Niwot Ridge/Green Lakes Valley.

Standardization of measurements, methods, and computer software is now receiving major attention in the LTER network. Researchers at the various sites were initially resistant to standardization, but they have become increasingly aware of its impor-

Table 1. Characteristics of the Long-Term Ecological Research Program sites.

Site abbreviation, name, and location	Institutional affiliation	Principal biome and main communities	Research topics
AND; H. J. Andrews Experimental Forest; Blue River, Oregon	Oregon State University; US Forest Service Pacific Northwest Research Station	Temperate coniferous forests. Douglas fir/western hemlock/western red cedar; true fir and mountain hemlock; streams	Successional changes in ecosystems; forest-stream interactions; population dynamics of forest stands; patterns and rates of log decomposition; disturbance regimes in forest landscapes
ARC; Arctic Lakes and Tundra, Toolik Lake; Brooks Range, Alaska	Marine Biological Laboratory; Universities of Alaska, Massachusetts, Minnesota, Cincinnati, and Kansas; Clarkson University	Arctic tundra, lakes, streams. Tussock and heath tundras; riverine willows; oligotrophic lakes; headwater streams	Movement of nutrients from land to stream to lake; changes due to anthropogenic influences; controls of ecological processes by nutrients and predation
BNZ; Bonanza Creek Experimental Forest; Fairbanks, Alaska	University of Alaska; Institute of Northern Forestry, US Forest Service, Pacific Northwest Research Station	Taiga. Areas of boreal forest including permafrost-free uplands and permafrost-dominated north slopes and lowlands; floodplain seres	Successional processes associated with wildfire and floodplains; facilitative and competitive interactions among plant species throughout succession; plant-mediated changes in resource and energy availability for decomposers; herbivorous control of plant species composition
CDR; Cedar Creek Natural History Area; Minneapolis, Minnesota	University of Minnesota	Eastern deciduous forest and tallgrass prairie. Old fields; oak savanna and forest; conifer bog; lakes; pine forest; wetland marsh and carr	Successional dynamics; primary productivity and disturbance patterns; nutrient budgets and cycles; climatic variation and the wetland/upland boundary; plant-herbivore dynamics
CPR; Central Plains Experimental Range; Nunn, Colorado	Colorado State University; US Department of Agriculture, Agricultural Research Service	Shortgrass prairie. Shortgrass steppe; floodplain; shrubland; salt meadow	Hydrologic cycle and primary production; community and population dynamics; organic matter aggregation or degradation; influence of erosion on redistribution of matter, nutrients, and pedogenic process; influence of atmospheric gases, aerosols, and particulates on primary production and nutrient cycles
CWT; Coweeta Hydrologic Laboratory; Otto, North Carolina	University of Georgia; US Forest Service, Southeastern Forest Experiment Station	Eastern deciduous forest. Hardwood forests and white pine plantations	Long-term dynamics of forest ecosystems including response to perturbation; input-output elemental dynamics in forested ecosystems; land-stream interactions; consumer regulation of ecosystem processes; atmospheric deposition
HFR; Harvard Forest; Petersham, Massachusetts	Harvard and Clarkson Universities, Universities of New Hampshire and Massachusetts	Eastern deciduous forest. Hardwood/white pine/hemlock forest; spruce swamp forest; conifer plantations	Long-term climate change, disturbance history and vegetation dynamics; comparison of community, population, and plant architectural responses to human and natural disturbance; forest-atmosphere trace gas fluxes; organic matter accumulation, decomposition, and mineralization; element cycling, fine root dynamics, and forest microbiology

Continued on next page

Table 1. Continued.

Site abbreviation, name, and location	Institutional affiliation	Principal biome and main communities	Research topics
HBR; Hubbard Brook Experimental Forest; West Thornton, New Hampshire	Yale and Cornell Universities; Institute of Ecosystem Studies; US Forest Service, Northeastern Forest Experiment Station	Eastern deciduous forest. Northern hardwood forests in various developmental stages, spruce-fir forests; streams and lakes	Vegetation structure and production; dynamics of detritus in terrestrial ecosystems; atmosphere-terrestrial-aquatic ecosystem linkages; heterotroph population dynamics; effects of human activities on ecosystems
JRN; Jornada; Las Cruces, New Mexico	New Mexico State University, US Department of Agriculture, Agriculture Research Service	Hot desert. Playa, piedmont, and swale; bajada, basin, mountain, and swale shrubland; mesquite dunes	Desertification; factors affecting primary production; nitrogen cycling; animal-induced soil disturbances; direct and indirect consumer effects; organic matter transport and processing; vertebrate and invertebrate population dynamics
KBS; Kellogg Biological Station; Hickory Corners, Michigan	Michigan State University	Row-crop agriculture. Conventional corn/soybean cultivation; low-input corn/legume cultivation; perennial biomass cultivation; native successional communities	Agricultural productivity; nutrient availability and organic matter dynamics; herbivory and microbial pathogens; plant competition and C and N allocation; gene transfer
KNZ; Konza Prairie; Manhattan, Kansas	Kansas State University	Tallgrass prairie. Tallgrass prairie; gallery forest; prairie stream	Role of fire, grazing, and climate-influencing ecosystem processes in a tallgrass prairie system
LUQ; Luquillo Experimental Forest; San Juan, Puerto Rico	Center for Energy and Environment Research, University of Puerto Rico; Institute of Tropical Forestry, US Forest Service, Southern Experiment Station	Tropical rainforest. Tabonuco forest; palo Colorado forest; palm brake; dwarf forest; montane streams	Patterns of disturbance in space and time; ecosystem response to different patterns of disturbance; land-stream interactions; effect of management on ecosystem properties; integration of ecosystem models and geographic information systems
NWT; Niwot Ridge/Green Lakes Valley; near Boulder, Colorado	Institute of Arctic and Alpine Research, University of Colorado	Alpine tundra. Fellfield; herbaceous and shrub tundras; cliffs and talus; glacial lakes, streams, and wetlands	Geomorphology; paleoecology; disturbance and recovery of plant communities; root and soil interactions; vertebrate populations; aquatic invertebrates; decomposition and nutrient cycling
NIN; North Inlet Marsh-Estuarine System; Georgetown, South Carolina	Belle W. Baruch Institute for Marine Biology and Coastal Research, University of the South	Coastal estuary. Salt marsh; estuarine benthic; intertidal; barrier island; open beach; inshore oceanic	Patterns and control of primary production; dynamics of selected populations; organic accumulation; patterns of inorganic contributions; patterns of site disturbances, including tidal effects
NTL; North Temperate Lakes; near Madison, Wisconsin	Center for Limnology, University of Wisconsin, Madison	Northern temperate lakes; eastern deciduous forests. Oligotrophic, dystrophic, and eutrophic lakes; temporary forest ponds; warm and cold streams; sphagnum-leatherleaf bog; conifer swamp; mixed deciduous and coniferous forests	Groundwater hydrology and geochemistry; physical, chemical, and paleolimnology; producer and consumer ecology, including introduced organisms and their effects; ecology of invasions; lakescape and landscape ecology
SEV; Sevilleta National Wildlife Refuge, near Albuquerque, New Mexico	University of New Mexico; US Fish and Wildlife Service	Multiple: intersection of dry mountain land, grassland, cold desert, and hot desert. Conifer woodland/savanna; creosote bush; desert grassland; mesquite and sand dunes; Great Basin shrub and shortgrass steppes; tallgrass swales; riparian communities	Landscape and organism population dynamics in a biome tension zone; semiarid watershed ecology; climate-change detection in a sensitive landscape; biospheric/atmospheric interactions; paleobotany; archaeology; microbial role in gas flux; control of landscape heterogeneity; scale effects on spatial and temporal variability
VCR; Virginia Coast Reserve, near Oyster, Virginia	University of Virginia	Coastal barrier islands. Sandy intertidal; open beach; shrub thicket; mature pine forest; salt marsh; estuary	Holocene barrier-island geology; salt marsh ecology; geology, and hydrology; ecology and evolution of insular vertebrates; primary/secondary succession; life-form modeling of succession

Figure 3. Most of the LTER sites include human-manipulated as well as natural ecosystems; secondary forests dominate the Harvard Forest LTER site (in Massachusetts), which was once almost entirely cleared for agriculture.

tance in achieving a truly functional network. Development of a graded series of standardized meteorological measurements was an early effort (Greenland 1986, 1987), as was a recommendation that sites become stations in the National Atmospheric Deposition Program. Climatic conditions, including climatic variability, are being subjected to a series of analyses (Greenland and Swift in press). Such analyses are helping to guide further development of comparable measurement schemes, including identification of additional parameters such as indicators of environmental pollutants.

In 1988, scientists at the LTER sites collectively decided that acquisition of some basic standardized communication, data handling, and analytic capabilities by all LTER projects was essential to development of the network. Hence a current emphasis is the acquisition of a "minimum standard installation" (MSI), which includes the common hardware and software needed to achieve computer networking capability. Another major element is standardized geographic information system (GIS) software and hardware; LTER projects will acquire both raster- and vector-based systems. Additional MSI elements are local-area computer networks and linkage to a national wide-area network so that rapid communication and data exchange with other sites are possible.

A network office has been established in the College of Forest Resources at the University of Washington to facilitate intersite activities including the development of multisite databases, analyses of remotely sensed images, and the exchange of data among long-term ecological sites, including non-LTER programs. This office has established and maintains an electronic mail forwarding system and bulletin board, which is heavily used by network and nonnetwork scientists. The network office also publishes a semiannual newsletter, an annual personnel directory, and other informational materials, such as a site guidebook (Brenneman 1989) and a data management newsletter.

Benefits of the program

LTER is the first major program to provide sustained, systematic support for long-term studies in ecology, and this continued support is probably the program's greatest single value. The recognition of and interest shown in LTER by scientific institutions in other countries confirms this value (Risser and Melillo in press).

The LTER program, however, is making a variety of other contributions. It is producing numerous scientific findings, providing focal points for ecological research, and creating opportunities for comparative and collaborative research. The following sections provide examples of each of these types of contributions.

Figure 4. Watershed-level manipulations have been used at many LTER sites, including the Coweeta Hydrological Laboratory in North Carolina. Photo: Wayne Swank.

Figure 5. Mirror Lake and its watershed have been a major limnological research site at the Hubbard Brook Experimental Forest LTER in New Hampshire.

Generation of scientific findings

The LTER sites are producing major scientific results, particularly regarding ecological processes whose study requires experimentation and observation over extended time periods. A long history of prior research at most sites is one major factor in this scientific productivity.

DISTURBANCES OF WATERSHEDS. A typical example of the long-term experiments characteristic of research at the LTER sites is the manipulation of watersheds in which ecosystem responses to various kinds of disturbances, including fire, cultivation, grazing, and several intensities of forest harvest, are being examined. Two areas with long histories of watershed-level manipulations are the Coweeta Hydrologic Laboratory (CWT; Figure 4) and Hubbard Brook (HBR) Experimental Forest (Figure 5). Both of these programs were established many years before LTER began.

CWT has more than 50 years of hydrologic data documenting the effects of land treatment, including clearcutting, on hydrologic regime and, more recently, on stream chemistry (Swank and Crossley 1988). Research on biological regulation of nutrient cycles at CWT includes a mix of long-term observations, experiments, and modeling. Documentation of significant increases in stream nitrogen from insect herbivory is one example from many scientific results.

The more than 25-year history of watershed-level studies at HBR has also produced major discoveries, such as the importance of vegetative regrowth in reducing nutrient losses after catastrophic disturbances, such as clearcutting (Borman and Likens 1979). A current study focuses on the effect of whole-tree harvesting on nutrient budgets. At HBR, aquatic research has focused on Mirror Lake and its watershed, resulting in numerous scientific findings regarding natural processes and anthropogenic influences (Likens 1985a; Figure 5).

A VARIETY OF PROCESSES. Other LTER programs also have long-term records that can be used to investigate specific processes. At North Temperate Lakes (NTL), changes in groundwater chemistry are being studied by examining water as it moves through and surfaces in a chain of lakes. This process requires decades of observation.

At Cedar Creek LTER (CDR), the dynamic interplay of vegetation, herbivores, and soil processes constitutes a major class of studies (Figure 6). Old-field succession, a classic topic in ecology, is studied at CDR by focusing on long-term, well-replicated experimental manipulations of such factors as soil nutrients, disturbance regimes, herbivore densities, fire fre-

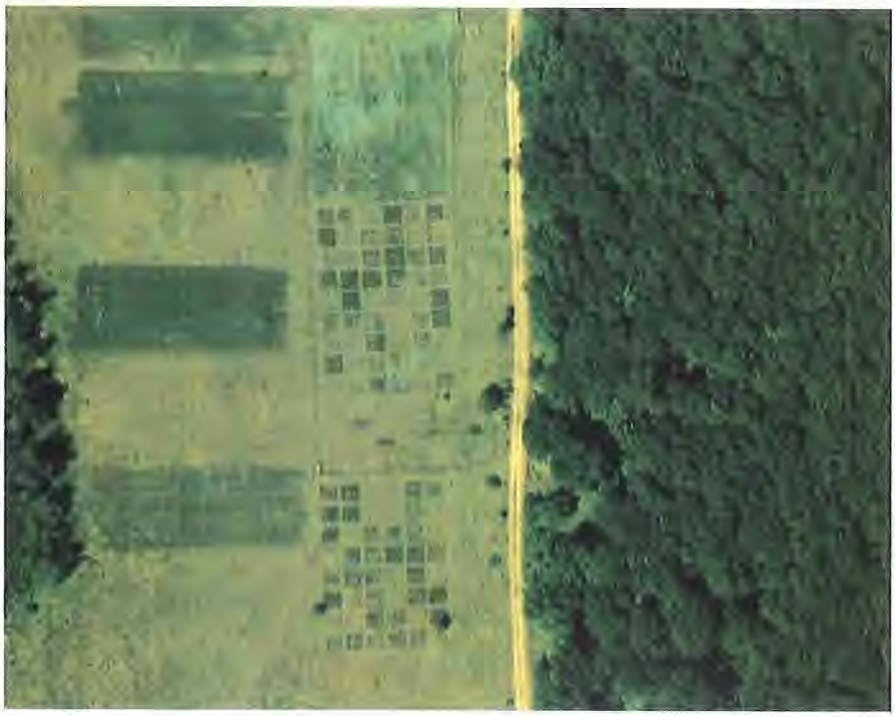


Figure 6. Studies of ecological change in old-field ecosystems are the focus of much of the research at the Cedar Creek LTER in Minnesota. Photo: David Tilman

Figure 7. Niwot Ridge LTER in Colorado represents an alpine ecosystem; research at this site includes long-term studies of the effects of altered snowpack duration on ecosystem composition.

quency, and plant colonization rates (Tilman 1988).

Studies at Niwot Ridge LTER (NWT) include effects of altered snowpack durations on plant community composition (Figure 7). A major detritivore, termites, has been eliminated from a desert ecosystem in a long-term experiment at Jornada LTER (JRN; Figure 8).

TREE MORTALITY. Long-term studies of tree mortality at many forested LTER sites provide quantitative information on patterns of this poorly understood process (Franklin et al.

Figure 8. Research at the Jornada LTER in New Mexico extends along a topographic gradient from mountain slope to playa; one experimental treatment has been the removal of termites, a major detritivore. Photo: Walt Whitford.

Figure 9. The two principal Luquillo Experimental Forest LTER study sites at El Verde and Bisley were severely affected by Hurricane Hugo: all four walk-up towers in the forest canopy access system were knocked down. Photo: Robert Waide.

Figure 10. LTER research at H. J. Andrews Experimental Forest in Oregon includes a study of decay processes and their controls in large logs; this project has a planned duration of 200 years. The log is being placed on netting within a forested site; it will subsequently be completely enclosed in netting as one experimental treatment. Photo: Mark Harmon.

1987). Much forest mortality research concerns gradual changes associated with successional development (Franklin and DeBell 1988), but abrupt changes are also important, such as effects of catastrophic disturbance on forest mortality.

Hurricane Hugo provided outstanding opportunities for studies at the North Inlet Marsh-Estuarine System (NIN) and Luquillo Experimental Forest (LUQ; Figure 9). At LUQ, early assessments have focused on forest structure, litter and nutrient input and export, as well as other effects. At NIN, scientists are studying effects of hurricane-induced tidal inundation of coastal forests and the import of saltwater into forests. Research on effects of hurricanes at Harvard Forest (HFR) includes both retrospective studies (Foster 1988a, 1988b) and experimental simulations of wind-thrown stands.

Figure 11. Although shortgrass steppe dominates at the Central Plains Experimental Range in Colorado, as shown here, the modeling studies at this site use data from throughout the Great Plains. Photo: D. P. Coffin.

Wood decomposition. Complete decomposition of coarse woody debris (standing dead trees and downed boles) is typically a slow and complex process (Harmon et al. 1986). During decomposition, these woody structures carry out many important ecological functions (Franklin et al. 1987, Maser et al. 1988). Two hundred years from now, scientists are expected to complete the last measurements in a log decomposition experiment at H. J. Andrews LTER (AND)—an exceptionally long timeline even for LTER (Figure 10).

At AND, more than 500 large (averaging 60 cm in diameter) freshly cut logs of four different tree species were placed in six undisturbed forest stands. Initial wood conditions were thoroughly documented. For the first six years, randomly selected logs are being removed annually, dissected, and analyzed biologically and physically. Subsequent removals are scheduled at increasing time intervals until the year 2185. Already scientists are developing a much better understanding of decomposition processes than was possible using the log chronosequence method (a series of logs of different ages). The information that leaching is an important process early in bole decay is one unexpected recent discovery, and the complex and critical role of invertebrates in inoculating logs with decay organisms is another (Carpenter et al. 1988).

Modeling. Mathematical and conceptual modeling are key components of LTER programs. Central Plains Experimental Range (CPR) and Virginia Coast Reserve (VCR) are projects with major modeling emphases (Parton et al. 1987a, Shugart 1988, Shugart et al. in press). At CPR (Figure 11), the Century soil organic computer model uses data from two other LTER sites, Sevilleta National Wildlife Refuge and Kellogg Biologi-

cal Station (SEV and KBS; Parton et al. 1987a, Parton et al. 1987b), as well as data from non-LTER grassland areas throughout North America. This model predicts changes in soil properties and productivity in grasslands under alternative management practices and climatic regimes.

Long-term field studies are providing data for tests of these model predictions of ecosystem response to short-term (5- to 50-year) and long-term (100- to 500-year) changes in climate and grazing intensity. Results show that short-term ecosystem responses are frequently opposite to long-term responses.

In the barrier island ecosystems at VCR (Figure 12), models and field data are being used to study long-term migration of barrier islands. Retrospective studies have shown that these islands were once several hundred miles further east in the Atlantic Ocean. Models predict migration rates for these islands as they move closer to the mainland.

Figure 12. The Virginia Coast Reserve LTER focuses much of its research on coastal Virginia barrier islands and their movement.

Several LTER programs include studies to develop, refine, and test ecological theory. Functional relationships between soil physical and chemical properties and vegetation succession in boreal floodplains are under way at the Bonanza Creek Experimental Forest LTER (BNZ), a subarctic boreal forest and floodplain ecosystem in Alaska (Figure 13). Nutrient flows at the landscape level (through terrestrial, lake, and river ecosystems) are under both observational and experimental study at the Arctic Lakes and Tundra LTER (ARC) on the North Slope in Alaska (Figure 14). Similarly, nutrient flows between forest and estuary and the role of outwelling (the export of materials from estuaries to the ocean) are under investigation at NIN (Figure 15).

Focus for ecological research. LTER programs provide focal points for research by other scientists and programs. Factors attracting outside users to LTER sites include the availability of long-term data sets, interdisciplinary scientific cadres, participation in a connected network of sites, potential for long-term experiments and protected research sites, and logistical support, sometimes including living and working facilities. Users of LTER sites include both individual research scientists and agencies with large projects.

LAKE ACIDIFICATION. The Little Rock Lake Experimental Acidification Project at NTL is a major national study on the effects of lake acidification sponsored by the US Environmental Protection Agency (Watras and Frost 1989). In 1983 the University of Wisconsin's Center for Limnology was chosen to play a major role among several institutions in conducting this study, largely because it maintains a long-term database on lake ecosystems and is associated with LTER. The Little Rock Lake project involves the acidification of half of a lake (Figure 16). The two lobes of this hourglass-shaped lake are separated by a neoprene barrier. One half of the lake has been acidified

Figure 13. Long-term changes in soils and vegetation are the focus of research at Bonanza Creek Experimental Forest LTER in Alaska; a broad gradient of conditions are represented on upland and floodplain areas. Photo: Keith Van Cleve.

Figure 14. Nutrient flows at the landscape level—through terrestrial, lake, and river ecosystems—are under investigation at the Arctic Lakes and Tundra LTER located on the North Slope in Alaska. Photo: Gaius Shaver.

from pH 6.1 to 4.6, in 0.5 unit increments, during three two-year stages between 1985 and 1990. The second half of the lake has been retained as a reference.

The power of this experimental study is the large, whole-ecosystem manipulation that allows researchers to quantify complex interactions within a natural system. This power is magnified by the availability of parallel data on seven nearby NTL study lakes, which provide a background of natural variability with which to compare responses to acidification. Using this information, the Little Rock Project has provided important insights not only into acidification effects (Frost and Montz 1988) but on the interpretation of whole-ecosystem experiments in general (Carpenter et al. 1989).

CLIMATOLOGY. Konza Prairie (KNZ) LTER was selected as the focal point for the First International Land Surface Climatology Project (ILSCP) Field Experiment (FIFE), another large interdisciplinary study (Figure 17). The National Aeronautics and Space Administration sponsored this study of the utility of remotely sensed (satellite) data for observing climatological phenomena. Data from a variety of observation vehicles (Landsat and Systeme Pour l'Observation de la Terre [SPOT] satellites, high- and low-flying fixed-wing aircraft, and a helicopter) are being compared with data obtained by scientists on the ground and in tall towers. Several intensive study periods in 1987 and 1988 provided unique data sets of coincident satellite, airborne, and surface measurements.

Figure 15. At North Inlet Marsh-Estuarine System LTER in South Carolina, the focus is on an estuary and its interactions with the terrestrial and marine environments. Photo: John Vernberg.

One focus in this study has been the influence of various manipulations, such as fertilization and burning, on the spectral reflectance of the vegetation. Preliminary results show that infrared bands in the Landsat thematic mapper are sensitive to differences between burned and unburned vegetation (Seastedt and Briggs in press). Differences in reflectance patterns are being related to patterns in sensible and latent heat fluxes (i.e., growing plants reflect more infrared radiation and convert a higher percentage of incoming solar radiation to energy in water vapor than do senes-

cent herbage). The resulting data allows scientists to address the question "How does vegetation affect regional climate?"

MICROORGANISMS. At Kellogg Biological Station (KBS), the new Science and Technology Center in Microbial Ecology is using the LTER site as its principal field site. A major focus of the center is understanding the diversity, function, and competitiveness of microorganisms in natural and managed habitats, chief among them the plant rhizosphere. Ongoing LTER research in plant carbon and nitrogen allocation, soil physical structure and organic matter turnover, and trophic relationships in soil communities ties closely into center-sponsored research on the genetics, physiological capacities, and environmental constraints of naturally occurring microbial populations.

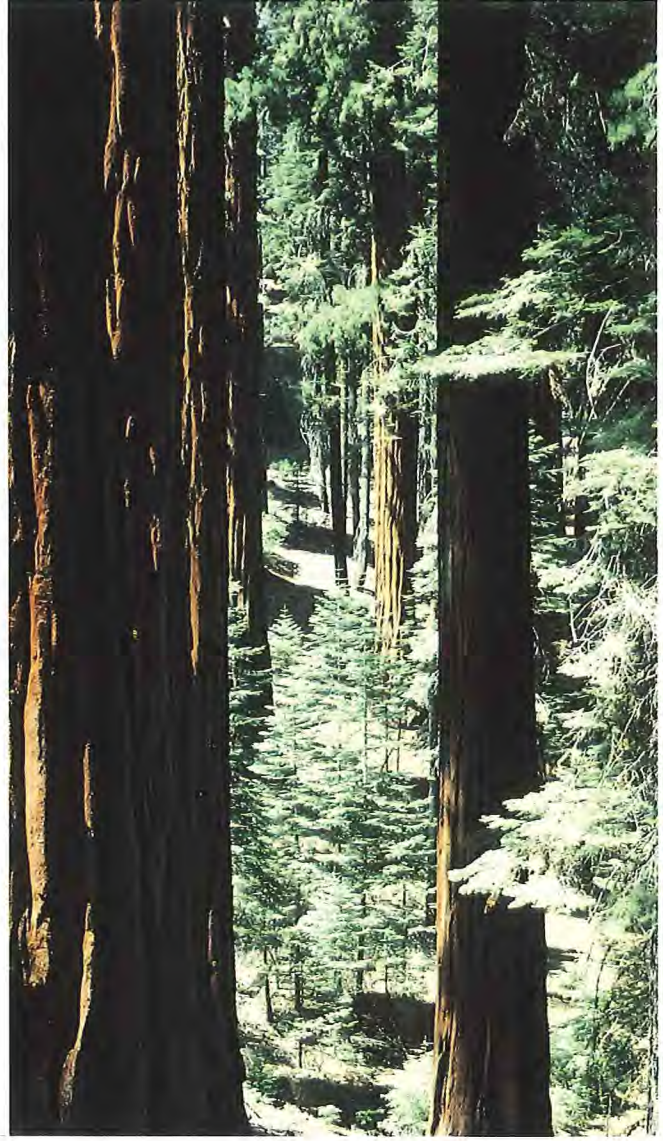
VARIED USES. Individual scientists are also finding that LTER sites provide ideal locations for many of their research projects. Lists of active studies at LTER sites as well as publication lists make clear their varied use in systematic, evolutionary, population, physiological, community, and landscape studies.

In 1988, NSF instituted a program called "Supplements for Research at LTER Sites" to facilitate more varied use of LTER sites by non-LTER scientists who were currently funded by the Biotic Systems and Resources Division at NSF. Awards under this program include research on a variety of topics, such as plant systematics (systematics and evolution of polyploid mosses at ARC), evolutionary biology (polyploid polymorphism in grasses in relation to adaptation to environmental variation at KNZ), physiology (physiological mechanisms and population parameters in the evolution of a plant-insect interaction at CDR), and community processes (process and mechanisms of plant competition in the Great Basin sagebrush-dominated ecosystem at Sevilleta National Wildlife Refuge [SEV]).

Figure 16. Many agencies are finding LTER sites to be ideal locations for their research projects. At North Temperate Lakes LTER in Wisconsin, the Environmental Protection Agency is sponsoring a study of effects of lake acidification using the two halves of Little Rock Lake. Photo: John Magnuson.

Figure 17. Prescribed burning is one of the major experimental treatments in the tallgrass prairie of the Konza Prairie LTER in Kansas. The National Aeronautics and Space Administration is also using the site to determine the sensitivity of remote sensing to the measurement of vegetation-atmosphere interactions. Photo: Donald Kaufman.

Figure 18. Work on the Luquillo Experimental Forest LTER in Puerto Rico (above) includes research related to the recovery of this endangered parrot. Photo: Robert Waide.



There are many non-LTER sites, such as Sequoia-Kings Canyon National Park in California (right), that have major projects focused on long-term ecological phenomena.

Figure 19. The program at Kellogg Biological Station LTER in Michigan is focused on agricultural ecosystems, in particular on ecological constraints on crop productivity. Photo: Philip Robertson.

Comparative and collaborative research opportunities

Comparative research is an important scientific frontier because of its potential contribution to the development of robust ecological theory—broadly applicable ecological principles. Much ecological theory has fallen victim to myopia. In many cases, investigators have constructed theory on a too-limited base of organisms, communities, or ecosystems and have proposed universal applicability. In fact, it is increasingly clear that ecological processes vary dramatically in importance along environmental, as well as spatial and temporal, gradients. This variation makes comparative studies critical to the development of a predictive science.

The LTER network offers outstanding opportunities for comparative studies, both within the network and as part of a larger network composed of both LTER and non-LTER projects. The LTER program provides high potential for coordinated and cooperative comparative research across diverse ecosystems. This coordination may take many forms, including the installation of standard experimental designs across many sites. A 17-site experiment, for example, is under way that will use enclosed bags of plant litter (roots and foliage) to evaluate litter decomposition over periods of up to 20 years, a much longer time period than litter decomposition is typically observed. Such standardized studies, including reciprocal exchanges of plant and animal materials, are expected to make major contributions to understanding and predicting how pathways and rates of ecological processes vary over large environmental gradients.

Multisite syntheses of existing information are essential to early progress in many areas of comparative ecological analysis. Several such efforts are already progressing under LTER sponsorship. Cross-site analyses of the role of geomorphology in ecological processes have already been completed (Caine and Swanson 1989, Swanson et al. 1988, Swanson and Sparks page 502 this issue).

Magnuson (Magnuson et al. in press) led a group in an investigation of spatial and temporal variability across the broad range of ecosystem types represented in the LTER program. They found that there were consistent differences in the variability of ecosystem type. For example, animal and plant characteristics were more variable among years than were climatic and edaphic variables. David Tilman of the Cedar Creek LTER, University of Minnesota, is leading a multisite investigation of factors that control primary productivity.

Individual LTER sites are contributing significantly to research on emerging environmental issues. Many sites have been critical in identifying and understanding environmental pollutant issues; examples include research on acid precipitation at HBR (Likens 1985a, 1989) and on nitrogen saturation from fossil fuel combustion at HFR (Aber et al. 1989).

Issues in conservation of biological diversity are part of the agenda at most LTER sites; for example, research at LUQ on the Puerto Rican parrot (Figure 18) and at AND on the northern spotted owl address threatened and endangered species. In an agricultural ecosystem (Figure 19), KBS is examining microbial gene transfer and the role of genetically altered organisms in the plant/soil community.

Collaborative efforts among holistic, large-scale programs are particularly critical, however, in addressing major environmental issues. The LTER network can be central in stimulating such comparative analyses because it is an existing system of linked sites. For example, at a November 1989 workshop, 25 LTER and non-LTER sites (including sites funded by the Department of Energy [DOE], the National Park Service, and the Smithsonian Institution) considered research needs associated with global climatic change and its effects. Position papers identified the unique potential and perspectives of each site. For example, because SEV is located at a transition among several biotic provinces (see cover), it may be particularly sensitive to global climatic change. Population processes, material cycles (including trace gases), and effects of altered disturbance regimes or sea-level rise are foci at other sites.

The 1989 workshop participants identified a multisite research program addressing global climatic change and building on the individual strengths and collective interests of each site. Critical elements included major experiments on effects of soil warming, especially on soil organic matter and trace gas emission, and effects of carbon dioxide enrichment on productivity and water use efficiency of representative ecosystems. Research on interactions between global environmental change and land-use patterns and disturbance regimes, especially frequency, intensity, and locality of catastrophic disturbances, was identified as another major component.

LTER in the long-term research community

Many scientists, sites, and programs are involved in long-term studies in ecology, and the involvement of a great many more is essential, given the pervasive need for research with extended time scales. The LTER program is far too limited to fill most of the needs for long-term ecological research. The LTER system of sites lacks coverage of some major biomes, such as Mediterranean chaparral and montane coniferous forests. Furthermore, the LTER sites represent a limited amount of the variability within biomes.

The need for collaborations among the numerous scientists and high-quality programs that are involved in long-term ecological studies is an even stronger argument for the development of a network larger than LTER. Important long-term data sets for individual organisms, communities, and environments have been collected by many scientists and institutions (Strayer et al. 1986). Many outstanding ecological research projects with larger temporal and spatial scales exist outside the LTER network (Likens 1985b) and are supported by a variety of agencies.

Programs at national laboratories, such as Oak Ridge, are supported primarily by DOE. Several national parks, such as Sequoia-Kings Canyon, California (see photo, page 520), are effective long-term study sites; Channel Islands National Park has developed an outstanding program in long-term monitoring of near-shore marine environments (Davis and Halvorsen 1988). The US Department of Agriculture (both the Forest Service

and the Agricultural Research Service) has numerous long-term study sites in its widespread system of experimental forests and ranges.

Other programs sponsored by NSF (at Kemmerer, Utah), as well as some sponsored by the Smithsonian Institution (at Chesapeake Bay, Maryland, and Barro Colorado Island, Canal Zone) and the Organization for Tropical Studies (La Selva, Costa Rica), also have a long-term focus. The LTER program is a major participant in planning direct communication links, common measurement programs, and joint studies with this larger collection of sites, including the in-house site networks created by (or being planned by) DOE, the USDA Forest Service, and the National Park Service.

LTER scientists are committed to collaborating with other scientists and programs in the development of an enlarged network of researchers involved in long-term studies. Although LTER represents a small set of sites, it can provide leadership by its exclusive focus on long-term studies. For example, approaches and standards developed in climate measurement (Greenland and Swift in press) and data management programs (Michener 1986) may be broadly useful.

As illustrated by the global change workshop, the LTER network has consistently involved scientists outside the LTER network in meetings to address topical issues or plan multisite comparative research. LTER programs can also help catalyze the creation of regional site networks, which are necessary to provide adequate representation of within-biome variability. For example, CPR and SEV are core elements in a network of grassland sites and programs that extends from Canada to Mexico. Integration of CWT LTER, Oak Ridge National Laboratory, and Great Smoky Mountains National Park through the recently established Southern Appalachian Man and the Biosphere (MAB) Program is another example of the potential for regional scientific cooperation.

Even broader collaborations in long-term ecological research are needed, however. The newly established Section on Long Term Studies in the Ecological Society of America will provide a forum for information exchange and development of collaborative efforts throughout the entire ecological community. LTER has established computer-based local-area networks that use existing wide-area electronic networks for information exchange. Many other ecologists also use NSF's Internet for electronic communication.

Networking at the international level is also possible. Exchanges of information are taking place as a part of bilateral programs, such as the exchange between LTER sites in the United States and the People's Republic of China. Multinational efforts are also under way, such as the 1988 meeting at Berchtesgaden, West Germany (Risser and Melillo in press) and the 1989 teleconference at Albuquerque, New Mexico, which included LTER and European ecologists involved in long-term studies.

Development of both regional and international collaborations under UNESCO's MAB Program is also possible. Ten of the 17 LTERs are already designated biosphere reserves. The MAB connection could be used in developing institutional links for monitoring, research, and education within particular biogeographical regions. At a recent meeting in Paris, a small MAB task force began planning for such an international program.

Conclusions

The program of long-term studies sponsored by NSF is now well-established, with a system of 17 sites representing a large variety of ecosystem types. Although each program incorporates long temporal and broad spatial perspectives, the LTER projects have varied scientific objectives and approaches.

Significant contributions to ecological science from LTER include: the production of specific scientific findings and theoretical constructs; the provision of sites with existing information bases and infrastructures for use by other ecological scientists; and the creation of opportunities for comparative research. Substantial efforts are being made for networking within the LTER program and between LTER scientists and others involved in long-term ecological studies. Such networking is critical in exchanging information, adopting standardized measurement and data management programs, designing and conducting comparative studies, and conducting high-level syntheses, including the construction and testing of theory.

References cited

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

Bormann, F. H., and G. E. Likens. 1979. *Pattern and Process in a Forested Ecosystem.* Springer-Verlag, New York.

Brenneman, J., ed. 1989. *Long-Term Ecological Research in the United States, a Network of Sites 1989.* LTER Network Office, College of Forest Resources, AR-10, University of Washington, Seattle, WA.

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

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

Carpenter, S. E., M. E. Harmon, E. R. Ingham, R. G. Kelsey, J. D. Lattin, and T. D. Schowalter. 1988. Early patterns of heterotroph activity in conifer logs. *Proc. R. Soc. Edinb. Sect. B (Biol. Sci.)* 94B: 33–43.

Carpenter, S. R., T. M. Frost, D. Heisley, and T. K. Kratz. 1989. Randomized intervention analysis and the interpretation of whole ecosystem experiments. *Ecology* 70: 1142–1152.

Conley, M. R., and W. Conley. 1984. *New Mexico State University College Ranch and Jornada Experimental Range: A Summary of Research, 1900–1983.* Special Report 56, New Mexico State University Agricultural Experiment Station, Las Cruces.

Dancik, B. P., ed. 1983. The structure and function of a black spruce forest in relation to other fire-affected taiga ecosystems. *Can. J. For. Res.* 13: 695–916.

Davis, G. E., and W. L. Halvorsen. 1988. *Inventory and Monitoring of Natural Resources in Channel Islands National Park, California.* National Park Service, Ventura, CA.

Foster, D. R. 1988a. Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah Forest, southwestern New Hampshire. *J. Ecol.* 76: 105–134.

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

Franklin, J. F. 1988. Past and future of ecosystem research—contribution of dedicated experimental sites. Pages 415–424 in W. T. Swank and D. A. Crossley Jr., eds. *Forest Hydrology and Ecology at Coweeta.* Springer-Verlag, New York.

———. 1989. Importance and justification of long-term studies in ecology. Pages 3–19 in G. E. Likens, ed. *Long-Term Studies in Ecology: Approaches and Alternatives.* Springer-Verlag, New York.

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: 663–639.

Franklin, J. F., H. H. Shugart, and M. E. Harmon. 1987. Tree death as an ecological process: the causes, consequences, and variability of tree mortality. *BioScience* 37: 550–556.

Frost, T. M., and P. K. Montz. 1988. Early zooplankton response to experimental acidification in Little Rock Lake, WI. *Verhandlungen Internationale Vereinigung Limnologie* 23: 2279–2285.

Gaskin, J. W., J. E. Douglas, and W. T. Swank. 1983. Annotated bibliography of publications on watershed management and ecological studies at Coweeta Hydrologic Laboratory, 1934–1984. General Technical Report SE-30, Southeast US Forest Experiment Station, Ashville, NC.

Greenland, D., ed. 1986. *Standardized Meteorological Measurements for Long-Term Ecological Research Sites.* LTER Network Office, College of Forest Resources AR-10, University of Washington, Seattle.

Greenland, D., ed. 1987. *The Climates of the Long-Term Ecological Research Sites.* Occasional Paper No. 44, Institute of Arctic and Alpine Research, University of Colorado, Boulder.

Greenland, D., and L. W. Swift, eds. In press. *Climate Variability and Ecosystem Response.* General Technical Report SE, USDA Forest Service, Southeast Experiment Station, Asheville, NC.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack Jr., and K. W. Cummings. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15: 133–302.

Kirchner, T. B., and W. K. Lauenroth. 1989. *Publications of the Central Plains Experimental Range 1939–1988.* Natural Resource Ecology Laboratory, Colorado State University, Fort Collins.

Likens, G. E., ed. 1985a. *An Ecosystem Approach to Aquatic Ecology and its Environment: Mirror Lake.* Springer-Verlag, New York.

_____. 1985b. Status and future of ecosystem science. *Occasional Publication of the Institute of Ecosystem Studies* 3:1–24. Millbrook, NY.

_____. 1989. *Long-Term Studies in Ecology: Approaches and Alternatives.* Springer-Verlag, New York.

Likens, G. E., F. H. Bormann, R. S. Pierce, J. S. Eaton, and N. M. Johnson. 1977. *Biogeochemistry of a Forested Ecosystem.* Springer-Verlag, New York.

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, B. J. Benson, R. Nero, and C. J. Bowser. 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. M. Melillo, eds. *LTER: An International Proposal.* John Wiley & Sons, Chichester, England.

Maser, C., R. F. Tarrant, J. M. Trappe, and J. F. Franklin. 1988. *From the Forest to the Sea: A Story of Fallen Trees.* General Technical Report PNW-GTR-229, USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

McKee, A., G. M. Stonedahl, J. F. Franklin, and F. J. Swanson. 1987. *Research Publications of the H. J. Andrews Experimental Forest, Cascade Range, Oregon, 1948–1986.* General Technical Report PNW-GTR-201, USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

Michener, W. K., ed. 1986. *Research Data Management in the Ecological Sciences.* University of South Carolina Press, Columbia.

National Science Foundation (NSF). 1977. *Long-Term Ecological Measurements: Report of a Conference.* National Science Foundation Directorate for Biological, Behavioral, and Social Sciences, Washington, DC.

_____. 1978. *A Pilot Program for Long-Term Observation and Study of Ecosystems in the United States: Report of a Second Conference in Long-Term Ecological Measurements.* National Science Foundation Directorate for Biological, Behavioral, and Social Sciences, Washington, DC.

Parton, W. J., D. S. Schimel, C. V. Cole, and D. Ojima. 1987a. Analysis of factors controlling soil organic levels in grasslands in the Great Plains. *Soil Sci. Soc. Am. J.* 51: 1173–1179.

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

Risser, P. G., and J. M. Melillo, eds. In press. *LTER: An International Proposal.* John Wiley & Sons, Chichester, England.

Seastedt, T. R. and J. M. Briggs. In press. Long-term ecological questions and considerations for taking long-term measurements: lessons from the LTER and FIFE programs on tallgrass prairie. In P. J. Risser and J. M. Melillo, eds. *International Workshop on Long-Term Ecological Research.* John Wiley & Sons, Stockholm.

Shugart, H. H. 1988. The role of ecological models in long-term ecological studies. Pages 90–109 in G. E. Likens, ed. *Approaches to Long-Term Studies in Ecology.* Springer-Verlag, New York.

Shugart, H. H., G. B. Bonan, D. L. Urban, W. K. Lauenroth, W. J. Parton, and G. M. Hornberger. In press. Computer models and long-term ecological research. In P. G. Risser, ed. *Long-Term Ecological Research and Global Ecology.* John Wiley & Sons, New York.

Strayer, D., J. S. Glitzenstein, C. G. Jones, J. Kolasa, G. E. Likens, M. J. McDonnell, G. G. Parker, and S. T. A. Pickett. 1986. Long-term ecological studies: an illustrated account of their design, operation, and importance to ecology. *Occasional Publication of the Institute of Ecosystem Studies* 2: 1–38. Millbrook, NY.

Swank, W. T., and D. A. Crossley Jr., eds. 1988. *Forest Hydrology and Ecology at Coweeta.* Springer-Verlag, New York.

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.

Swanson, F. J., and R. E. Sparks. 1990. Long-term ecological research and the invisible place. *BioScience* 40: 502–508.

Tilman, D. 1982. *Resource Competition and Community Structure.* Princeton University Press, Princeton, NJ.

_____. 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities.* Princeton University Press, Princeton, NJ.

_____. 1989. Ecological experimentation: strengths and conceptual problems. Pages 136–157 in G. E. Likens, ed. *Long-Term Studies in Ecology: Approaches and Alternatives.* Springer-Verlag, New York.

VanCleve, K., F. S. Chapin III, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness, eds. 1986. *Forest Ecosystems in the Alaska Taiga.* Springer-Verlag, New York.

Watras, C. J., and T. M. Frost. 1989. Little Rock Lake (Wisconsin): perspectives on an experimental ecosystem approach to seepage lake acidification. *Arch. Env. Cont. Toxicol.* 18: 157–165.

Wessman, C. A., J. D. Aber, D. L. Peterson, and J. M. Melillo. 1988. Remote sensing of canopy chemistry and nitrogen cycling in temperate forest ecosystems. *Nature* 335: 154–156.

Whitney, G. 1989. *Research Bibliography of the Harvard Forest 1906–1988.* Harvard University Press, Cambridge, MA.