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Long-Term Research on Biosphere–Atmosphere Interactions

DAVID GREENLAND, BRUCE P. HAYDEN, JOHN J. MAGNUSON, SCOTT V. OLLINGER, ROGER A. PIELKE SR., AND RAYMOND C. SMITH

Selected findings from the Long Term Ecological Research (LTER) program are described in the field of biosphere–atmosphere interactions. The Palmer, Antarctic, site contributes evidence to the debate on the ecological effects of increased ultraviolet-B radiation; the ecological response to a warming trend over the past half-century has been clearly documented there. The North Temperate Lakes site in Wisconsin was the principal LTER site for an international study to document a 100-year trend of change in freeze and thaw dates of boreal lakes. A multidisciplinary approach to soil warming studies benefited from observations over decades and demonstrated the importance of initial conditions. The LTER Network permits investigation of atmosphere–ecosystem interactions over a long period encompassing storm events and quasi-periodic climate variability. LTER studies show that ecosystem dynamics often cannot be decoupled from atmospheric processes. Atmospheric processes are an integral component of the ecosystem and vice versa. Finally, we provide an example of how regionalization studies, often grounded in atmospheric data, add a spatial context to LTER sites and identify controls on ecological processes across broader environmental gradients.

Keywords: atmosphere, climate, biosphere, ice, land use

Ecologists and climatologists recognize that climate research has a key role in long-term ecological research. This role arises because climate forcing has a large influence on ecological and hydrological processes at all sites in the Long Term Ecological Research (LTER) Network. Research by LTER investigators has also demonstrated that many biological processes are an integral part of the climate system. Comprehending the ecological consequences of variability in the global climate system requires an understanding of how climate varies and what the potential is for rapid directional change. LTER studies have helped address both of these issues.

Climate research at LTER sites has unique characteristics. First, LTER climate research is focused on sites that have legacies of ecosystem research. Second, the climate research, often oriented to specific ecosystem processes, is performed at sites that have ongoing programs of ecosystem investigation. Third, LTER climate research sometimes occurs at places rarely sampled by national weather observing systems. Climate research is pursued at individual sites and in intersite studies across the LTER Network (4 November 2002; <http://intranet.lternet.edu/committees/climate/>).

Although there have always been strong ties between the fields of ecology and climatology, the connection is often taken for granted or overlooked. Because ecologists have a specific perspective on climate, ecological research often generates climatological information that would not otherwise be obtained. The reverse is also true. The case studies

in this article, and the LTER climate program in general, demonstrate this interplay. Other monitoring studies such as the US National Atmospheric Deposition Network may have certain advantages, but a strength of biosphere–atmosphere interaction investigations at LTER sites is that the study of ecological processes over a long period of time has added value. Although this article focuses on LTER contributions, we cannot claim that all of the results mentioned here would be unavailable without the LTER program. Consequently, in most of the sections below, we guide the reader to an important general review of work similar to the LTER studies described in the section.

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The LTER Network samples a broad range of climates (figure 1). The 24-site network represents about half the possible Köppen classification climate types worldwide (McKnight 1999) and over 80% of the climate types of the North American continent and Puerto Rico. Most sites measure and record meteorological variables hourly. Many sites also use proxy data to provide climate information for longer time periods, sometimes extending through the Holocene and into the Pleistocene geological epochs. The broad range of sites has permitted networkwide investigations into climate variability and ecosystem response (Greenland and Swift 1990), the impact of the El Niño–Southern Oscillation (ENSO) at LTER sites (Greenland 1999), and temporal climate variability (Greenland and Kittel 2002).

LTER sites provide an important opportunity for exploring atmosphere–ecosystem process studies. For example, early results from the Niwot Ridge, Colorado, ongoing experiment in which snow fences are used to enhance snowpack suggested that microbial activity increases in the deeper snow accumulation, because the insulation provided by the enhanced snowpack raises soil temperatures (Brooks et al. 1996). One of the most innovative studies has led to the discovery that lightning-strike data may be used as a proxy for summer precipitation observations at the Sevilleta, New Mex-

ico, site. Researchers at this site developed algorithms that related lightning and precipitation quantity and used lightning location to determine rainfall amount and distribution for areas in New Mexico (Gosz et al. 1995).

LTER sites play an important role as atmosphere–ecosystem observatories. To aid this research, the LTER Climate Committee and the LTER Information Management Committee established ClimDB—an interactive electronically accessible data system for LTER climate data (4 November 2002; <http://sql.lternet.edu/climdb/climdb.html>). Meteorological observations are standardized at LTER sites, but in several instances innovative monitoring devices have been designed to attain more accurate observations than could be achieved with standard National Weather Service equipment. For example, at the Andrews LTER site in Oregon, rain and snow gauges located several meters (m) above the ground are equipped with a variety of windshields and heated orifices to more accurately capture winter precipitation. Heated orifices on the gauges melt snow and ice that would otherwise build up and possibly block the catch of later liquid precipitation. Meteorological observing equipment designed at LTER sites continues to focus directly on particular ecosystem issues, as in the soil warming experiments (Shaver et al. 2000) discussed below. Several LTER sites are associated with important ecotones and as such may be used as observatories to monitor the effect of climate change on vegetation at the biome scale. Hayden (1998a), focusing on the Konza Prairie LTER site in Kansas, used a principal components analysis of floral and faunal species ranges to pioneer a method of relating these ranges to air mass boundaries. He showed quantitatively how the flora and fauna of the Konza Prairie serve as a sensitive indicator for environmental change. In a similar way, changes in location and species composition of ecotones may indicate climate change at the Sevilleta LTER site, where three biomes meet. LTER sites are certain to play a major role in any enhanced biometeorological observing network, such as the proposed National Environmental Observation Network.

The LTER Climate Program is many-faceted. This article emphasizes LTER site-level studies that have contributed to the investigation of global change, climate change and ecosystem experiments, meteorological disturbances and ecosystem dynamics, decadal and longer quasi-periodic behavior in climate and ecosystem dynamics, ecosystem processes within the climate system, and regional climate studies in support of ecosystem modeling.

Global climate change studies

Many LTER climate studies have a direct relationship to some of the more important global climate changes that the world is experiencing. The effects of stratospheric ozone depletion in the Antarctic have been well documented at the Palmer Station LTER site. Warming at the surface of some mid- and higher-latitude locations is exemplified by the shorter duration of lake ice at the North Temperate Lakes (NTL) LTER site in Wisconsin and at other locations.

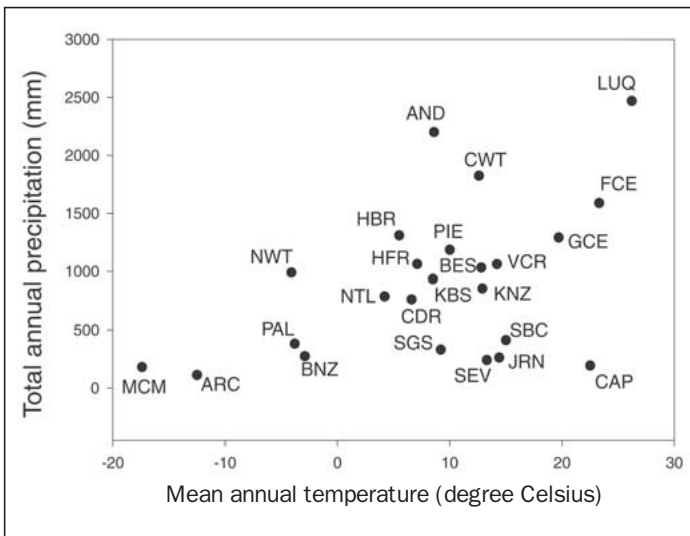


Figure 1. Distribution of LTER sites by annual mean temperature and total annual precipitation (millimeters). Key to sites is as follows: AND, Andrews Forest; ARC, Arctic Tundra; BNZ, Bonanza Creek; BES, Baltimore Ecosystem Study; CAP, Central Arizona–Phoenix; CDR, Cedar Creek; CWT, Coweeta; FCE, Florida Coastal Ecosystems; GCE, Georgia Coastal Ecosystems; HBR, Hubbard Brook; HFR, Harvard Forest; JRN, Jornada; KBS, Kellogg Biological Station; KNZ, Konza Prairie; LUQ, Luquillo; MCM, McMurdo Dry Valleys; NTL, North Temperate Lakes; NWT, Niwot Ridge; PAL, Palmer; PIE, Plum Island Ecosystem; SBC, Santa Barbara Coastal; SEV, Sevilleta; SGS, Shortgrass Steppe; VCR, Virginia Coast Reserve. Data are for the period 1961–1990.

The ocean at Palmer Station, Antarctic. LTER investigators have employed an understanding of time and space variations in the stratosphere and Antarctic waters, radiation transfer theory, remote sensing, and sea-surface and hydrographic observations to provide one of the first pieces of evidence of an ecosystem response to decreasing levels of stratospheric ozone. The decrease of ozone concentrations over the high latitudes of the Southern Hemisphere, commonly called the “ozone hole,” is most marked during the austral spring (Farman et al. 1985). As a result, more ultraviolet-B (UV-B) radiation (280 to 320 nanometers [nm]) reaches the ocean surface. Phytoplankton blooms are found at and near the ocean surface during spring and summer in the Antarctic marginal ice zone (MIZ), the circumpolar, equatorward edge of the pack ice surrounding the continent. The blooms occur near the surface because ice loses some of the salt in seawater during and after freezing; therefore, when the ice melts in the spring, the upper layers of the ocean are stabilized by the meltwater, which is relatively fresh and less dense than the underlying sea water. Consequently algal blooms may be concentrated and restricted to the near-surface waters of the MIZ, and these blooms proceed southward with the retreating ice edge. Palmer LTER investigators (Smith et al. 1992) directly measured the increase in and penetration of UV-B radiation into Antarctic waters and provided the first conclusive evidence of a direct ozone-related effect on a natural population. Higher UV-B levels within the ozone hole were consistently associated with a 6% to 12% reduction of water-column production (figure 2; Smith and Cullen 1995). Recent reviews of the influence of enhanced ozone-related UV radiation on aquatic ecosystems are given by Häder (1997) and de Mora and colleagues (2000).

Further work has shown that because of complex interactions, an assessment of UV-B effects across Antarctic ecosystems requires experimentation on the ecosystem as a whole. The work demands a concurrent effort toward understanding the overall role of UV-B within the context of environmental and biological forces that drive the Antarctic marine system. Many large areas of uncertainty remain, including the possibility that in enhanced UV-B situations, changes in species composition might be a more important change to the ecosystem than a decrease in total primary productivity (Worrest et al. 1978, Vernet and Smith 1997). In addition, Palmer investigators have used SeaWiFS (Sea-viewing Wide Field-of-view Sensor) satellite data to extend their observations seasonally and regionally; they have found that the temporal and spatial variability of biomass is much larger than previously had been thought (Smith et al. 2001). This variation makes it difficult to separate direct climate effects on ecosystems from the effects of increased UV-B. For these reasons, the ecological significance of enhanced UV-B continues to be debated. In contrast, the ecological response to a statistically significant warming trend in the western Antarctic Peninsula region over the past half-century, with corresponding reduction in sea-ice extent, has been demonstrated at all trophic levels (Smith and Stammerjohn 2001).

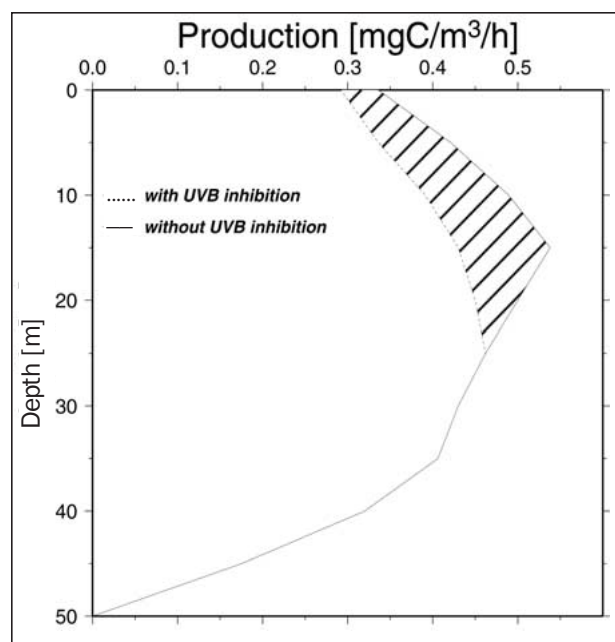


Figure 2. Average values for in situ phytoplankton productivity (milligrams of carbon per cubic meter per hectare) versus depth (meters) within the marginal ice zone of the Bellinghausen Sea in austral spring of 1990. Comparison of productivity inside the ozone hole (poleward of an isoline of stratospheric ozone levels < 200 Dobson units) with productivity outside the hole (equatorward of an isoline of stratospheric ozone levels > 300 Dobson units). Higher ultraviolet-B (UV-B) levels (inside the ozone hole) are consistently associated with reduced (dotted-line curve) levels of production. Integration of these curves shows that higher UV-B levels within the ozone hole lead to a reduced water column production (6% to 12%). Reprinted with permission from American Geophysical Union.

North temperate and boreal lakes and streams. LTER investigators at the North Temperate Lakes site have analyzed data on the duration of ice cover on lakes and streams to better understand the role of climate change and variability in driving temporal dynamics of lake ecosystems (Magnuson et al. 2001). The first data on freeze and breakup dates recorded by residents of Madison, Wisconsin, for nearby Lake Mendota (figure 3) started in 1853. The time series for this LTER lake has depended on at least five generations of direct human observation.

The long-term linear slopes from 1853 to 2000 are for later freeze (7 days later per century) and earlier breakup (9 days earlier per century) (Magnuson 2002). These circa 150-year trends explain 6% to 11% of the variation; the remainder is explained by interdecadal and interannual variation, as well as by measurement error and chance events associated with the passage of weather fronts, such as wind and precipitation. The 20-year duration of the LTER program is too short



Figure 3. Photograph of the ice breaking up on Lake Mendota, Wisconsin, in the spring of 2000. Photograph: J. J. Magnuson.

to observe the slower drivers of climate change. With regard to Lake Mendota data, Wynne (2001) has pointed out that when successive 20-year and 50-year windows are analyzed across 100 years of breakup dates, the slopes oscillate from negative to positive, in a quasi-sinusoidal pattern, between trends of earlier breakup and later breakup.

Even though we know that large-scale climate drivers influence Lake Mendota's dynamics, multiple sites are needed to provide the spatial context for more regional or global perspectives. To provide a larger spatial context, the NTL LTER site formed a Lake Ice Analysis Group with international colleagues who had, or were familiar with, other long-term time series of data on lake and stream ice throughout the Northern Hemisphere. The Global Lake and River Ice Phenology Database (4 November 2002; <http://nsidc.org/data/g01377.html>) contains 748 sites, of which 170 have data records longer than 50 years and 28 have data records longer than 100 years.

Some of the variation and patterns in the time series of lake and stream ice phenology are correlated with large-scale climate drivers such as ENSO and the interdecadal oscillations in the strength of the Aleutian Low (a low-pressure center near the Aleutian Islands) and the North Atlantic Oscillation (NAO, the normalized pressure difference between a station in the Azores and one in Iceland). The drivers of these dynamics often originate at great distances from the lake or stream under consideration, but the effects of the drivers are not consistent across the Northern Hemisphere. For example, in recent decades Lake Mendota ice breakup has occurred earlier in the year following the onset of El Niño (Anderson et al. 1996). This pattern was strong from 1940 to 1995 for Lake

Mendota and other lake and stream ice sites in North America, but from 1900 to 1940 the pattern was reversed, with El Niños being associated with later ice breakup (Robertson et al. 2001). The correlation of breakup date with NAO and the Pacific–North American (PNA) pattern varies among sites and between North America and Europe (Livingstone 2001). The relation to the PNA pattern was stronger at latitudes due east of the North Pacific and in North America than in Europe (Benson et al. 2001).

The longer-term trends noted above for Lake Mendota are also apparent around the Northern Hemisphere (figure 4; Magnuson et al. 2000). Thirty-seven of the 39 records change in the direction of later freeze or earlier breakup. On average, the freeze date was 5.7 days per 100 years later, and the breakup date was 6.3 days per 100 years earlier between 1846 and 1995. Thus, the long-term trends seen for Lake Mendota were characteristic for lakes and streams around the Northern Hemisphere. The long-term trends in dates translate to an increase in air temperature of about 1.2 degrees Celsius (°C) per 100 years (Magnuson et al. 2000).

Therefore, lengthening the extent of the record and examining different sublengths of it can reveal patterns and trends not apparent from short-term data sets. The ice phenology data allow analyses of long-term, 100- to 150-year trends and shorter interyear and interdecadal dynamics; they allow analyses of the spatial consistency and, conversely, the spatial heterogeneity of response over broad regions (Magnuson et al. 2001, Magnuson 2002).

Possible future conditions, however, must come from model simulations rather than observation. Not surprisingly, ice cover is expected to continue declining as greenhouse gases increase. Simulations indicate that a doubling of greenhouse gases could be associated with a decline in ice duration on small inland lakes in the Great Lakes region of 1.5 to 2 months (Stefan and Fang 1997, Fang and Stefan 1998). For the Laurentian Great Lakes (i.e., Lakes Erie and Superior) simulation study, the duration of cover is projected to decline 10% to 52% by 2030 and 33% to 88% by 2090 (Lofgren et al. 2002).

Atmospheric change and variability and ecosystem experiments

Although the investigations discussed above document atmospheric change and ecosystem response, many LTER sites are engaged in manipulative experiments designed to investigate some of the possible future ecosystem responses to projected continued climate change. Some sites, such as the Shortgrass Steppe (SGS) LTER site in Colorado, are directly examining the effects of enhanced carbon dioxide (CO₂) concentrations on their ecosystem. At the Niwot Ridge site, as mentioned above, investigators are undertaking a snowpack enhancement experiment. The responses that ecosystems might have to soil warming are being investigated at several LTER sites.

Soil warming studies at LTER sites make a unique contribution in several ways. With a multidisciplinary approach, the

whole ecosystem can be studied, and with long-term funding, changes can be observed over decades. Results from the variety of sites also led to the realization that the initial conditions at a site are extremely important in controlling what might happen when the soil is warmed. Shaver and colleagues (2000) point out that examining the effects of soil warming is a more complex problem than anticipating the effects of increased ambient CO₂ alone, because higher temperatures affect virtually all chemical and biological processes, not just a limited subset of processes.

One important issue is that response to warming in already cold environments is anticipated to have different effects on the net flow of carbon (C) to either the ecosystem or the soil as time progresses following the warming. Experiments at the Harvard Forest LTER site in Massachusetts show that, immediately after warming, there is a rapid oxidation of the labile C pool by decomposing organisms and a consequent net C loss from the ecosystem. During the second stage of the response, a redistribution of nitrogen (N) results in net C storage in the ecosystem, although there is a loss of soil C (Rastetter et al. 1997). In the third phase, N pools in the soil decrease, such that little N can be redistributed from the soil to the plants. At this stage, the ecosystem may have a net loss of C because of increased respiratory losses from plants and soils. Interesting from the climatic point of view, the hurricane studies at Harvard Forest suggest that this decline might be reversed if trees are felled during disturbances such as a hurricane and the dead biomass is later decomposed.

A somewhat similar overall temporal pattern of C budget response to warming occurs at the Arctic Tundra LTER site in Alaska (Shaver et al. 2000), but with the phases having different lengths and being highly sensitive to soil moisture availability. This similar temporal pattern occurs only when the soil moisture does not change markedly. At the present time, decomposition and N mineralization are strongly limited by the low soil temperature and high soil moisture in the arctic tundra. An increase of soil organic matter turnover attributable to increased warming results in net C storage in the ecosystem, except that in water-saturated soil conditions the response is minimized. In the Arctic, the response to warming in the first 1 to 3 years is a decrease in net ecosystem production (NEP) because of increased respiration. In phase two (3 to 10 years after warming), net primary production (NPP) increases. Finally, it is anticipated that NEP returns to near zero after about 50 to 100 years, because the increase in NPP leads to increased litter production and a higher heterotrophic respiration rate. However, a warming when soil moisture is low in this environment will cause a long-term loss of both C and N because of large increases in respiration, combined with losses of N by drainage from the system.

Meteorological disturbances and ecosystem dynamics

One advantage of continuous long-term monitoring at LTER sites, in many cases backed up with past meteorological and ecological observations, is that the effects of meteorological

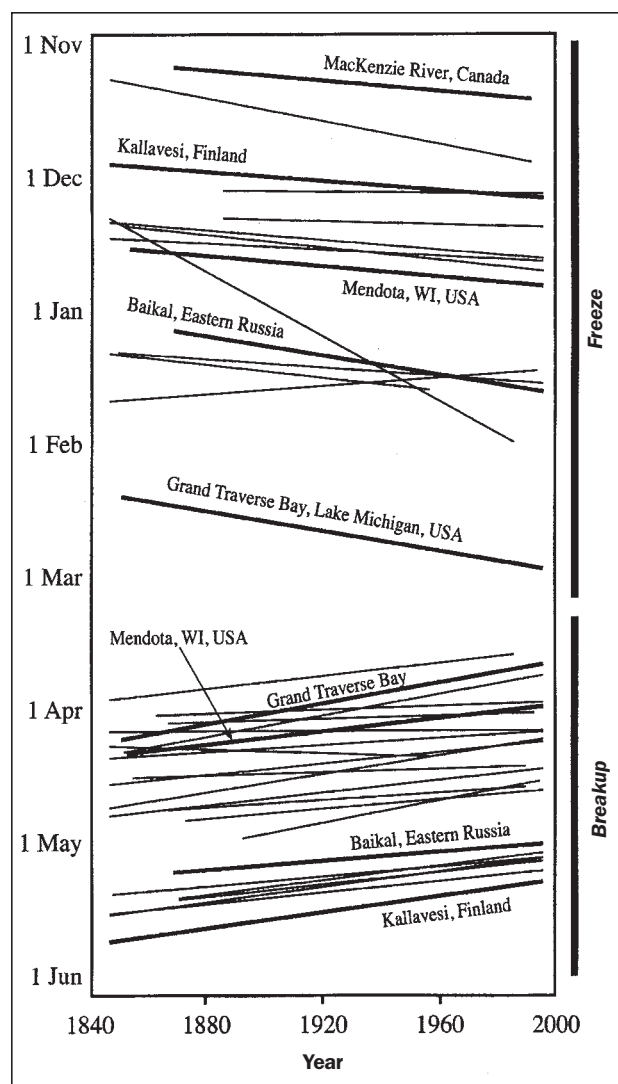


Figure 4. Linear trends of ice freeze and breakup dates from lakes and streams around the Northern Hemisphere. Several sites are identified on the figure. The others are, in Canada: Miramichi and Red Rivers and Toronto Harbor; in Minnesota: Detroit, Osakis, and Minnetonka Lakes; in Wisconsin: Monona, Rock, and Geneva Lakes; in New York: Oneida, Otsego, Casenovia, and Schroon Lakes; in Maine: Moosehead Lake; in Finland: Torionjoki River and Vesijärvi, Paijanne, and Näsi-järvi Lakes; in Switzerland: Lej da San Murrezzan Lake; in Russia: Angara River; and in Japan: Lake Suwa. Reprinted with permission from the Intergovernmental Panel on Climate Change, World Meteorological Organization. The figure is from Gitay and colleagues (2001), modified from data in table 1 of Magnuson and colleagues (2000).

disturbances on ecosystem dynamics are open to intensive investigation. A variety of such meteorological disturbances have occurred during the more than 20-year history of the LTER program. A 100-year rainfall event (an event that could

be expected to occur in 1 year out of 100) filled a playa at the Jornada LTER site in New Mexico with over 1 m water. A flood at the Andrews LTER site was so severe that stream erosion uncovered wood more than 44,000 years old. Some frequent disturbances have been the hurricanes and winter storms on the East Coast.

Currently nine LTER sites in the Caribbean and the US East Coast are well positioned to observe tropical storms that make landfall. Three LTER, or former LTER, sites have been directly affected by tropical storms. Hurricane Hugo passed over the Luquillo, Puerto Rico, site and the North Inlet, South Carolina, site in September 1989, and Hurricane Opal passed over the Coweeta, North Carolina, site in October 1995. Current sites provide opportunities for observation of a range of ecosystems, including tropical and temperate forests, several coastal barrier islands and wetlands, and an urban site.

LTER hurricane studies have yielded many specific results. Stream water export of potassium and nitrate ions increased markedly after Hurricane Hugo and remained elevated for 18 to 24 months, until the canopy leaf cover returned. Other ions were much less affected (Schaefer et al. 2000). Luquillo investigators concluded that biogeochemical cycling in this forest is resilient to hurricane damage, or at least that there is a damage threshold for biogeochemical cycling that has not been crossed recently. (See Turner and colleagues [2003] for their review and discussion of many of the other findings from the LTER Network with regard to tropical storms as disturbance factors.)

Winter storms have large effects on East Coast LTER sites as well. The 35 to 40 winter extratropical storms that pass off the coast of Virginia each year are of sufficient magnitude to result in a reworking of the sands of the barrier islands of the Virginia Coast Reserve (VCR) LTER. Of these, about one-third generate waves and storm surges of sufficient magnitude to drive sand across the beach zones and into the interior of the islands. The frequency of such overwashes of sand varies along the coast and with distance inland. In fact, Hayden and colleagues (1995) found that the frequency and intensity of coastal storms controlled the zonation of plant species typical of barrier islands. In addition, investigators established that the higher elevation of sands on the islands caused by the inland movement of beach sands during storms determined the magnitude of the freshwater resources within the islands, and thus the degree of development of terrestrial vegetation communities.

As beach sands are driven across the island or lost to the offshore zone during large storms, the beach may become eroded. The rates of change of the shorelines of each of the VCR barrier islands have been estimated from 1949 to the present using aerial photographs; survey charts extended the estimates back to the 1850s. The trends in erosion and accretion (land buildup) of the Virginia coast have not been constant over the last 150 years. For the period of aerial photographic record, Fenster and Dolan (1994) found that currently eroding reaches of the Virginia coast were accreting before the late 1960s.

Studies of other Atlantic coast beaches from Florida to Long Island confirmed this observation from the VCR LTER site; the average date of the change from accretion to erosion or vice versa was 1967. Its great geographic extent indicates that the change was not a local phenomenon but rather a large-scale event, probably related to historical changes in storminess. Studies of the period from 1850 to 1949, when only survey charts are available for analysis, indicate that previous reversal of the erosion–accretion pattern of the shorelines of Hog Island (Virginia), Cape Hatteras (North Carolina), and New Jersey occurred in the 1870s. It appears, therefore, that there has been a century-long, quasi-periodic behavior in the sedimentary dynamics of Atlantic coast barrier islands (Fenster and Dolan 1994). At the present time, about one-third of the US Atlantic coastline is accreting and two-thirds is eroding. Geomorphological studies at the VCR site indicate that at least three other reversals in erosion happened before the 1850s.

Quasi-periodic behavior in atmospheric and ecosystem dynamics

The VCR studies show that the frequency of individual meteorological events may itself have longer-term, quasi-periodic behavior. The long-term direct and proxy measures of these events have been examined at a number of LTER sites.

While investigating the climate of the H. J. Andrews Forest LTER site, Greenland (1996) found an apparent relationship between quasi-periodic behavior of atmosphere and ecosystem dynamics in relation to Coho salmon. When temporally smoothed data are used for the period 1925–1985, there is a close inverse statistical relationship, acting on an interdecadal time scale, between the Andrews site air temperatures (which represent temperatures in the Pacific Northwest) and Coho salmon catch off the coasts of Washington and Oregon (figure 5). A cascading set of events has been suggested to explain this finding.

A five-level cascade starts at the first level with a coupled ocean–atmosphere variability now called the Pacific Decadal Oscillation (PDO). The two major modes (in this context typified by a deep, extensive, well-developed Aleutian low pressure zone and the opposite) of the PDO affect air circulation over the northeast Pacific Ocean. This circulation change leads to changes in the direction of the winds (level 2 of the cascade) in the area and the intensity of the ocean currents (level 3 of the cascade). It is the changes in wind direction that give rise to the changes in the air temperatures of the Pacific Northwest. The air temperatures are a byproduct in this cascade and have little to do with salmon catch. It is hypothesized that the operation of the ocean current leads to the provision of greater or lesser amounts of nutrients, and therefore greater or lesser amounts of C and energy are passed along the food chain (level 4 of the cascade); eventually the result is a variable abundance of salmon and subsequent salmon catch (level 5 of the cascade). There can be several more levels in this cascade, depending on the degree of detail in which the food chain is resolved. It remains to be seen how robust this rela-

tionship is over extended periods of time. Updates of and the context for this work have been given by the leaders in this research area at the University of Washington (Mantua et al. 1997, Francis et al. 1998).

A variety of proxy climatic data extending over several centuries illuminated linkages at the Sevilleta LTER site between quasi-periodic behavior in climate and ecosystem dynamics (Betancourt et al. 1993). Tree-ring and pack rat-midden analysis indicated that widespread piñon pine mortality may be attributed to a severe drought between 1942 and 1957, the most extreme drought at the site during the past 400 years. Infrequent “killer” droughts like those of the 1950s reset demographic clocks in woody perennials; broadscale mortality is eventually followed by surges in recruitment. The structure and composition of any southwestern woodland and shrubland reflects in part the time elapsed since the last catastrophic drought.

The Sevilleta LTER site provides an interesting laboratory to study the long-term interaction of ENSO-scale (2- to 7-year) and PDO-scale (10- to 30-year) climatic events. For example, the drought of the 1950s was broken by the rains of the 1958 El Niño. Following the PDO shift to more El Niño-like (wet) conditions in 1976, and coincident with generally warmer springs, an unprecedented surge in tree-ring expansion is evident within millennia-length chronologies at the highest elevations, as is vigorous tree recruitment at all elevations (Swetnam and Betancourt 1998). Research at this LTER site and elsewhere in the Southwest has also begun to connect wet years, when vigorous vegetative growth provides more food for rodents, to an increase in associated parasites and pathogens, including smallpox, plague, and, more recently, hantavirus (Parmenter et al. 1999, Yates et al. 2002).

Swetnam and Betancourt (1998) have demonstrated that ecosystem responses to climate variability are sometimes surprising. For example, mesoscale fire activity in the Southwest does not simply correlate with drought; instead, wet conditions and the lag between climate and fuel production are also involved. Another surprise is that outbreaks of western spruce budworm generally do not occur during droughts; instead, they coincide consistently with wet periods. Swetnam and Betancourt (1998) note the importance of reconstructing, observing, and assessing ecological processes and patterns at meso- (regional) scales and over centuries-long time periods. They argue that ecological synchronicity at these scales is the hallmark of climatic effects on ecosystems and a key to separating cultural from natural causes of environmental change. No matter how difficult, the regional climatic signal needs to be extracted before variations in ecosystem components can be attributed to other causes or biocomplexity can be evaluated. Betancourt and colleagues (1993) also show how the 1950s drought and its impacts provide a tracer—a regional perturbation that cascades from one scale to another.

Ecosystem processes within the climate system

It is not only the effect of climate on ecosystems that is of interest to LTER scientists. It is becoming increasingly obvious

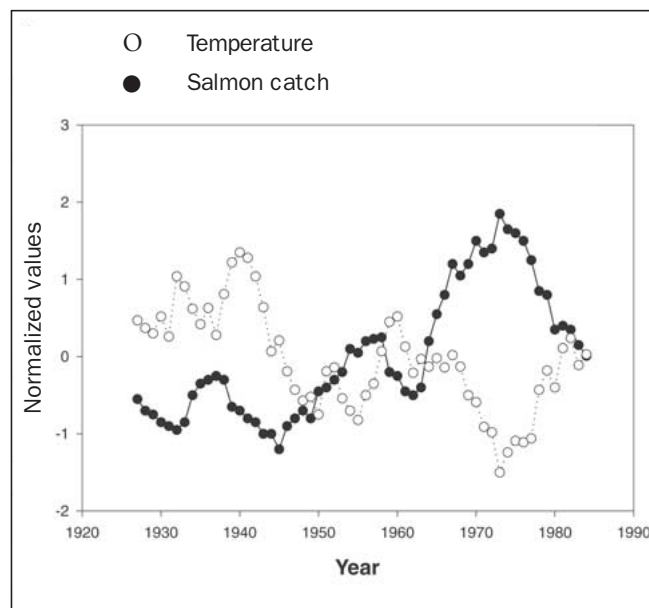


Figure 5. Five-year moving average of annual mean temperature at the H. J. Andrews LTER site (open circles) and 7-year moving average of Coho salmon catch off the coast of Washington and Oregon (filled circles). Reprinted with permission from the California Department of Water Resources. Salmon data are from Frances and Sibley (1991).

that the biosphere plays important roles in working as an integral part of the climate system. This may be seen in the effect of landscape heterogeneity on the overlying atmosphere, as well as in the role of biogenic emissions in temperature change. Both of these examples emerge from LTER–NSF-funded work, in part related to the efforts of the LTER program to place its individual LTER site studies into their respective regional context.

Recent studies have documented the role of landscape heterogeneity in organizing atmospheric wind circulations, including preferential locations of thunderstorms (Pielke 2001). The reason for this organization involves the spatial variations of heating and cooling of the land surface. Such variations include differences in the amount of solar irradiance absorbed at the surface, the rate of long-wave irradiance to space, and the relative magnitudes of sensible and evaporative fluxes of water vapor into the atmosphere. Each LTER site has such variations in surface energy and moisture budgets. These variations also explain the spatial differences in geochemical trace-gas fluxes (Eastman et al. 2001a, 2001b, Lu et al. 2001).

The spatial variation in land use and in greenness has been extensively studied around the SGS LTER site (figures 6, 7). Aircraft and balloon observations at selected locations across this region (Segal et al. 1989) document the profound influence of these variations in landscape on atmospheric structure. The introduction of irrigation in this region has altered the weather patterns over the SGS site even though that site is predominately a native shortgrass area (Stohlgren et al.

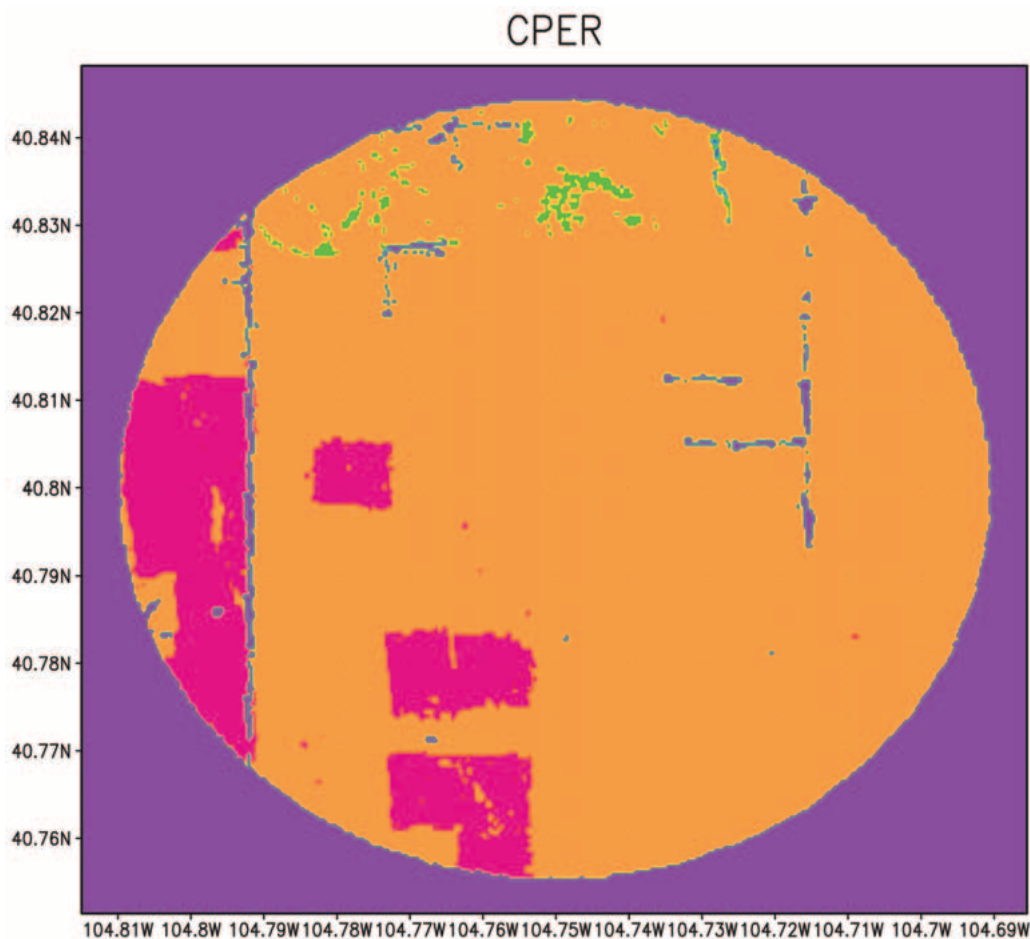


Figure 6. Five-kilometer radius circle of 30-meter resolution land-use data for the Shortgrass Steppe (SGS, formerly CPER) climate-observing site. The orange is shortgrass, the magenta is cultivated crops, the blue is residential, and the green is groves of trees. Reprinted with permission from Capt. James R. Hanamean (Hanamean 2001).

1998). Rainfall and cloudiness appear to have increased in this region as a result of the additional water supplied to the atmosphere through transpiration from the irrigated land. Eastman and colleagues (2001a) have also shown that the removal of bison from the region has resulted in a somewhat wetter and cooler summer environment. The absence of bison grazing and the consequent greater aboveground biomass result in a greater fraction of the turbulent fluxes occurring as latent heat, which has a cooling and moistening effect on the air, as opposed to sensible heat flux.

In the winter, the variation in landscape also has an effect on the region's climate. Segal and colleagues (1989) have shown that the height of vegetation relative to the depth of snow cover significantly influences temperatures and atmospheric boundary layer depth. For instance, when snow completely covers the vegetation, most of the impinging sunlight is reflected into space. Temperatures in the air above the snow are relatively low. In contrast, when vegetation extends well above the snow, the albedo is lower and more of the sun-

light is absorbed. The air above the snow and protruding vegetation is therefore somewhat warmer.

Weather may be altered as a result of a conversion of earlier natural landscape heterogeneity to the current landscape. As shown in the study by Pielke and colleagues (1999), the generation of different local circulations over south Florida and an aggregate change in the heat energy, moisture, and trace gas fluxes associated with the current landscape have produced an altered climate over the Everglades National Park, the location of the Florida Coastal Everglades LTER site, even though the park itself is relatively unchanged (figures 8, 9). Over northern Alaska, Sturm and colleagues (2001) made a suggestion, not yet confirmed by LTER studies' longer-term data, that recent landscape changes may include an increase in shrubs. The distribution and amount of shrubs in this region control the distribution of drifted snow and its subsequent snowmelt evolution in the spring (Liston et al. 2002). In the central grasslands of the United States, for example, Eastman and colleagues (2001b) used a coupled atmospheric-

biophysical model to show that a doubling of CO₂ could lead to cooler maximum and warmer minimum warm-season temperatures. The effect of enhanced CO₂ on the vegetation, including its feedback to the atmosphere, was on the same order as that associated with the conversion of the natural landscape in the region to the current landscape.

One conclusion from these studies is that ecosystem dynamics cannot, in general, be decoupled from atmospheric processes. The atmospheric processes are an integral component of the ecosystem and vice versa. Indeed, climate is similarly an integration of effects across land, ocean, continental ice, and atmosphere interfaces (Pielke 1998). Neither a current climate assessment nor a proper assessment of the predictability of future climate will be possible unless climate and the ecosystem are considered as intimately related earth-system processes. The interdisciplinary nature of the LTER projects helps to ensure that this intimate connection remains in focus. Kabat and colleagues (2002) give a comprehensive review of the influence of land surface processes on weather and climate, which includes work that is not part of the LTER effort.

Most of the feedbacks on the atmosphere described above are associated with mass and energy fluxes from the biosphere into the atmosphere, but feedbacks may also include the physical and chemical properties of individual molecules released into the atmosphere. In most vegetated landscapes, plants release hydrocarbons (terpenes, hemiterpenes, and aromatics), which are physically and chemically active in the subcloud layer of the atmosphere. They form particulates of a size that scatters light in the blue wavelengths, giving rise to the characteristic blue haze seen in dry, clear air conditions and the milky white haze seen in humid conditions (Hayden 1998b). Both these forms of haze alter the radiation budget of the subcloud layer in the visible and infrared portions of the electromagnetic spectrum (Fuentes et al. 2001). In humid air, the particulates, which become enveloped in water molecules and grow larger, scatter at all wavelengths and thus appear white, as in the haze of the Great Smoky Mountains near the Coweeta LTER site. The condensation of water onto these hydrocarbon particles results in the release of latent heat, which warms the surrounding atmosphere and makes the subcloud layer more isothermal with altitude (Fuentes et al. 2001).

Under dry air conditions at the Central Arizona–Phoenix, Jornada, and Sevilleta LTER sites, and during periods of continental polar air masses at the VCR LTER site, the gaseous hydrocarbons and the particulate hydrocarbons are strong greenhouse gases that result in reduced nocturnal cooling and higher minimum temperatures than would occur under other conditions (Hayden 1998b). Where the atmosphere is humid at night, temperatures fall to the dew-point temperature each night. In vegetated arid regions with dry air, temperatures do not fall to the dew-point temperature, and in fact minimum temperatures may be 10° to 15°C warmer than the dew-point temperature. Over nonvegetated deserts, this failure of nocturnal cooling and elevated minimum temperatures

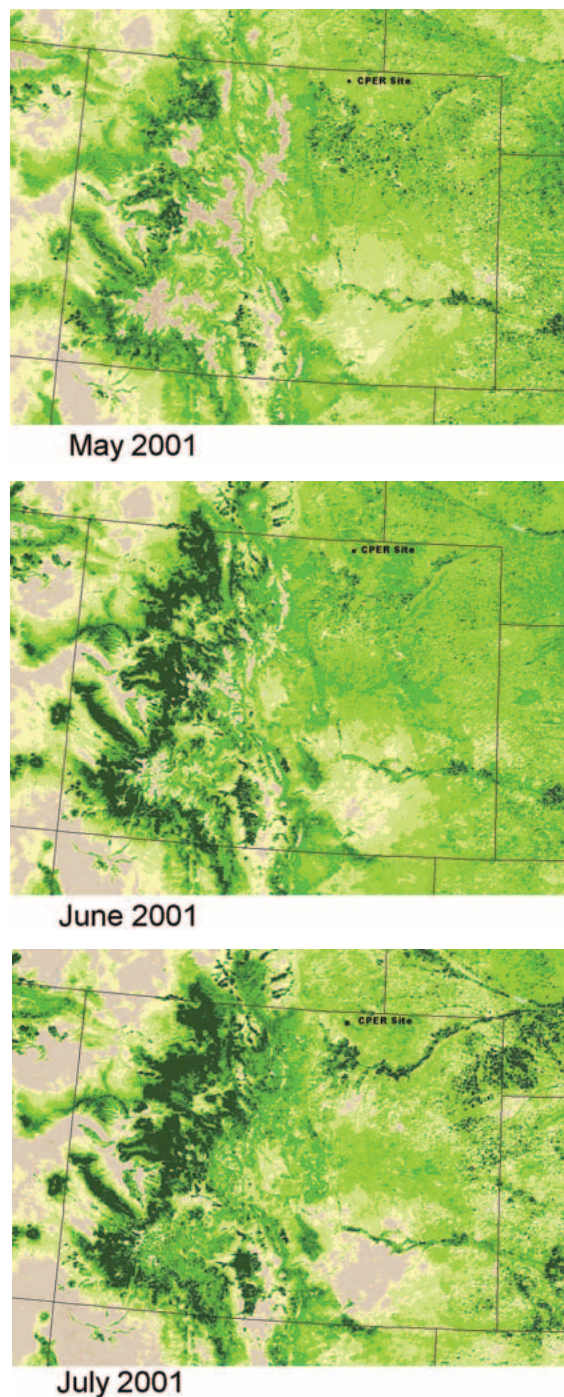


Figure 7. Greenness of the central Great Plains region for the months of May, June, and July 2001. Reprinted with permission from EROS Data Center (Brad Reed).

does not occur, and nighttime low temperatures fall to the dew point. The notion that vegetation plays a role in modulating temperatures in the lower atmosphere is new.

Regional climate studies in support of ecosystem modeling

The preceding sections illustrate the interplay between ecological and atmospheric research in the LTER program. Two

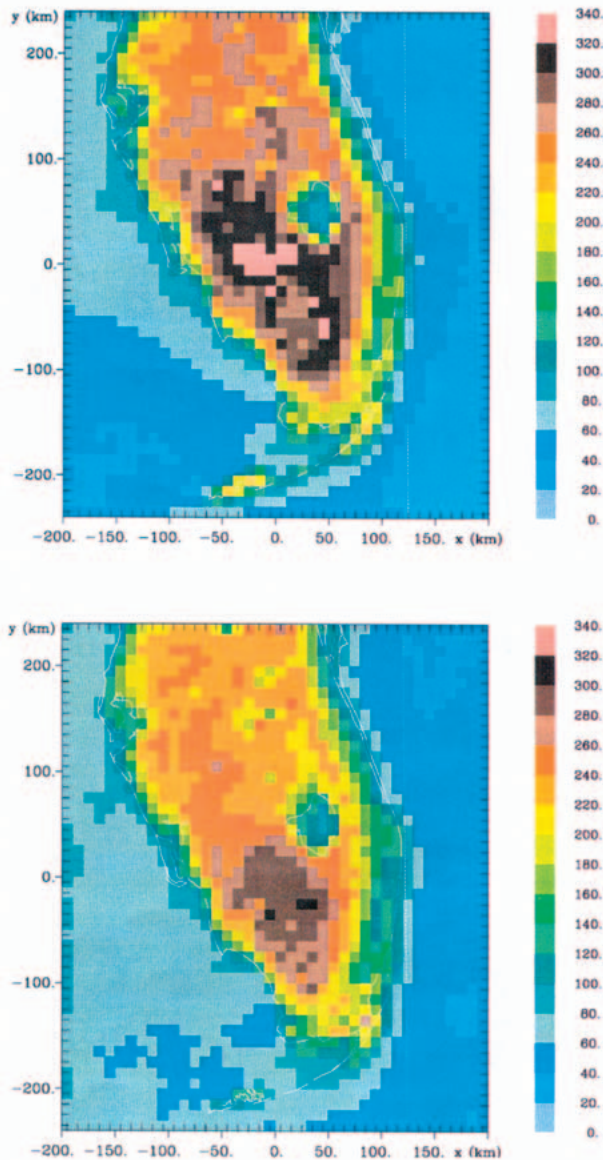


Figure 8. South Florida June–July total convective precipitation in millimeters (mm) for 1900 (top picture) and 1993 (bottom picture) landscapes. The spatially averaged accumulated precipitation over land was 238 mm in 1900 and 213 mm in 1993. Data are from Pielke and colleagues (1999). Reprinted with permission from the American Meteorological Society.

themes that emerge from these discussions are that (1) atmosphere–biosphere interactions occur over spatial and temporal scales that cannot be fully characterized through site-specific research alone, and (2) our appreciation for the degree to which atmosphere–biosphere interactions are truly interactive has probably just begun. As our understanding of these interactions grows, another contribution of the LTER program will be to take on an increasingly important role in support of ecosystem modeling through long-term climatic and ecological data collection.

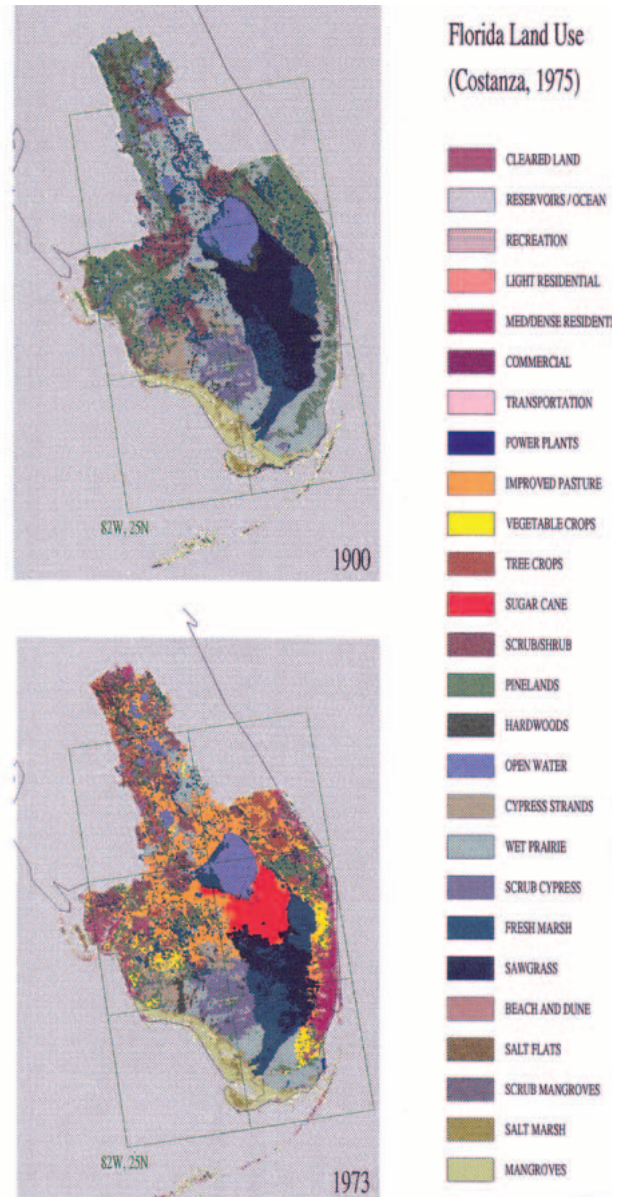


Figure 9. The spatial distribution of land use and its change from 1900 (top picture) to 1973 (bottom picture). Reprinted with permission from Robert Costanza (Costanza 1975).

The synthesis of LTER data into process-based ecosystem models is important, because models can offer a productive means of extending site-specific knowledge across broader spatial and temporal scales (e.g., Burke et al. 1990, Coops and Waring 2001, Rastetter et al. 2003). Regionalization was the theme of the 1993 LTER All Scientists Meeting; a primary goal established at that meeting was the need for regional-scale climate and environmental data sets. Regionalization studies conducted since then have added a spatial context to LTER sites and have helped to identify controls on ecological processes across broader environmental gradients.

One example of such an effort is the development of the PnET ecosystem models (a suite of three nested computer models that simulate C, water, and N dynamics of forest ecosystems), which have drawn heavily on work from the Harvard Forest and Hubbard Brook LTER sites (e.g., Aber et al. 1995, 1997). Extension of these models to the Northeast has been made possible by directly comparable analyses of the region's physical and chemical climate (Ollinger et al. 1993, 1998). Temperature and precipitation patterns have been evaluated using regression analysis of long-term weather station data against geographic coordinates and elevation. The resulting trends indicate seasonally shifting gradients that reflect latitude and distance from the seacoast, while elevation coefficients reflect orographic effects and environmental lapse rates.

Similarly, regional patterns of atmospheric N deposition were evaluated using data from atmospheric deposition and air quality monitoring networks. For wet deposition, spatial patterns of ammonium and nitrate concentrations in rain and snowfall were combined with regional estimates of amount of precipitation. For dry deposition, gradients of particulate ammonium and nitrate, as well as nitric acid vapor, were combined with deposition velocity estimates to yield a dry deposition flux. Across the northeast, wet N deposition exhibited a clear west- to-east gradient, declining from western New York to Maine. Dry deposition exhibited an equally clear trend but had a predominantly south to north orientation. These contrasting spatial patterns suggested that the two deposition forms are received in different proportions from different source areas: wet-deposited materials primarily from industrial areas to the west and dry-deposited materials from urban areas along the southern portions of the region. The combination of the two trends produced a southwest-to-northeast gradient in total N deposition, which varied from a high of approximately 14 kilograms (kg) per hectare (ha) per year (yr) in New York's Catskill Mountain region to a low of around 3 kg per ha per yr in northern Maine (Ollinger et al. 1993).

The spatial data that resulted from these analyses provided a means of linking process studies at Harvard Forest and Hubbard Brook to their surrounding regional landscapes. For example, whereas Whittaker and colleagues (1974) and Goulden and colleagues (1996) provided site-specific measurements of NPP and ecosystem CO_2 flux at Hubbard Brook and Harvard Forest, validation of model estimates against those measurements provided confidence in extending simulations to the regional level (Aber et al. 1995, Ollinger et al. 1998). Spatially driven process models can also provide insights into large-scale controls on ecosystem function by facilitating geographically explicit sensitivity analyses that are constrained by known climatic and ecological variation (Schimel et al. 1996). For instance, spatial patterns of predicted NPP in northeastern US deciduous forests were strongly correlated with patterns of annual precipitation (figure 10), suggesting that moisture limitations play a key role in this forest type. In contrast, predictions for conifer forests were more strongly

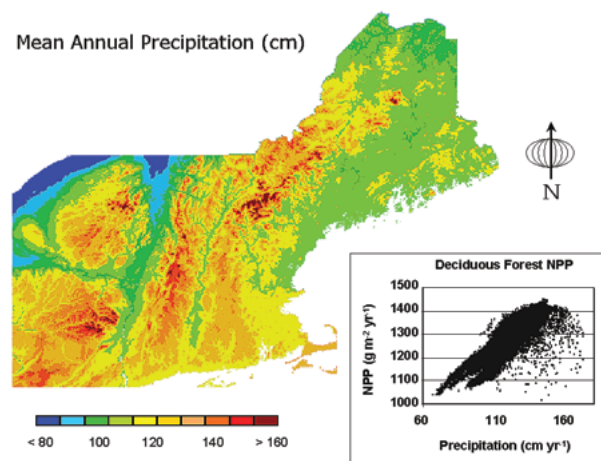


Figure 10. Modeled mean annual precipitation for the northeastern United States for input into the PnET forest ecosystem model. Also shown is the predicted relationship between annual precipitation (centimeters per year) and net primary production (NPP; grams per square meter per year) for areas dominated by deciduous forests, suggesting an important moisture control on growth rates in this forest type. Data points falling off the relationship to the upper right indicate higher elevation areas where temperature limitations become increasingly important. Reprinted with permission from Landscape Ecology, Kluwer Academic Publishers.

related to annual growing degree days (a heat index based on accumulated environmental temperature values), suggesting that energy limitation has a greater influence than moisture availability.

More recent PnET model development has allowed interactive analysis of multiple environmental stress factors as they vary over a region and over historical time (Ollinger et al. 2002). The factors considered include elevated CO_2 , N deposition, tropospheric ozone pollution, and land-use history. Changes in each of these over the past several centuries have been suspected of altering ecosystem functioning, but the potential for positive or negative interactions among them has made it difficult to assess their combined net effect. Here too, a synergy between regional-scale research and long-term site records is evident. Whereas spatial data sets for climate and air pollution have come from regional gradient analyses, the ability to conduct meaningful simulations over historical time periods required reconstruction of long-term records that were available only for LTER sites. This was particularly true in the case of disturbance and land-use history, for which there are few regional data but good local documentation at both Hubbard Brook and Harvard Forest. Harvard Forest has a long agricultural history, whereas Hubbard Brook disturbance has come from timber harvesting.

Careful reconstruction of these records made it possible to perform controlled multifactorial model experiments that compared the effects of varying atmospheric conditions

across these two contrasting land-use scenarios (Ollinger et al. 2002). It appears that, over the past several centuries, increases in atmospheric CO₂ and N deposition have stimulated forest growth and C uptake regionally. However, the degree of stimulation varied for regions where the prior land use was agriculture or forest harvesting. The key process is the long-term effects of each land-use scenario on soil N availability. When tropospheric ozone is included in the analysis, a substantial portion of the potential increases in forest growth caused by CO₂ and N deposition is offset. Collectively, the combined effects of all disturbance and atmospheric factors that were addressed produced present-day growth estimates that were surprisingly similar to estimates obtained in the absence of any form of disturbance. The implication of this finding is that multiple stress factors have been largely compensatory—intact forests may show relatively little evidence of altered growth since preindustrial times, despite substantial changes in their physical and chemical environment.

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