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Long-Term Trends in Ecological Systems:

A Basis for Understanding Responses to Global Change

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Cross-Site Studies “By Design”: Experiments and Observations That Provide New Insights

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In many cases, cross-site comparisons from similar experiments, often with different questions and designs, are conducted after the studies are completed to address new questions that require multiple sites. Here, we describe cross-site studies that are “by design” in which the questions, experimental layout, methods, and measurements included multiple sites from the beginning. Broad-scale questions and patterns can be addressed explicitly in these studies because the experiment or observation network was designed for comparisons among sites that are distributed spatially across one or more environmental gradients. The same design and methods of sampling allow powerful comparisons to be made without assumptions about differences in plot size, number, or sampling frequency and intensity on the results. However, these studies also have limitations:

- All sites need a similar experimental design, which can limit the types of questions that can be addressed.
- These studies typically involve large amounts of resources (time, personnel, supplies) that can limit the number of samples collected.
- Time and travel involved can also often limit graduate student involvement.
- Collaborators are needed at different sites for site selection and design details and to conduct the sampling and interpret the results.
- These studies often take longer to get started because of the coordinated efforts required by many people.

Cross-site studies are well suited to addressing large-scale questions that cannot be adequately addressed with local studies because of the uncertainties associated with extrapolation of results from one site to a much broader area. There has been a recent increase in the interest for large-scale ecological questions driven by the need to predict the consequences of global change on ecosystem functioning (IPCC 2007). Another independent demonstration of the increasing interest in regional- and continental-scale ecology is the emerging National Ecological Observatory Network (NEON) project that will be deployed throughout the continental United States (http://www.neoninc.org).

The objectives of this chapter are to present examples of the kinds of questions and results that require a priori cross-site experiments or observations and to describe new insights provided by these studies that would not have been possible with cross-site comparisons conducted from existing studies.

There are two types of cross-site studies described below: experimental manipulations of drivers or system properties and observations or monitoring of natural or managed ecosystems located along environmental gradients.

Experimental Manipulations of Ecosystems

Ongoing or Completed Cross-Site Experiments

Temperature manipulations. Global warming is occurring as a result of elevated concentrations of carbon dioxide and other greenhouse gases in the atmosphere (IPCC 2007). Regions of particular concern for increasing air temperatures are the Arctic and Antarctic, where ecosystems are dominated by cold-adapted plants and animals. The International Tundra Experiment was designed to study how ecosystems in arctic and alpine tundra respond to experimental warming (http://www.geog.ubc.ca/itex). At present, the project includes 50 sites from 13 countries (including three LTER sites) located in Antarctica (MCM), Asia, Australia, Europe, and North America (NWT, ARC). Each site follows standard protocols for experimental design. Response variables include those at the individual level (for example, height and cover of plants) and at the community level (for example, plant species richness). In one key result, canopy height and cover of deciduous shrubs and graminoids increased with elevated air temperature, and cover of mosses and lichens decreased; species richness and evenness decreased (figure 10-1) (Walker et al. 2006).

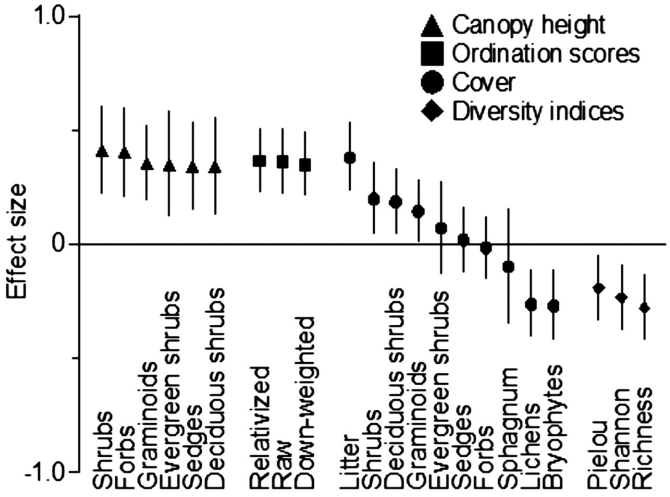


Figure 10-1. Effects of elevated air temperature on alpine and arctic tundra plants at 11 International Tundra Experiment (ITEX) sites. The mean effect size and the 95 percent confidence interval were obtained from meta-analyses of 22 variables (Walker et al. 2006). Reprinted with permission from the National Academy of Sciences, USA.

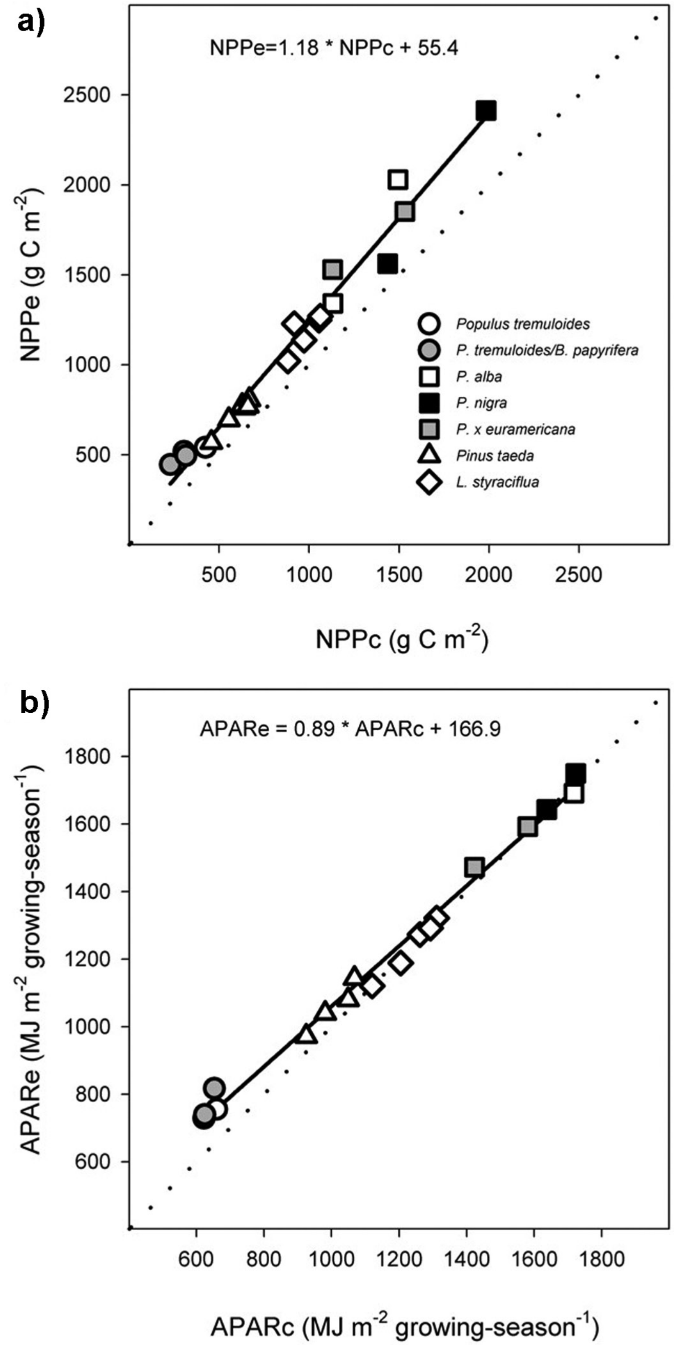


Figure 10-2. Effect of elevated CO2 concentration on forest primary production of seven species at four sites using Free Air CO_2 Enrichment (FACE) technology (Norby et al. 2005). (a) Comparison of forest net primary production at elevated (550 ppm, NPP_e) and current CO_2 concentrations (376 ppm, NPP_c). Regression: $R^2 = 0.97$, $p<0.001$, slope is significantly different from 1. (b) Comparison of absorbed photosynthetically active radiation at elevated ($APAR_e$) and current CO2 concentrations ($APAR_c$). Regression: $R^2 = 0.99$, $p<0.001$, the slope is significantly different from 1. Reprinted with permission from the National Academy of Sciences, USA.

CO_2 manipulations. Effects of increasing atmospheric carbon dioxide (CO_2) on ecosystems is being studied using the Free Air CO_2 Enrichment technology that has been adopted by 30 sites in 16 countries in Australia, Asia, Europe, and North America, including one LTER site (CDR) (http://public.ornl.gov/face/). The technology allows plant and ecosystem responses to elevated CO_2 concentration to be studied under natural conditions. Examples of response variables include plant photosynthesis and respiration and plant and soil nitrogen and carbon dynamics (Nösberger et al. 2006). Recent analyses from four sites showed that the forest's net primary production (NPP) increased at a median of 23 percent at an elevated CO_2 concentration (550 ppm) compared to forests growing under current CO_2 concentration (figure 10-2a) (Norby et al. 2005). The increase in NPP at the lower end of production was due to an increase in the ability of plants to absorb more light, as measured by Absorbed Photosynthetically Active Radiation (APAR), while the increase in NPP at the higher end was due to increase in plants' efficiency in using light (figure 10-2b).

Nutrient manipulations in streams. The Lotic Intersite Nitrogen Experiment (LINX) was designed to examine how hydrodynamic, chemical, and metabolic characteristics of streams control nitrogen uptake, retention, and cycling through the experimental addition of a stable isotope of nitrogen (^{15}N) (http://www.biol.vt.edu/faculty/webster/linx/). Ten U.S. sites participated in LINX 1 (1996 to 2001). During LINX 2 (2001-2006), effects of land use on nitrogen cycling were examined across 72 streams at 9 U.S. sites. Each site measured nitrogen uptake and denitrification rates as well as potential explanatory variables including physical, chemical, and biological characteristics of a stream and rates of stream metabolism by algae and microbes. Streams from agricultural and urban areas were found to contain higher concentrations of nitrate (NO_3^-) than streams from areas with vegetation typical of the biome (figure 10-3a) (Mulholland et al. 2008). The rates of total biotic nitrate uptake, one of two ways of nitrogen removal in streams, were higher in streams from agricultural and urban areas (figure 10-3b), stimulated by the increased nitrate concentrations. However, the nitrate uptake efficiency decreased with increasing nitrate concentration.

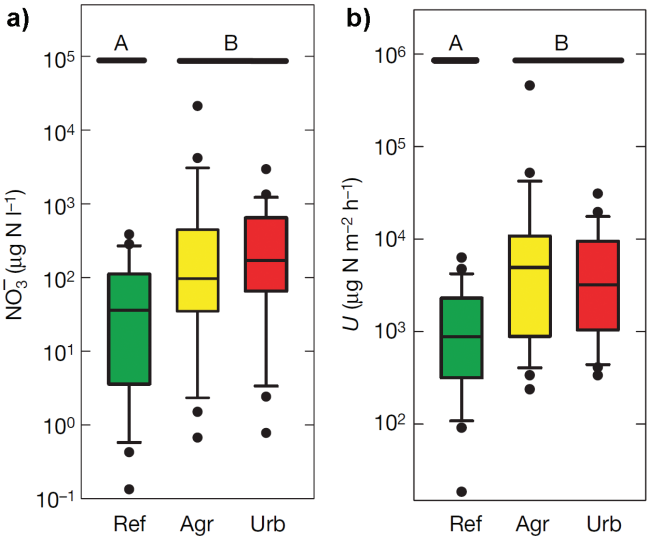


Figure 10-3. Nitrogen in streams located in different areas in the LINX2 project (Mulholland et al. 2008). (a) Nitrate (NO_3^-) concentration. (b) Total biotic nitrate uptake rate. Ref: streams in areas with vegetations typical of the biome; Agr: streams adjacent to agricultural practices; Urb: streams in urban areas. Reprinted with permission from Macmillan Publishers Ltd.

Animal removal. Removal of animals combined with monitoring of environmental variables has been used to investigate interactions among components of ecosystems that show similarities across sites. For example, results of removing seed-eating rodents or ants from desert shrublands were compared with removal of insect herbivores in a tree-dominated system (Brown et al. 2001). Each system was monitored for over 20 years; data recorded included variable precipitation. In the desert site (Portal, AZ), interactions were found among precipitation, food supply, and rodent populations. At the forest site (Sunset Crater, AZ), complex dynamics emerged from the interactions among abiotic stress, dominant tree growth and morality, keystone herbivores, and other trophic levels (Brown et al. 2001).

These results were used as the basis for an ongoing study at three sites in the Chihuahuan Desert: Sevilleta LTER (SEV), Jornada Basin LTER (JRN), and Mapimi Biosphere Reserve near Durango, Mexico (D.C. Lightfoot, unpublished data). The project was initiated in 1993 to experimentally determine how small mammals affect Chihuahuan Desert ecosystems, either grasslands or shrublands, and how small mammals are affected by climate change (http://tierra.unm.edu/projects/chihuahuan-desert-small-mammal-exclosure).

Litter manipulation. Litter decomposition is an important ecosystem process in which biochemical molecules in plants are broken down by microorganisms and made available in simpler forms for uptake by other organisms. The Long-Term Intersite Decomposition Experiment Team (LIDET) studied the effects of substrate quality (species and type of litter) and climate on long-term decomposition and nitrogen accumulation in litter (http://andrewsforest.oregonstate.edu/research/intersite/lidet.htm). Twenty-eight sites from seven biomes, including 15 LTER sites, followed the same methods. Response variables included litter mass, total nitrogen, lignin, and cellulose in material remaining in litter bags. Results during a 10-year period found that net nitrogen immobilization and release from leaf litter in six of the seven biomes depended strongly on initial nitrogen concentration in litter but did not depend on climate, other litter qualities, or local site characteristics (Parton et al. 2007). At high initial nitrogen concentration in leaf litter (1.98 percent), net nitrogen immobilization was close to 0; nitrogen release started when about 60 percent of the mass remained in a litter bag (figure 10-4a). At low initial nitrogen concentration (less than 0.39 percent), net nitrogen immobilization was high, and nitrogen release started when about 40 percent of the mass remained in a litter bag (figure 10-4d).

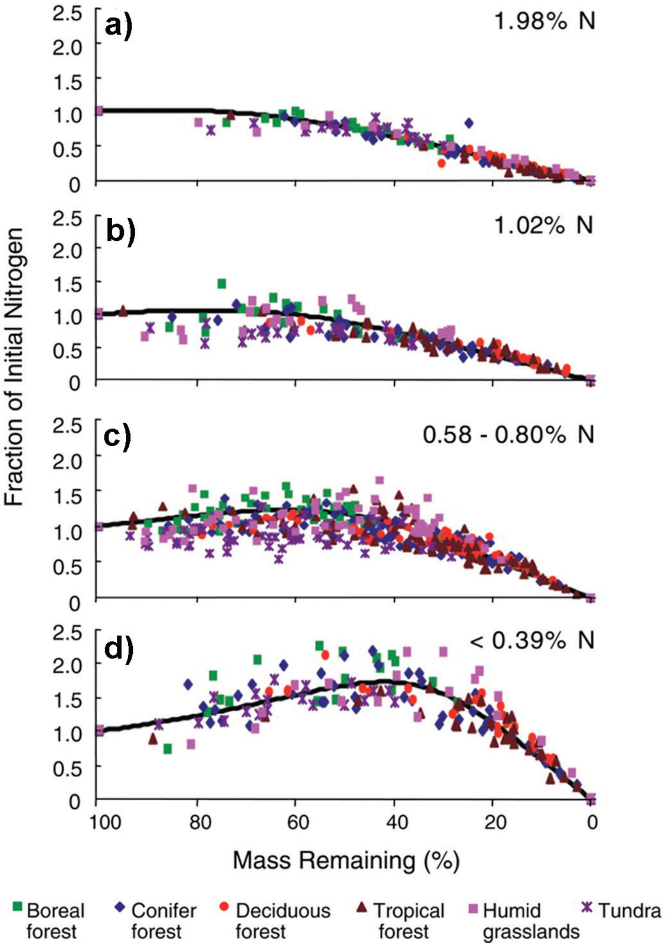


Figure 10-4. Pattern of nitrogen (N) immobilization and release from the LIDET study depends on the initial N concentration of leaf litter, shown as percentage in the upper right corner of each panel (Parton et al. 2007). N immobilization refers to the conversion of N from inorganic (usable by plants and microbes) to organic form (not usable). N release refers to the conversion of N from organic to inorganic form. Values of fraction of initial N > 1 indicate N immobilization while values < 1 indicate N release. Reprinted with permission from AAAS.

Biodiversity manipulations. Long-term studies that manipulated species richness in grasslands at the CDR LTER site found that aboveground net primary productivity (ANPP) and biomass increase as species richness (biodiversity) increases (Tilman et al. 1997, 2001, Reich et al. 2004, Fargione et al. 2007, Fornara and Tilman 2009). Similar biodiversity manipulations were conducted in Europe for eight sites in the Biodiversity and Ecological Processes in Terrestrial Herbaceous Ecosystems (BIODEPTH) project. Results confirmed the patterns found at CDR: ANPP increased as plant species richness increased at seven sites. The effect of biodiversity on production became stronger over time at most sites (Hector et al. 1999, Spehn et al. 2005). However, comparisons across ecosystem types have shown that the relationship between productivity and richness can take a variety of forms (Mittelbach et al. 2001).

New or Developing Cross-Site Experiments

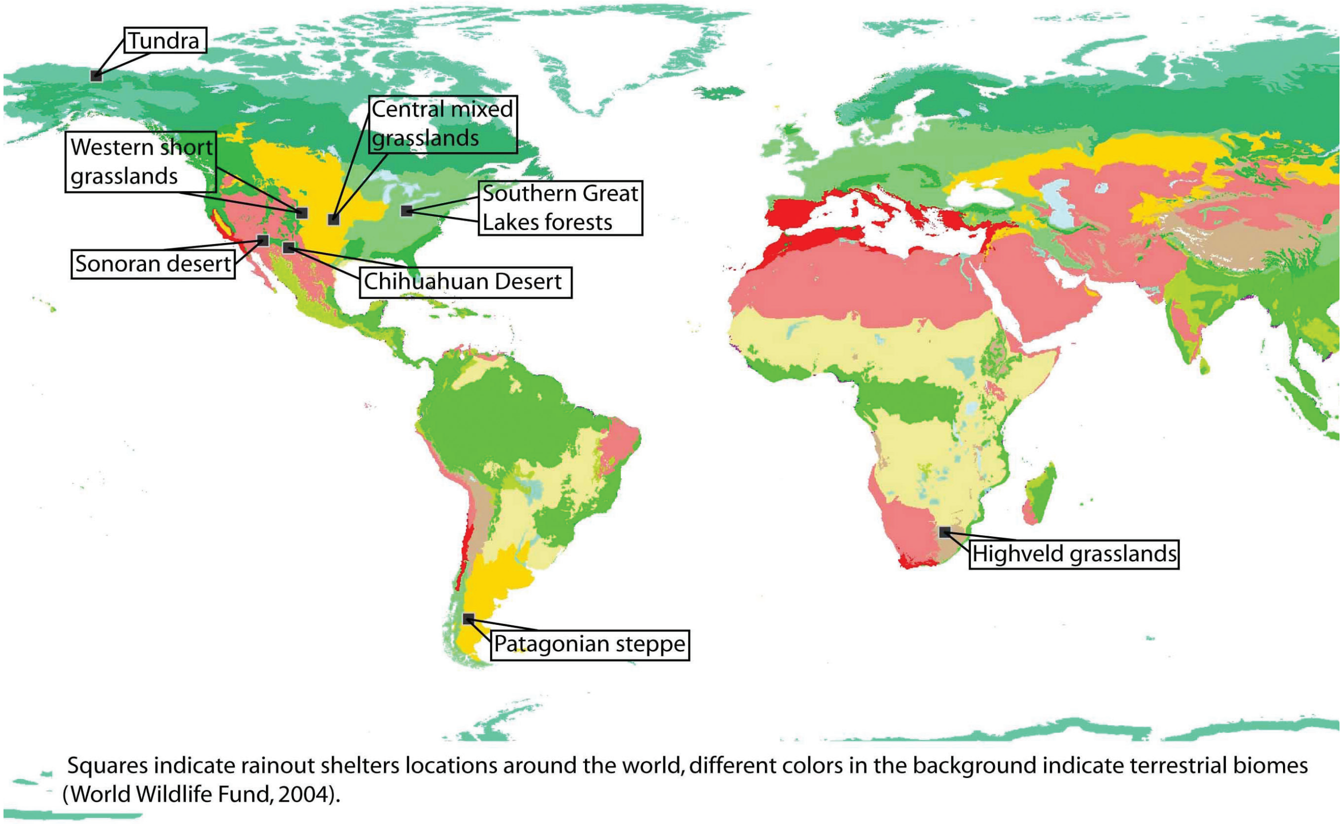
Nutrient additions in grasslands. Nutrient Network is being designed to study the effects of nutrient (nitrogen, phosphorus, and potassium) additions in grasslands (http://nutnet.science.oregonstate.edu/). The research questions are:

- How general is current understanding of productivity-diversity relationships?
- To what extent are plant production and diversity co-limited by multiple nutrients in herbaceous-dominated communities?
- Under what conditions do grazers or fertilization control plant biomass, diversity, and composition?

All sites follow the same experimental protocol and collect similar data (Adler et al. 2011). The project started in 2009 with 52 sites in eight countries in Africa, Asia, Australia, Europe, and North America, including six LTER sites (AND, CDR, KNZ, NWT, SEV, SGS).

Anthropogenic manipulations in streams. A stream experimental and observational network (STREON) is part of the emerging NEON program. This study is expected to examine effects of nutrient loading, species losses, and hydrologic change on the structure and functioning of streams (http://www.neoninc.org/science/experiments). All sites will follow the same experimental protocols. Natural hydrologic events (flood and drought) will be recorded. Biological variables and other variables related to material flux and rates of nutrient transformations and metabolism are expected to be measured (Dodds 2008).

Rainfall manipulations. Rainfall is the most important determinant of ANPP in grasslands, steppes, and deserts (Sala et al. 1988). Manipulations of rainfall are often used to study how systems may respond in the future under altered rainfall regimes (IPCC 2007). Most rainfall manipulations require expensive installations that constrain the spatial extent of the manipulation, the number of replications, and the power of the experimental design (Hanson 2000). An inexpensive rainout shelter design (Yahdjian and Sala 2002) has recently been adopted in many locations around the world, from South Africa and Patagonia to the Alaskan Tundra (figure 10-5), including three LTER sites (JRN, SGS, ARC). These experiments use the same method to manipulate incoming precipitation, although there is not a formal network of rainfall manipulations. Future synthesis of results is expected to provide unique insights into the response of ecosystems to water availability along gradients of temperature and precipitation.



Squares indicate rainout shelters locations around the world, different colors in the background indicate terrestrial biomes (World Wildlife Fund, 2004).

Figure 10-5. Sites using the rainout shelter design of Yahdjian and Sala (2002).

Monitoring of Ecosystems

Ongoing Monitoring Networks

Observations of the environment, such as climate (http://www.ncdc.noaa.gov), atmospheric chemistry (http://nadp.sws.uiuc.edu/NADP/), and human populations (http://census.gov) have been made in the United States over the past century or longer. Data from these networks form the basis for cross-site comparisons in chapters 11 to 14. Here we focus on networks of sites collecting information about ecosystem dynamics in response to these environmental and human drivers.

Carbon dioxide and water vapor fluxes. Two existing networks of sites are collecting data on carbon, water, and energy fluxes. The two networks use different technology to address similar questions.

The Rangeland Carbon Dioxide Flux Project is examining the effect of management practices on the global carbon balance for eight U.S. sites (including one ARS-LTER site: JRN) (Svejcar et al. 1997). The Bowen ratio-energy balance system is being used to measure energy, water vapor, and carbon dioxide fluxes. An analysis of net ecosystem exchange of carbon during 1996-2001 showed that five sites are sinks for atmospheric CO_2 (figure 10-6) (Svejcar et al. 2008). The three sites that are sources of atmospheric CO_2 are in the Great Plains and Southwestern deserts of the United States.

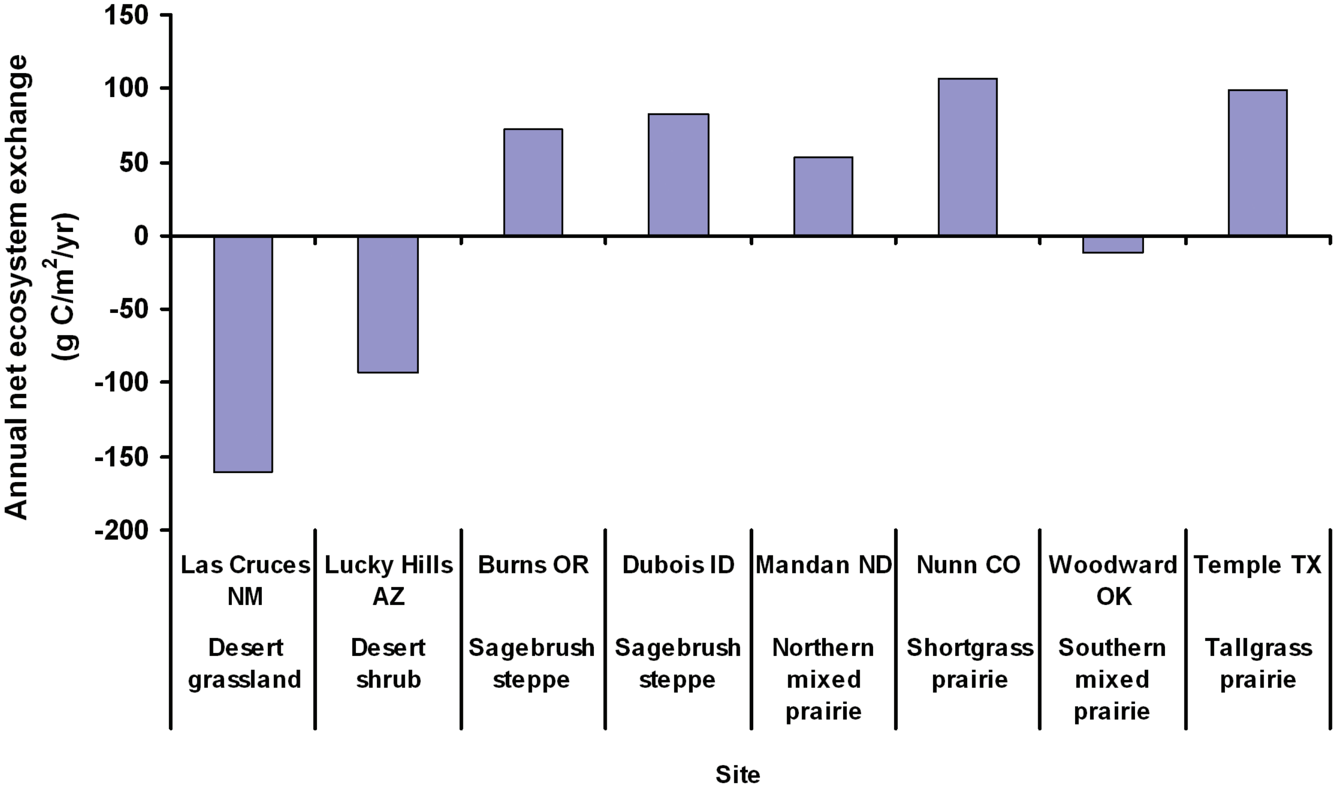


Figure 10-6. Average annual net ecosystem exchange of carbon (g/m/yr) at eight sites from the rangeland carbon dioxide flux project. Sites with positive values are carbon sinks because carbon accumulates in vegetation and soil. Sites with negative values are sources of atmospheric carbon dioxide because carbon is released into the atmosphere. Two ARS-LTER sites are included: desert grassland (JRN) and shortgrass prairie (SGS). Data from Svejcar et al. (2008).

FLUXNET is a network of regional networks monitoring carbon dioxide and water vapor fluxes in terrestrial ecosystems using eddy covariance towers, an alternative approach to Bowen ratio systems (http://www.fluxnet.ornl.gov/fluxnet/). The goals are to characterize spatial and temporal variation in CO_2 and water vapor fluxes and to understand the drivers causing this variation. Started in the 1990s, currently more than 500 sites in Africa, Asia, Australia, Europe, and North and South America participate. Variables related to vegetation, soil, hydrology, and meteorology are collected. The first global standardized dataset was established in 2007 (http://www.fluxdata.org/).

The AmeriFlux network, started in 1996, is a network within FLUXNET (http://public.ornl.gov/ameriflux/). Its research questions are—

- What are the magnitudes of carbon storage and the exchanges of energy, CO_2, and water vapor in terrestrial systems? What are the spatial and temporal variability?
- How is this variability influenced by vegetation type, phenology, land use change, management, and disturbance history, and what is the relative effect of these factors?
- What is the causal link between climate and the exchanges of energy, CO_2, and water vapor for major vegetation types? How do seasonal and interannual climate variability and anomalies influence fluxes?
- What is the spatial and temporal variation of boundary layer CO_2 concentrations, and how does this vary with topography, climatic zone, and vegetation?

Currently the AmeriFlux network consists of 133 sites in 5 countries in North and South America.

New or Developing Monitoring Networks

A number of observational networks have emerged over the past decade to collect similar ecological data from a number of sites (Peters et al. 2008). Existing or emerging networks funded at least in part by the National Science Foundation to collect ecologically relevant data from U.S. sites include the Ocean Observatories Initiative (OOI; http://www.oceanleadership.org/programs-and-partnerships/ocean-observing/ooi/), WATERS Network (http://www.watersnet.org), the Arctic Observing Network (AON; http://www.arcus.org/search/aon.html), the Global Lakes Ecological Observatory Network (GLEON; http://www.gleon.org/), and the National Phenology Network (http://www.usanpn.org/). Here we describe in more detail two networks that include a number of LTER sites, NEON and the Microbial Inventory Research Across Diverse Aquatic (MIRADA) LTERs.

NEON is being designed to study the effects of land use, climate change, and invasive species on structure and functioning of ecosystems in the United States (http://www.neoninc.org/). Observational data will be collected from sites selected to represent one of 20 eco-climatic domains based on vegetation, landform, and climate. All sites will follow the same sampling protocols and collect the same core data, expected to include biological, hydrological, and atmospheric variables (Keller et al. 2008). NEON sites will also use eddy covariance towers to study carbon, water, and energy fluxes, similar to the AmeriFlux network.

The MIRADA LTERs started in 2007 with the goal of building an inventory of microbial operational taxonomic units in marine and freshwater ecosystems (http://amarallab.mbl.edu/mirada/). Both diversity and relative abundance of microbes will be documented, and the physical and chemical drivers behind the observed patterns of microbial diversity will be studied. The project includes 13 LTER sites that study aquatic ecosystems. All sites use a standardized gene sequencing protocol.

Summary

This chapter has presented examples of cross-site experimental manipulations and observations that have yielded unique and extraordinary results. Insights resulting from these cross-site experiments could not have been obtained with another approach. Cross-site experiments allow scientists to address large-scale questions and to isolate cause-and-effect relationships, which are more difficult in observational studies. The importance of large-scale studies across sites has grown in the last decade as society has recognized the need to understand the phenomenon of global change and to predict its impacts on ecosystems and society (MEA 2005). Global change is a large-scale phenomenon that demands studies at this scale (IPCC 2007). However, not all studies can be done at a large scale. For example, elevated carbon dioxide studies can be done only in small plots. Replication across sites provides the means to address differential responses that occur at large scales.

Cross-site experimentation is an ideal tool to address novel and urgent questions, yet this approach faces some difficulties. Costs are usually higher than standard experiments and require major investments in coordination. In addition, funding opportunities for cross-site experimentation are scarce compared with standard grants. Funding agencies and the academic community may need to modify their approaches to allow for this new type of research tool to flourish and yield the results that society demands.

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