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The US Long Term Ecological Research Program

JOHN E. HOBBIE, STEPHEN R. CARPENTER, NANCY B. GRIMM, JAMES R. GOSZ, AND TIMOTHY R. SEASTEDT

The 24 projects of the National Science Foundation's Long Term Ecological Research Network, whose sites range from the poles to the Tropics, from rain forests to tundras and deserts, and from offshore marine to estuarine and freshwater habitats, address fundamental and applied ecological issues that can be understood only through a long-term approach. Each project addresses different ecological questions; even the scale of research differs across sites. Projects in the network are linked by the requirement for some research at each site on five core areas, including primary production, decomposition, and trophic dynamics, and by cross-site comparisons, which are aided by the universally available databases. Many species and environmental variables are studied, and a wide range of synthetic results have been generated.

Keywords: LTER Network, long-term ecological research, LTER accomplishments, LTER history, LTER description

From its start in 1980 with six projects, the Long Term Ecological Research (LTER) program has now grown to 24 projects involving more than 1100 scientists. This article describes why the program exists and what it does. But the success of a scientific program cannot be measured by the number of sites or scientists involved in a project. Instead, the question must be, What have the LTER program and its long-term data sets contributed to the intellectual progress of ecological and environmental sciences? This special section takes direct aim at this question in six articles focusing on accomplishments of the LTER program in discrete areas of ecological research.The goal of each article is to highlight LTER contributions, not to provide an extensive review of an ecological topic. Readers should keep in mind that LTER projects make many other contributions than those described here.

This article introduces the justification for long-term studies in ecology and describes the history of these studies, from Rothamsted in the 1840s through the International Biological Program of the 1970s to today's Hubbard Brook ecosystem study and LTER and other intensive research sites. Long-term projects make use of their year-to-century life span to identify the nonequilibrium and nonlinear characteristics of ecosystems and processes through monitoring and through experiments that may last decades. Much of this article is devoted to the LTER program today—its mission (box1), databases, cross-site synthesis activities, and cooperative research with government agencies—as well as the International LTER (ILTER) effort and LTER involvement with societal issues, including policy and education. The article concludes with a discussion of the value of LTER sites as indicators of regional and global change and as test beds for new technologies, from miniature chemical analyzers to satellite remote sensing.

Why do we need long-term studies in ecology?

In ecology, historical change is the key to understanding the present and anticipating the future. Thus, observation of long-term change is central, yet some ecological changes take place at scales that match or exceed human lifetimes. These changes are not recognized by most people; they lie in the "invisible present" of Magnuson (1990). Trees grow for hundreds of years, hurricanes may decimate a site every 50 years, and droughts may last for decades; thus, a long-term perspective is needed to understand the ecological response to these slow changes or rare events.

Environmental problems often develop slowly and are difficult to identify and solve without a long-term baseline. For example, a careful record of animal species in Wisconsin lakes identified exactly when a nonnative crayfish invaded

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Box 1. The mission and aims of the US Long Term Ecological Research Network

The central, organizing intellectual aim of the Long Term Ecological Research (LTER) Network is to understand long-term patterns and processes of ecological systems at multiple spatial scales. To achieve this aim, the mission of the LTER Network is implemented in six interrelated ways:

1. Understanding: Gaining ecological understanding of a diverse array of ecosystems at multiple spatial and temporal scales
2. Synthesis: Using the network of sites to create general ecological knowledge through the synthesis of information gained from long-term research and development of theory
3. Information dissemination: Creating well-designed, documented databases that are accessible to the broader scientific community
4. Legacies: Creating a legacy of well-designed and well-documented long-term observations, experiments, and archives of samples and specimens
5. Training: Developing a cadre of scientists who are equipped to conduct long-term, collaborative research to address complex ecological problems
6. Outreach: Providing knowledge to the broader ecological community, general public, resource managers, and policymakers to address complex environmental challenges

(Turner et al. 2003). In some cases the records reveal a clear trend, such as the continued increase of carbon dioxide (CO_2) concentration in the air at the top of Mauna Loa, carefully monitored since 1958. Long-term records are frequently consulted when resource managers attempt to set goals for restoration programs, such as those for the hydrology of the Everglades or the elk herd of Yellowstone. Ecological research requires observations of organisms and their interactions with each other and with their physical environment. Given the natural variations over time in the numbers of organisms and in the physical environment, the relevant observations are repeated over days, months, or years, depending on such things as the pattern of change of leaf mass or temperature over the seasons. But each year is different, and multiyear observations expand our perspective. For example, we may realize that our 1-year study took place during a decadal drought, or that we need 50 years of lake ice data to detect the pattern of recurring El Niño climate disturbance (Magnuson 1990, Greenland et al. 2003).

Much of the natural world is responding dynamically to past or present disturbance. Even the tundra of northern Alaska, unchanged for thousands of years, is undergoing subtle changes caused primarily by warming of the climate (Serreze et al. 2000). In Wisconsin, the 120-year record of water clarity in Lake Mendota revealed close correlations with changes in nutrient discharges and food web structure (box 2). Forest vegetation may take hundreds of years to show change.

In many ecosystems, a rare event can reset a vegetation succession or drastically change geomorphology. The effects of hurricanes, such as those of Hugo at the Luquillo Forest in Puerto Rico, are well documented (Turner et al. 2003), but unusually heavy rainfalls or even floods can be important. In some regions the history of droughts that can last for decades or centuries is important for understanding the present-day distribution of vegetation.

Milestones in the development of the long-term approach

Many of the long-duration data sets of natural phenomena come from Asia. For ice cover on lakes, Magnuson and colleagues (2000) report that the record in Lake Suwa, Japan, began in 1443, and records in the Angara River in Siberia began in 1720. Long-term research, however, began much later.

Rothamsted. One of the earliest examples of long-term ecological research is the work begun in 1843 at Rothamsted, an experimental farm in England (described in Taylor 1989). The Broadbalk experiment at Rothamsted had as its initial objective a simple test of Liebig's theory that plants draw the nitrogen they need directly from the air. The experiment tested the growth of wheat in an untreated plot, a manured plot, and a plot fertilized with ammonium chloride and sulfate. The answer came quickly, and later nitrogen was demonstrated to be the limiting element. According to Taylor (1989, p. 38), "When R. A. Fisher subsequently tried to analyze it [the Broadbalk experiment], he was led to devise the new experimental field statistics and randomized factorial designs" (e.g., Fisher 1925). Another experiment, on the effect of fertilizers on the diversity of plant species in an ungrazed hayfield, continued for over a century until only one species remained—and it was inedible to cows. More recently, a 150-year set of stored soil samples provided a unique record of the effect of atom bomb detonations on radiocarbon dating.

Intensive sites: Hubbard Brook and the International Biological Program. In the United States, the Forest Service set up large-scale experiments to investigate the yield of water to streams in forests under various harvest regimes. In 1964, ecologists F. H. Bormann and G. E. Likens suggested the measurement of concentrations of various materials in stream water at the experimental watersheds of the Forest Service's Hubbard Brook site in New Hampshire (Likens et al. 1977). This effort soon led to estimates of the budgets of various ions (e.g., calcium, sodium, potassium, carbonate, and sulfate). The budgeting activity, in turn, led to measurements of the ions in precipitation (box 3).

Box 2. Understanding big effects from gradual changes

Long-term data contribute to discoveries of ecosystem change and possible mitigations. In Lake Mendota, Wisconsin, water clarity has been measured since the 1880s using Secchi disks. By obtaining the original disks and intercalibrating them, LTER researchers reconstructed an extensive record of water clarity (Lathrop et al. 1996). Over the same period of time, nutrient levels and food web structure were inferred from indicators other than water clarity (such as records of sewage discharge, fertilizer usage, or fish kills). Long-term changes in water clarity were related to nutrient discharges into the lake and food web structure. The abundance of planktivorous fishes, especially cisco *(Coregonus artedii)*, is inversely related to abundance of the voracious grazer *Daphnia pulicaria*, which affects water clarity. The effect of grazing on water clarity is roughly as large as that of nutrient input. Together, these two factors created considerable variability, which could only be understood from the long-term perspective.

A more recent and intensive LTER study showed how land-use activities, climate, and food web dynamics interacted to control clarity of the lake (Lathrop et al. 1999). While the lake's food web has been manipulated to enhance grazing, trends in development of the watershed seem likely to increase nonpoint pollution and thereby diminish water quality. An interdisciplinary analysis showed substantial economic losses due to poor water quality (Carpenter et al. 1999). The economically optimal level of phosphorus loading to the lake is about a third of current loading. Analyses of LTER time series showed that by cutting the phosphorus load in half, the probability of toxic algae blooms could be reduced from the current two days in three to only one day in five (Lathrop et al. 1998). An aggressive nonpoint pollution control program is now under way for the lake. LTER will play a key role in scientific assessment of the ecological and socioeconomic impacts of this program.

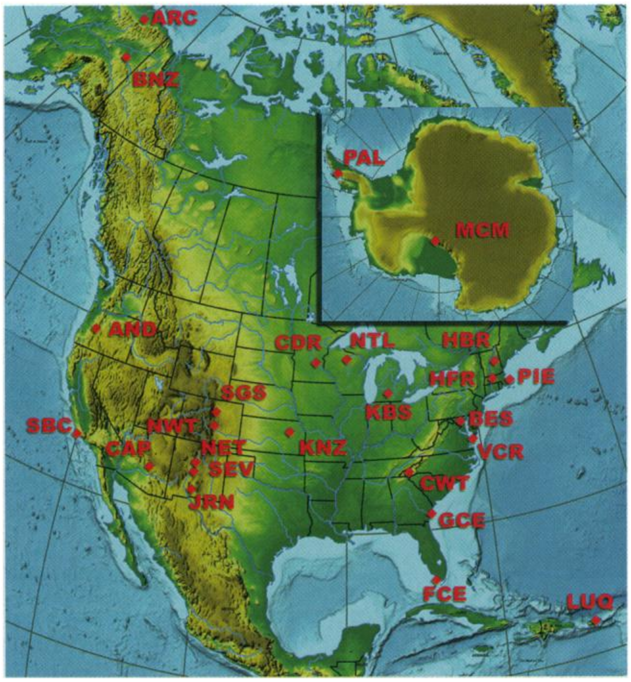

Figure 1. Map of location of LTER sites, courtesy of LTER Network office.

Soon the studies at Hubbard Brook expanded beyond chemical budgets to include questions about the species and biomass of the vegetation—that is, the structure of the forest—and about ecosystem functions such as the processes of nitrogen cycling and plant growth. As new questions came to the fore, measures were added such as changes in bird abundance and tree size, the rates of water and material movement in soils, and the rate of formation of dissolved organic carbon as water moves through the litter layers. The result was the formation of an intensive study site, that is, a location where a wide variety of information was assembled on climate; soil chemistry; biomass of plants, microbes, and animals; rates of processes; controls of ecosystem function; and so forth.

A 5-year study of intensive sites or biomes (deciduous forest, grassland, desert, western coniferous forest, and tundra) became the focus of the US contribution to the International Biological Program (IBP), which took place from 1970 to 1975. Availability of environmental and ecological data was a criterion for the selection of sites. One common theme was documentation of the cycling of carbon, nitrogen, and phosphorus. Ecosystem models and centralized databases were developed as tools for synthesis and understanding. Data and synthetic understanding were summarized in a series of 16 books. The studies were extraordinarily complete, and many of the rate functions, process constants, and environmental relationships used in today's regional and global mathematical models (Rastetter et al. 2003) come from the IBP data of the 1970s.

LTER and other intensive research sites today. In 1980, following the US IBP projects, the National Science Foundation (NSF) began a program of site-based research, with an emphasis on long-term studies (Franklin et al. 1990). Today, there are 24 projects (figure 1) located in a wide variety of habitats, ranging from the Arctic and Antarctic to the tropics of Puerto Rico, from the deserts of New Mexico to the forests of Oregon and Massachusetts, and from the lakes of Wisconsin to the mangrove wetlands of Florida. Two projects are located in the urban areas of Baltimore and Phoenix.

The US LTER Network facilitates the development of long-term research programs around the world. Relationships between international and US programs include scientist-to-

Box 3. A long-term record of acid precipitation

Acid precipitation apparently began to fall on much of the eastern United States in the 1950s or earlier (Likens et al. 1972); the longest record of pH in precipitation in the United States began in 1964 at Hubbard Brook, New Hampshire (figure 2; Driscoll et al. 2001). However, values of pH varied for each storm; between 1964 and 1974 the range at Hubbard Brook was 3.0 to 5.95 (Likens et al. 1977). This variability in concentration made it difficult to determine any trend over time. Instead of the average of values for each storm, the total input of hydrogen ion—that is, the pH-derived concentration multiplied by the volume of the precipitation—proved a valuable way to determine that the annual input increased 1.4-fold during the 1964–1974 period. These authors reported that sulfate amounts did not change over this period, while nitrate amounts increased 2.3-fold. Not only did the long-term record prove invaluable in the identification of the onset of acidity in rainfall in the United States, but the breadth of the Hubbard Brook study allowed researchers to identify the shift in the cause of acidity from the sulfur gases emitted by power plants to the nitrogen gases emitted by automobiles.

scientist exchange, intersite research, organization of international meetings, and global-scale research planning and collaboration. Long-term research sites in the United States are also associated with the Department of Energy's national laboratories (e.g., Savannah River Laboratory, Oak Ridge National Laboratory), with the Department of the Interior's National Park Service (e.g., Denali National Park, Shenandoah Watershed Study, Cape Cod National Seashore) and National Wildlife Refuges (e.g., Arctic National Wildlife Refuge), with the National Oceanic and Atmospheric Administration (e.g., Estuarine Research Reserves), and with private organizations (e.g., Black Rock Forest, The Nature Conservancy) and public groups (e.g., university field and marine stations).

What types of research require a long-term approach? The need for long-term ecological studies is compelling from many points of view (Strayer et al. 1986, Likens 1989, Risser 1991). From a theoretical viewpoint, the nonequilibrium status of ecosystems and the nonlinearity of many ecological processes provide the rationale for multiple measurements of ecological phenomena in space and in time. From the process-based viewpoint, long-term studies are needed for those ecological phenomena that occur as a result of slow, subtle, or complex processes (Pickett 1991). Thus, the process of forest succession requires observational periods longer than a human lifetime. Another viewpoint stresses the importance of natural disturbances in shaping ecological communities (Foster et al. 2003). Many of these disturbances, such as fire and drought, return only at long intervals and thus require long-term study. Even disturbances at geological time scales, such as the eruption of Mount St. Helens, are overwhelmingly important to the terrestrial and aquatic ecosystems and biogeochemical processes of the regions in which the disturbances occur.

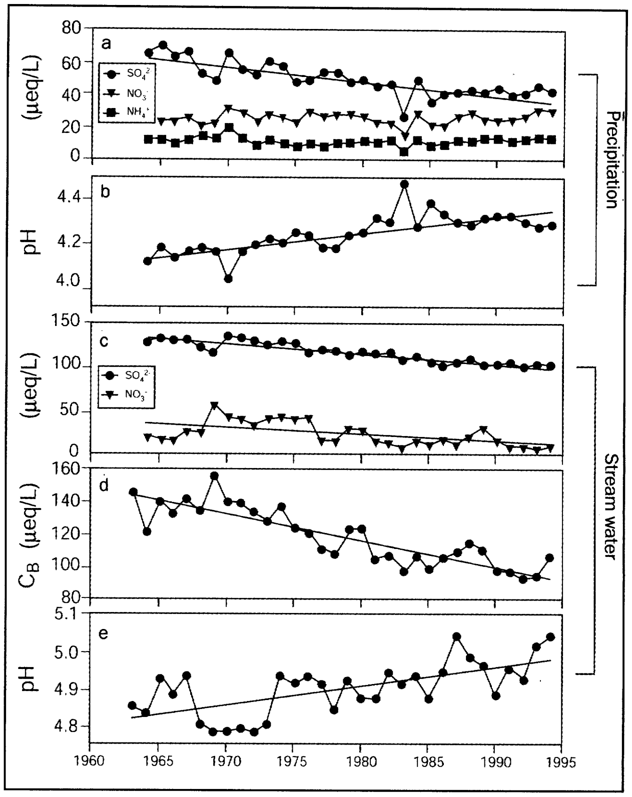

Figure 2. Time series from Watershed 6 of the Hubbard Brook Experimental Forest: (a) volume-weighted annual mean concentrations in microequivalents per liter (µeq/L) of sulfate (SO_4^{2-}), nitrate (NO_3^-), and ammonium (NH_4^+) in precipitation; (b) pH in bulk precipitation; (c) SO_4^{2-} and NO_3^- in stream water; (d) the sum of base cations (C_B) in stream water; and (e) pH in stream water. Redrawn from Driscoll and colleagues 2001 with permission.

Many of these viewpoints are combined in studies that seek to address current concerns about changes in the environment in general and effects of climate change in particular. For these studies to successfully serve their purpose, we must understand the extent to which ecological systems interact with the atmosphere to change temperatures and precipitation. Will these interactions amplify or attenuate the storage of carbon and the production of greenhouse gases? We do know that very small but unidirectional changes in the exchange of materials between the atmosphere and the surface of the earth can be of critical importance to global change, and long-term measurements are generally essential to detect, validate, or disprove the existence of such changes.

The LTER program has traditionally focused on ecological questions that require time scales of years, decades, or centuries to evaluate (figure 3). As Magnuson (1990, p. 495)

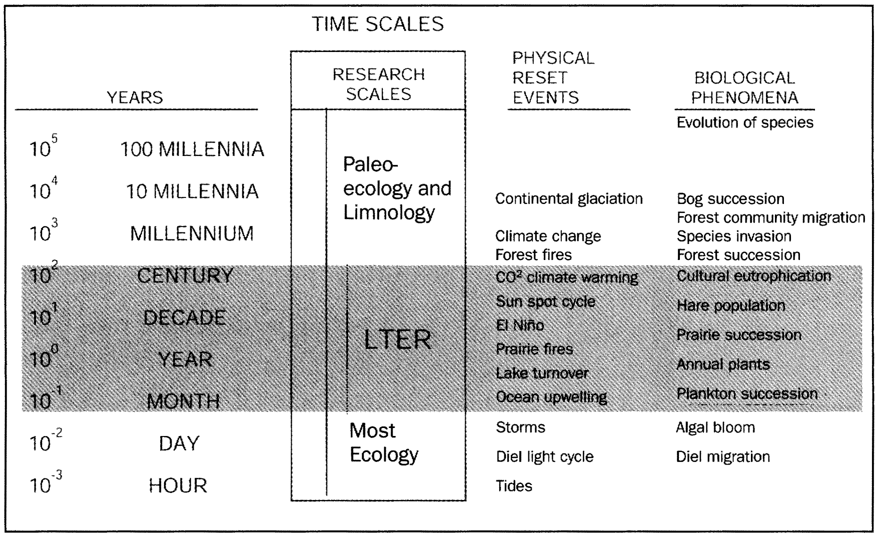

Figure 3. Long-term ecological studies emphasize ecological activities that operate on year to decade to century time scales. Redrawn from Magnuson 1990, with permission.

emphasizes, "This is the time scale of acid deposition, the invasion of non-native plants and animals, the introduction of synthetic chemicals, CO_2-induced climate warming, and deforestation. In the absence of the temporal context provided by long-term research, serious misjudgments can occur not only in our attempts to understand and predict change in the world around us, but also in our attempts to manage our environment." Without a long-term temporal context, or without a large spatial scale or comparative context, short-term ecological findings can be difficult to interpret.

We should also emphasize the value of the long-term approach to experimental research. Rothamsted scientists manipulated the amount of manure or inorganic nutrients added to agricultural fields. The Forest Service manipulated the tree harvest methods to investigate water runoff in Hubbard Brook and Coweeta research forests. Clearly, experiments involving nutrients in agriculture and forest harvest, such as the nutrient addition experiments at Cedar Creek LTER (Symstad et al. 2003), require a long-term approach. But it is now known that manipulations of nutrients and soil heating in arctic tundra and temperate forests also take decades to arrive at new equilibria of structure and function. The same can be said for aquatic ecosystems; the continual addition of phosphorus to an arctic river is still producing unexpected changes after 20 years (Bowden et al. 1994).

The US Long Term Ecological Research program

In response to the clear need for research extending beyond the traditional 2- or 3-year grant period, NSF began in 1980 to support research on long-term ecological phenomena in the United States. The many facets of the LTER program include databases, cross-site synthesis, cooperative research with government, an international connection, and education of students and teachers.

In 2003, the US LTER Network consists of 24 sites representing diverse ecosystems and research emphases, and a network office that coordinates communication, network publications, and research planning.The initial 6-year funding for a site is made after an open competition decided by a special panel. Subsequent 6-year awards, also made after panel evaluation of a full proposal, are made only if goals are fulfilled and the site is scientifically productive. Some LTER sites have been funded for 20 years.

During the first decade of the LTER program, individual sites focused on their own long-term research projects. In the 1990s, often called the large-scale research decade, the scale of many of the projects or groups of projects expanded to large areas. Indeed, models have been used to predict ecological changes over entire landscapes and regions (Rastetter et al. 2003). As spatial scales were expanded and regional phenomena considered, incorporation of human-dominated ecosystems was inevitable. Researchers began using multidisciplinary tools to address these new phenomena, and they received support from NSF to expand existing research into new disciplines and human-dominated landscapes (Coweeta, North Temperate Lakes) and to fund new agricultural (Kellogg Biological Station) and urban–suburban (Baltimore Ecosystem Study, Central Arizona–Phoenix) LTER sites.

LTER sites today span the planet's range of biomes and ecosystem types (figure 4). Most LTER sites have some research on aquatic ecosystems within their boundaries, while others have an exclusive aquatic focus (e.g., Palmer Station, North Temperate Lakes). Some have expanded to a broad region and have begun to look at legacies of prior land use (e.g., Coweeta, Harvard Forest). Large-scale experiments are the centerpiece of the research program at some sites (Konza Prarie, Arctic, North Temperate Lakes, Cedar Creek), whereas at many other LTER sites smaller-scale experiments supplement careful long-term monitoring.

The LTER mission. The central, organizing intellectual aim of the LTER program is to understand long-term patterns and processes of ecological systems at multiple spatial scales. The implementation goals of the program are listed in box 1.

While each site determines its own questions and themes, all sites are expected to maintain a broad spectrum of research to ensure that intersite and network-level comparisons are possible. This concept is formalized in the requirement that all sites perform at least some research in each of five core research areas: (1) pattern and control of primary production; (2) spatial and temporal distribution of populations selected to represent trophic structures; (3) pattern and control of organic matter accumulation and decomposition in surface layers

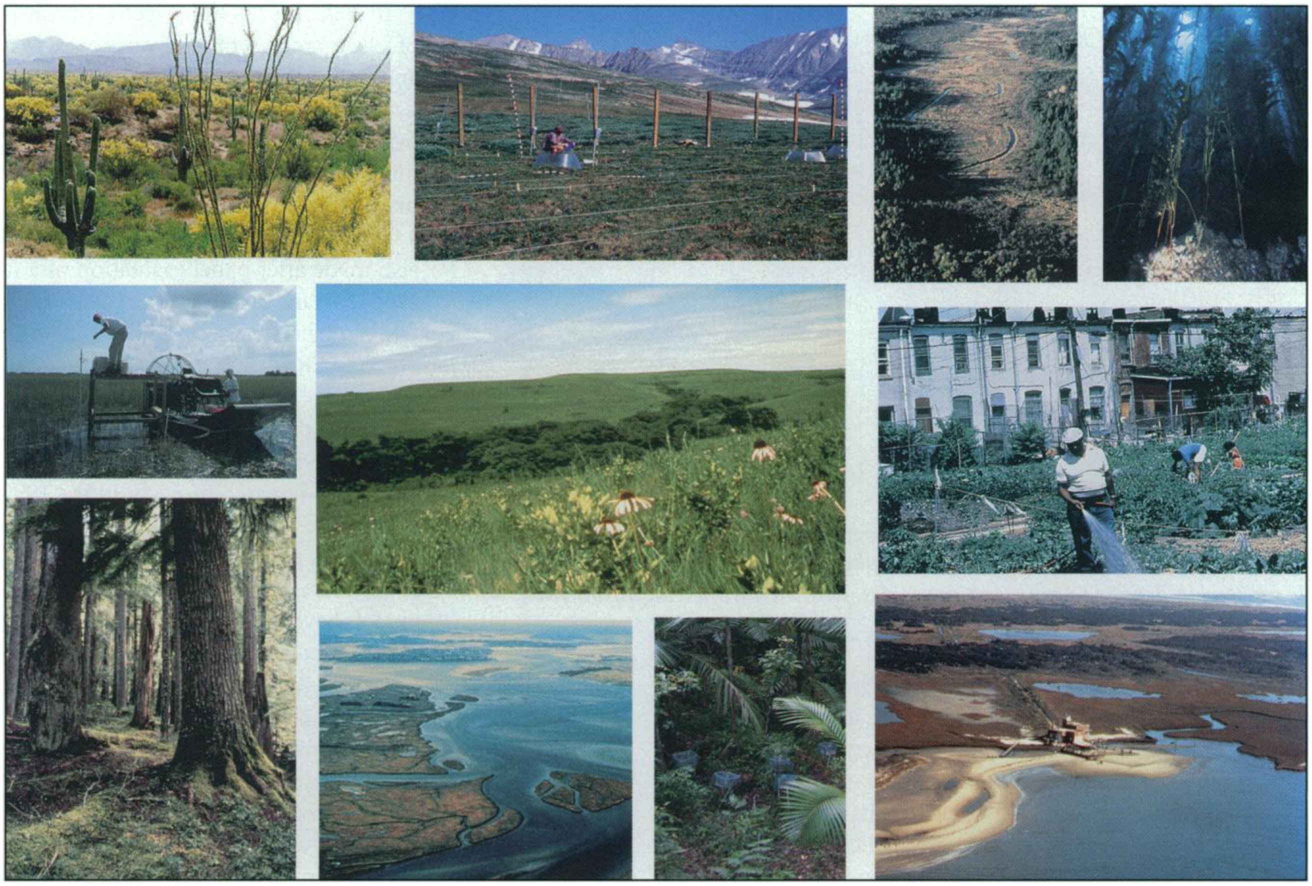

Figure 4. Various LTER habitats. From the upper left, the photographs on the outer border depict the following LTER site habitats: desert (CAP), alpine tundra (NWT), tall-grass prairie/oak woodland (CDR), kelp forest (SBC), urban (BES), salt marshes and barrier beach (VCR), tropical forest (LUQ), estuary (PIE), old-growth forest (AND), and everglades (FCE). The middle picture shows prairie (KNZ) habitat. Site codes are given in Table 1. Photographs by Brenda Shears (CAP), Tim Seastedt (NWT), Dave Tilman(CDR), Ron McPeak (SBC), Morgan Grove (BES), Linda Blum (VCR), and Robert Waide (LUQ), courtesy of Chuck Hopkinson (PIE), Fred Swanson (AND), Dan Childers (FCE), and Alan Knapp (KNZ).

and sediments; (4) patterns of inorganic inputs and movements of nutrients through soils, groundwater, and surface waters; and (5) patterns and frequency of disturbances. There is no doubt that site-based research remains the most basic and essential element of the LTER program, because the long-term nature of its core studies provides a context for understanding interannual variability, disturbance effects, and gradual or rapid change (natural or human-induced).

Many research foci are shared by multiple LTER sites. For example, the theme of work at 12 sites is interactions among atmosphere, land, and water, and the research theme of 11 projects is climate forcing and climate change (table 1).

Value added to research sites by the LTER program. When a research site becomes part of the LTER program, a number of positive changes happen simply because the project will likely continue for decades. First, there is a shift in the planning horizon of the scientists. In the Arctic LTER project, for example, research had been carried out at the site for 12 years under a series of 3-year grants, but serious climate observations began only with the advent of LTER funding. Second, there is a surge of interest in research at the LTER site by non-LTER scientists who will have access to a wide variety of site observations and knowledge. Thus, an LTER site is an attractive place to include in surveys of small mammals, microbes, or soil invertebrates. The result is that ecological understanding grows faster than the LTER-funded research. Third, there is the opportunity for outreach—that is, the chance to interact with nearby educational institutions, local citizens' groups and nongovernmental organizations, and local and state resource managers. Relationships with all these groups take years to develop and are nearly impossible to make work unless all parties make a long-term commitment.

The LTER databases. The creation, maintenance, and dissemination of LTER-produced data is an essential part of the program. The database created is a resource for the broader scientific community. Each LTER project has a Web site that provides easy access to the collected data as well as the additional information (metadata) needed to interpret the data. These Web sites also provide information about the

Table 1. Research themes for the 24 LTER sites.

Theme	Site
Climate forcing and climate change	ARC, CDR, HFR, KNZ, MCM, NTL, NWT, PAL, SEV, FCE, SBC
Disturbance, disturbance regimes, disturbance legacies	AND, BNZ, CWT, HFR, KNZ, LUQ
Human–ecosystem interactions	BES, CAP, NTL
Legacies of human activity and land-use change	BES, CAP, CWT, HFR, HBR, KBS, LUQ, PIE, SGS, FCE, SBC
Atmosphere–land–water interactions	AND, ARC, CAP, CWT, HBR, LUQ, MCM, NWT, PIE, FCE, GCE, SBC
Biodiversity	CDR, JOR, KBS, LUQ
Controls of food web structure (nutrients or predation)	ARC, NTL, PAL, KNZ, JOR, GCE, SBC
Invasive species effects	KNZ, NTL, LUQ, CAP
Succession	AND, BNZ, CDR, VCR
Physical forcing factors	PAL, NWT, MCM, GCE, VCR
Human infrastructure/built-environment effects on ecosystems	BES, CAP

Site codes: AND, Andrews (OR); ARC, Arctic (AK); BES, Baltimore Ecosystem Study (MD); BNZ, Bonanza Creek (AK); CAP, Central Arizona–Phoenix (AZ); CDR, Cedar Creek (MN); CWT, Coweeta (NC); FCE, Florida Coastal Everglades (FL); GCE, Georgia Coastal Ecosystem (GA); HFR, Harvard Forest (MA); HBR, Hubbard Brook (NH); JOR, Jornada Basin (NM); KBS, Kellogg Biological Station (MI); KNZ, Konza Prairie (KS); LUQ, Luquillo Forest (Puerto Rico); MCM, McMurdo Dry Valleys (Antarctica); NWT, Niwot Ridge (CO); NTL, North Temperate Lakes (WI); PAL, Palmer Station (Antarctica); PIE, Plum Island Ecosystem (MA); SBC, Santa Barbara Coastal (CA); SEV, Sevilleta (NM); SGS, Shortgrass Steppe (CO); VCR, Virginia Coast Reserve (VA).

ecological setting of the field site, about the goals of the project, and about the interpretations and publications from the project. Web sites may be accessed through the LTER Network home page *(http://lternet.edu/)*. The timely and widespread sharing of data within and outside the LTER Network encourages regional, national, and global syntheses far beyond the dreams of the original collectors.

Value added to ecological science by LTER. Long-term sites provide ecology with sustained intellectual attention to fundamental ecological issues that can only be understood by a long-term approach. Examples are slow processes (soil development, forest succession, life histories of long-lived organisms), rare or saltational events (large infrequent disturbances, recruitment events of organisms that reproduce episodically), associations between complex disturbance regimes and biotic change, and subtle changes that are discernable only through persistent study (Franklin 1989). Slowly changing variables pervade ecology, and their complex interactions with more rapidly changing variables create many of the phenomena that ecology seeks to explain (Carpenter and Turner 2000). Consequently, formulating and testing ecological theory demands long-term study and long-term experiments. Experience with long-term change is essential for creating, criticizing, adjusting, and ultimately improving ecological theories and models (Ford 2000). In addition, long-term sites provide information, such as parameter estimates, that is needed routinely for simulation models.

The LTER Network provides ecologists with a physical framework for long-term research, analogous to a fleet of research vessels in oceanography. Information is managed by state-of-the-art methods and shared widely through the Internet. The concentration of expertise, technical capability, and quality-assured data streams attracts diverse research projects to LTER sites. Colocation of research projects makes efficient use of costly data and long-term experimental manipulations; it also increases the possibilities for creative breakthroughs from interdisciplinary collaboration.

Cross-site synthesis in LTER. The LTER Network connects hundreds of scientists asking similar questions in a wide variety of habitats. Synthesis projects designed to work across sites are as follows.

Variance in North American Ecosystems. This project compared the scale-dependency and magnitude of variance in population dynamics and ecosystem processes across both space and time at 12 LTER sites representing different ecosystem types (Kratz et al. 1995). In some cases, patterns in variance could be explained by geomorphic processes or by turnover times of key species or processes. For example, water movement across the landscape was the most important factor explaining patterns in temporal variability across topographic gradients (Kratz et al. 1991).

Long-Term Intersite Decomposition Experiment Team. This project, known as LIDET, determines the effects of substrate quality and macroclimate on carbon and nutrient dynamics of decomposing leaves, wood, and fine roots (Moorhead et al. 1999, Gholz et al. 2000, Kratz et al. 2003). The team consists of the scientists at 28 different sites (17 of them LTER sites) who set up the incubations, a group that models carbon, nitrogen, and phosphorus dynamics, and a central analysis group that performs chemical analyses and manages data (Harmon et al. 1999).

The Biodiversity/Productivity Project. This project examines the association of species diversity with ecosystem productivity in experimental and comparative studies. That association, which appears to involve many mechanisms, changes qualitatively with geographic extent, range of ecological sys-

Box 4. Invasive Species

The impact of the introduction of nonnative species on native species populations is a major concern of environmentalists and conservation biologists (Vitousek et al. 1996, Wilcove et al. 1998). Insights on the causal mechanisms that allow invasion come from LTER long-term manipulative experiments and inventories of species (Kotanen et al. 1998, Smith and Knapp 1999, 2001). These experiments have shown that management activities such as fire and grazing do not have uniform effects on species' ability to invade in different ecosystems. Rather, the unifying mechanism involves the response of the dominant vegetation to a particular disturbance or manipulation. If the dominant, native vegetation is adapted to the disturbance, then invasion is reduced or minimal. For example, the nitrogen enrichment experiments conducted at a number of LTER sites provide the basis for a mechanistic interpretation of vegetation response to enhanced nitrogen at regional scales (LeJeune and Seastedt 2001). North American grasslands historically were nitrogen-limited (Hooper and Johnson 1999), and the dominant species thrived under these conditions. Removal of this limitation by any number of different mechanisms results in a decline in the dominance of native grasses and enhances the vulnerability of these ecosystems to invasions by nonindigenous species. With this knowledge about causation, both preventative and mitigation management activities can be instigated to substantially reduce the negative impacts associated with species introductions.

tems considered, and taxonomic level or energy source for the food web (Waide et al. 1999). In lakes, for example, species richness (adjusted for effects of lake area) is quadratically related to productivity (Dodson et al. 2000).

Lotic Intersite Nitrogen eXperiment. LINX, the Lotic Intersite Nitrogen eXperiment, used a standard experimental design and methodology to investigate characteristics of nitrogen cycling and movement of nitrogen through food webs in small streams from Alaskan tundra to the desert Southwest and Puerto Rican rain forest. Despite the diversity of landscapes, small streams were always extremely important sites of nitrogen retention (Peterson et al. 2001).

While these projects originate in and center on the US LTER Network, they typically include researchers from other long-term sites around the world. For example, a comparison of long-term ice data from the world's lakes revealed a significant pattern of decreasing ice duration throughout the Northern Hemisphere (Magnuson et al. 2000).

Cooperative research with government: LTER–government partnerships. Science-based management requires knowledge of how ecosystems work and how they respond to natural and anthropogenic changes. Management-based studies of ecosystems preceded the LTER program, and in many cases these studies evolved into LTER sites. As Tom Callahan wrote (1984, p. 364), "The roots for federal support for long-term research are deeply embedded in a family of preceding efforts including national parks, wildlife refuges and preserves, and experimental forests and ranges." The hydrologic studies at the Coweeta LTER site were initiated by the Forest Service in the 1930s and used the services of the Civilian Conservation Corps to conduct watershed-scale manipulations. The Hubbard Brook, H. J. Andrews, Luquillo, and Bonanza Creek forest studies evolved as outgrowths of Forest Service collaborations, often in conjunction with other funding programs. For example, the Luquillo site in Puerto Rico was the location of a major Department of Energy effort to study the energy dynamics of a tropical rain forest (Odum and Pigeon 1970). The passage of the National Environmental Protection Act of 1969 provided the impetus for federal agencies to support and promote ecological research necessary for the understanding of sustainability issues (Callahan 1984), and this policy decision further reinforced government support of long-term studies.

Most of the US IBP studies in the late 1960s and early 1970s were conducted in conjunction with other governmental research programs and on sites managed by federal agencies. Four of the six original LTER sites were IBP sites, and all were located on federal lands. While preexisting federal research sites formed the majority of initial LTER sites, state and private foundations have also contributed research lands and facilities to the LTER effort. Universities wholly own some sites. The Nature Conservancy largely owns two (Virginia Coast Reserve and Konza Prairie). Among the recent additions to the LTER Network are the two urban LTER sites. These sites have unique collaborative relationships with city and county personnel. Researchers at the Baltimore LTER site are studying patch dynamics of built, social, biological, and hydrological components of the Baltimore metropolitan area; they also are studying the feedbacks between social, economic, and ecological components of an urban ecosystem. The Central Arizona–Phoenix LTER project asks the question, How does the pattern of development of the city alter the ecological conditions of the city and its surrounding environment, and how do these changes feed back to the social sytem and result in further ecological changes (Grimm et al. 2000)?

International LTER. In 1993, the LTER Network hosted a meeting on international networking in long-term ecological research. At that meeting, representatives of scientific programs or networks that focus on ecological research over long temporal and large spatial scales decided to form the International Long Term Ecological Research network. They planned to develop a worldwide program and the infrastructure necessary to facilitate communication and information management. In addition to embracing the long-term research and educational training mission of the US LTER program, the ILTER network proposed to do the following:

- Promote and enhance the understanding of long-term ecological phenomena across national and regional boundaries
- Contribute to the scientific basis for ecosystem management at local, regional, and global scales
- Facilitate international collaboration among comprehensive, site-based, long-term ecological research programs
- Facilitate development of such programs where they currently do not exist

As of April 2002, 25 countries have established formal LTER programs and joined the ILTER network. Ten more are actively pursuing the establishment of national networks, and many others have expressed interest in the model. (A complete list is available at *http://lternet.edu/*.) The structure of individual ILTER sites does not necessarily follow the US model. Some programs are much more structured and top-down, with a more rigid emphasis on monitoring. Other programs have a greater regional focus and a much stronger human dimension than most US LTER sites.

The potential collaborative benefit of ILTER is large. Besides enhancing information exchange, ILTER offers an opportunity to evaluate different approaches to interdisciplinary science. Sites within ILTER offer examples of ecosystems that have contained a strong human component for thousands of years and may provide insight about human influences on US ecosystems.

LTER and society: Environmental concerns, public policy, and ecosystem management. The analysis of human impacts on ecological systems has been a cornerstone of LTER efforts. Clear-cutting, grazing by native and nonnative species, land conversion, changes in fire regimes, and alterations in the quantity and quality of inputs into lakes, streams, and estuaries are among the many impacts that LTER scientists have studied extensively. Three features of the LTER program have provided critical information to these areas of interest. First, most LTER sites provide baseline measurements, which are essential to understanding the magnitude of novel impacts. Second, the long-term databases obtained on management activities and disturbances have been essential to establishing the short- and long-term impacts of these manipulations. Third, comparisons among LTER sites have contributed to the extent to which findings from one site can be extrapolated and generalized to other ecosystems (Gross et al. 2000, Shaver et al. 2000).

The extent to which scientific information obtained by LTER sites has been transformed into management decisions or policy is not easily quantified. There is little doubt, however, that policy decisions affecting local and regional economic, social, and environmental concerns have been affected by LTER efforts. For one example, research from Andrews Forest has had a significant impact on logging and watershed management practices in the Northwest (Luoma 1999). For another, data from LTER research at the Sevilleta National Wildlife Refuge (Parmenter et al. 1999) defined the relationships between climate, productivity, rodent abundance, and outbreaks of hantavirus now used by public health officials to identify periods of increased human risk. Virtually all LTER sites can identify local and regional policy and management issues that have been influenced by their findings.

The LTER program was initiated before current concerns about global changes were identified. These changes are the collective result of changes in climate, atmospheric chemistry, land use, and the biotic composition of the landscape (Huenneke 1996). Many LTER studies were designed specifically to evaluate these impacts (Shaver et al. 2000). However, a major benefit of the presence of preexisting, well-documented information on ecosystem structure and function is that these data, initially collected to test a specific hypothesis, can be used to address a suite of new issues. The use of old data to address new societal concerns adds substantial value to LTER efforts (for example, invasive species in box 4).

Education of students and teachers. Graduate student education is a major activity within the LTER program. Student research at an LTER site provides an ideal combination of intensive work on a specialized topic and broad exposure to many types of research. Because extensive data on climate and other environmental factors are collected continuously and because there is an extensive database already collected, students can concentrate on the novel parts of their research. Graduate students from all sites participate in an association, and the LTER Network office provides funds for students to attend LTER All Scientists Meetings.

Undergraduate education at LTER sites includes student participation in studies, class field trips to LTER sites, and use of LTER findings as classroom material. Students may also participate in the NSF-sponsored Research Experience for Undergraduates activity. At many sites, undergraduates were authors or coauthors of research publications; given the 20-year history of this program, a number of these former undergraduates are now professional scientists.

There are also many opportunities to involve kindergarten through 12th-grade students and their teachers in LTER-sponsored activities. The overall goal of these activities is to promote outdoor learning about local ecosystems, learning about long-term ecological changes, and learning about the earth's ecosystems. Each site uses its unique resources, facilities, and personnel to achieve program objectives. The key to a successful project appears to be involving the teachers whenever possible and having them use their educational prowess to convert research activities into learning activities. One type of activity common to several LTER educational efforts is student contributions of data to ongoing research databases. A book written and illustrated by third-grade students, entitled *My Water Comes from the Mountains,* has been produced through the Schoolyard activity of the Niwot Ridge–Green Lake Valley LTER site.

Looking forward

The LTER sites range from pristine locations in the Arctic and Antarctic to agricultural and urban human-dominated locations. Because of their long-term databases and range of habitats, LTER projects are ideally suited to document change. They are also well suited to test new technologies for ecological application.

LTER sites as indicators of regional and global change. The documentation of a changing climate is difficult because of the year-to-year variation. In addition to interannual variation, various periodicities of wet, dry, hot, and cold intervals form a complex set of patterns in the climate for any given site. The two most valuable approaches to identifying global change and its effects are (1) the collection of long-term records that document the complex of changes and (2) the analysis of change over a range of locations that allows the identification of regional patterns. Even negative correlations are valuable, because they may substantiate a synchrony in regional changes that reflect global dynamics. For example, the oscillation between El Niño and La Niña phenomena results in an inverse relationship of precipitation in the northwestern and southwestern United States. Data from the LTER sites in those two regions are important in understanding the temporal and spatial ecological effects of these regular periodicities in climate.

The range of locations represented by the LTER Network provides an understanding of other regional effects of climate change. For example, glaciers in the McMurdo Dry Valley in the Antarctic have increased in mass since 1993, a change that coincides with a period of cooler than normal summers and more than average snowfall. The larger glaciers seem to be advancing, but this is primarily a legacy of past climate, roughly 103 years before the present. In contrast, the Bonanza Creek and Arctic LTER sites in Alaska have recorded a warming period unprecedented in the past 200 years. Glaciers in the Brooks Range are rapidly diminishing. Warmer air and soil temperatures and drought are associated with increased melting of ice-rich permafrost, fire, insect outbreaks, diminished growth and reduced seed production in dominant tree species, extensive grassland development following disturbance, reduction in moss abundance, and increased shrub and birch densities in the far north (Greenland et al. 2003). Increased warming is associated with changed dominance of grass species in the shortgrass steppe in Colorado (Lauenroth and Sala 1992); however, at the alpine Niwot Ridge site in Colorado, the same period demonstrated no directional change in temperatures but an increase in precipitation (Caine 2002). The Sevilleta site in central New Mexico also had a recent period of cool climate and unusually high precipitation (1980s to early 1990s) that allowed increased tree establishment and growth unprecedented in the past 500 years (Milne et al. 2003). These complex stories make sense only from a regional or continental perspective and from the vantage point of long temporal records that demonstrate the coherence of changed conditions.

Retrospective and paleoecological studies at LTER sites are important for placing these recent dynamics in perspective. These studies can identify other climate changes that occur at longer intervals than our historical records. Tree-ring analyses at the Sevilleta LTER in central New Mexico, for example, demonstrate periodicities in droughts occurring at 11, 22, and 60 years (Milne et al. 2003).The event occurring every 60 years is an especially severe, decade-long drought that causes long-lasting ecological effects. The last two occurred during the decades of the 1890s and 1950s; the landscape still shows evidence of the 1950s drought. The region may be entering another cycle of decadal drought leading to further ecological changes.

LTER sites as test beds for new technologies. A fundamental property of site-based research is that the knowledge base and the comprehensive understanding increase over time. Not only are dynamics more apparent over time, but the breadth and integration of the knowledge increases. This enhances the attractiveness of the site for other investigations whose interpretations ultimately depend on the knowledge base. Many basic capabilities are provided (e.g., climate data, site equipment, data management system, and other research infrastructure) that make it convenient to do research. LTER sites also become target areas for testing new technologies because of their existing infrastructure.

Many exciting methodological innovations are now emerging from fields such as nanotechnology, biotechnology, materials science, and information technology. Miniaturization of robotic systems and sensors allows us to monitor the environment in new ways. Miniature telemetry systems make it possible to follow the movements and behaviors of animals as small as insects. New chemical sensors are now available to solve old sampling problems. For example, in work with hantavirus and rodents at the University of New Mexico, "smart traps" can capture a rodent, identify it, analyze its urine, and release the animal, all without human involvement. New developments in microengineered materials allow the formulation of microscopic particles (i.e., aerogels) with physical properties capable of holding particular chemical compounds that are sensitive to chemicals in the environment ("smart dust"). Researchers use insects such as bees and cockroaches to carry these particles as they move through the environment. The particles, which react with specific compounds that they encounter, can be analyzed for the presence of those compounds in the environment. Currently, this technology is being developed to sense materials such as explosives, sarin, Venezuelan equine encephalitis virus, anthrax, or botulism-causing bacteria.

LTER sites will continue to be prime areas for new developments in remote sensing. New satellites provide hyperspectral imagery containing hundreds of bands of fine resolution. Such spectral data will allow many hundreds of useful analyses based on combinations of anywhere from 3 to 25 bands. Massive data storage capacity is increasing rapidly and also decreasing in cost. High-performance computing is also developing rapidly, and software is being developed to manage, manipulate, and analyze problems of this scale. The wide array of environmental data at LTER sites will be critical to successful validation of many of these new techniques.

Conclusion

The LTER program of the National Science Foundation expands on the experimental forests of the US Forest Service and the US IBP biome studies of the 1970s. Its unique features are the emphasis on understanding long-term patterns and processes of ecological systems, the long-term funding to carry out its goals, and the data sharing and site comparison activities of the LTER Network. The 24 research sites stretch from the Arctic to the Antarctic and include terrestrial, aquatic, and urban systems. Recently, a cooperating network of International LTER sites has developed. The LTER program's present-day vitality is evidenced by the more than 1100 scientists participating, the more than 10,000 scientific publications since its 1980 beginnings, and the many graduate students and postdoctoral scientists taking part in the program. As the long-term record grows at each site, the LTER program becomes more and more valuable as an observatory for discovering and predicting the ecological effects of climate and land-use changes. Even more valuable than the data sets, however, are the intellectual contributions to ecological and environmental understanding of our world. Many of these contributions are detailed in the six articles that follow.

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