

Ecosystem Dynamics

Ecosystem responses to manifold biotic and abiotic influences, both natural and anthropogenic, are the overriding factors in productivity and carbon biosequestration. A system's dynamics—including age-related natural variations in carbon use efficiency (CUE), responses to chronic stress arising from global change and interannual variability, and modified functions triggered by climate and man-made disturbances—significantly affect the fate of ecosystem carbon. Further study is needed to determine the combined impact to Earth systems from these influences and other system factors discussed previously, including plant traits, soil characteristics, and microbial populations.

Stand Development in Forests: Baseline Maturation and Aging of Ecosystems

The terrestrial biosphere is a mosaic of plant communities with widely divergent characteristics. As communities develop on a plot of land, gross primary production (GPP) and the relationships between it and net primary production (NPP) change. Since this natural variation must be understood amid a changing climate, anticipating the trajectory of these relationships is especially important for predicting the future productivity of long-lived, woody communities (i.e., forests). Comprising a central role in the global carbon cycle, forest ecosystems sustain about 80% of terrestrial NPP and 50% of global NPP and thus are a major part of the terrestrial carbon sink that removes some 30% of anthropogenic carbon emissions each year. Consequently, understanding the complex dynamics directing carbon flow through forests is critical.

An important measurement of this flow is carbon use efficiency. Defined as the ratio of NPP to GPP, CUE is a measure of the capacity of forests to transfer carbon from the atmosphere to terrestrial biomass. CUE for forests is widely assumed in many landscape-scale carbon cycling models to be a constant value of 0.5—that is, about half of GPP is made into biomass. To achieve a constant CUE, tree respiration must be a constant fraction of canopy photosynthesis. However, a literature survey of research indicated that CUE values calculated from independent estimates of GPP and NPP were not constant but varied, ranging from 0.23 to 0.83 for different forest types (DeLucia et al. 2007), a finding consistent with theoretical considerations (Amthor 2000). This uncertainty in observed or experimental values is significant because a 20% error in current estimates of carbon use efficiency used in landscape models (0.4 to 0.6) could misrepresent an amount of carbon equal to total annual anthropogenic emissions of CO₂ when scaled to the terrestrial biosphere (DeLucia et al. 2007).

Some of the variation in forest CUE probably is related to the stage of stand development. For example, aboveground forest NPP certainly declines with age, potentially diminishing the capacity of old-growth forests to sequester atmospheric CO₂. Although poorly understood, the mechanisms governing the age-related decline in forest NPP are embodied in two competing hypotheses.

The “respiration hypothesis” [see Fig. 5.1. “Respiration Hypothesis” (a) and “GPP Hypothesis” (b), p. 72] suggests that GPP remains constant but NPP declines following canopy closure early in stand development because of increasing

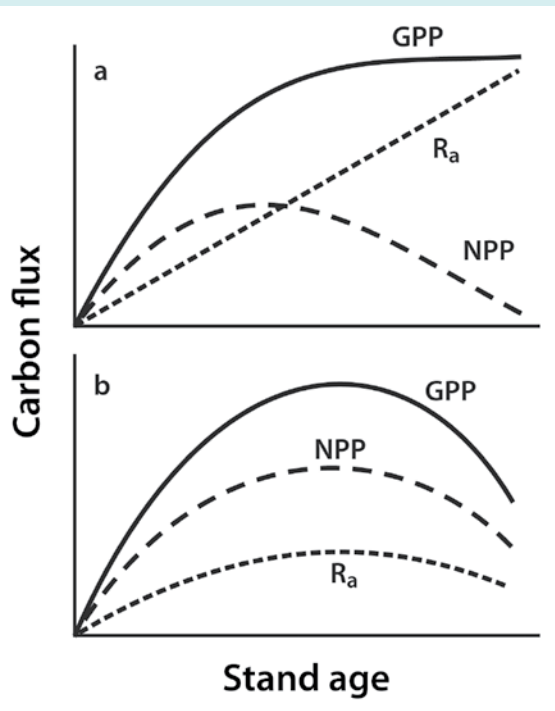


Fig. 5.1. “Respiration Hypothesis” (a) and “GPP Hypothesis” (b). Graphs a and b describe how changes in autotrophic respiration (R_a) and gross primary production (GPP) contribute to age-related decline in forest net primary production (NPP). For additional information, see Barnes et al. (1998) and Ryan et al. (2004) for (a) and Ryan, Binkley, and Fownes (1997) and Gower, McMurtrie, and Murty (1996) for (b).

autotrophic respiration (R_a) associated with the accumulation of woody biomass. This hypothesis has been modified to include increased partitioning of carbon below ground as a factor contributing to the decline in NPP as forests age. The decrease in CUE with stand age suggests that increasing R_a does have a role in age-related NPP decline.

In contrast, the “GPP hypothesis” [see Fig. 5.1 (b), this page] posits that R_a is a fixed fraction of GPP whose age-related decline causes NPP to decrease. Several factors, including increasingly unfavorable water relations and nutrient limitations in large trees, may contribute to GPP decline in old forests. The near-constant GPP fraction partitioned to R_a supports this hypothesis and should lead to a constant CUE with stand age.

Further research is necessary to gain a clear understanding of the factors affecting NPP as forests age. In addition to accurately discerning the relationships among GPP, NPP, and R_a during various stages of stand development, greater insight is needed into the controlling regulatory and metabolic processes in primary producers and their symbiont microbial communities. The ability to model how forest carbon cycling will respond to global change depends critically on a thorough understanding of all these factors.

The Role of Plant-Trait Variation in Ecosystem Response to Chronic Stress Arising from Climate Change

Ecosystems undoubtedly will differ in their responses and vulnerability to global climate change (IPCC 2007). A mechanistic understanding of the complex interplay of various factors dictating these responses is critical for forecasting climate effects on plant productivity and carbon biosequestration (see Fig. 5.2. Factors in Species Composition of Ecosystems, p. 73). Such an understanding could reveal the incredible variability in how ecosystems react to chronic alterations in resources and how particular ecosystem attributes influence a system’s ability to adjust to these and other shifts brought on by climate change. Knowing how ecosystems differ in their response and susceptibility to changes in a single resource—and eventually multiple types of resources—will improve capabilities for simulating trajectories of climate change impacts. Also important is how different resource types and amounts will vary the shape, direction, or rate of such response trajectories. Further influencing these projections are multiple ecosystem attributes, such as the variation in phenotypic traits within populations and among plant and other species, sizes and turnover rates of nutrient pools, the nature and responsiveness of soil biota, and trophic complexity. Thus, to advance understanding of the nature and pace of ecosystem reactions to climate change and improve predictive capabilities, new research must examine the relative importance of the different mechanisms underlying response trajectories [see Fig. 5.3. Hierarchical Response Model (HRM), p. 73]. Specifically needed is more insight into ecosystem response to key aspects of dynamic climate

change, such as elevated CO₂, warming, ozone level, and altered precipitation regimes, as well as interactions with other global shifts.

Numerous factors are expected to contribute to ecosystems' different responses and vulnerability to climate change. However, variation in traits within populations of and among different plant species is likely critical for determining rates and trajectories of ecosystem response, particularly NPP and carbon biosequestration. For example, global climate change represents chronic and directional shifts in resource availability, either directly via elevated CO₂ and altered precipitation regimes or indirectly as, for instance, through the impacts of warming and elevated CO₂ on water balance. Ecosystem reactions to these chronic resource

Fig. 5.2. Factors in Species Composition of Ecosystems.

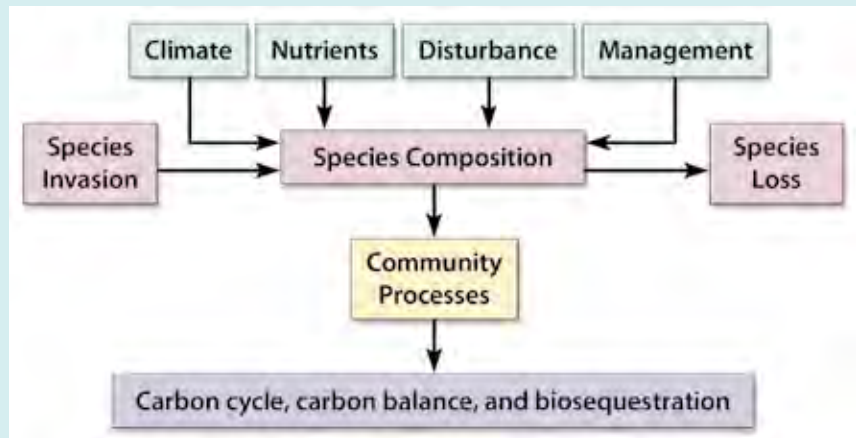
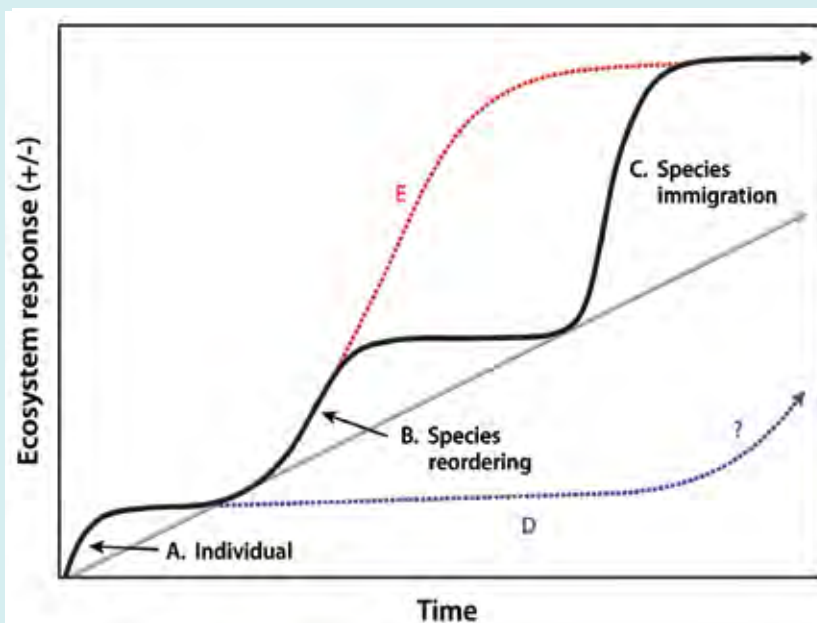


Fig. 5.3. Hierarchical Response Model (HRM). This graph depicts the hierarchy of mechanisms underlying ecological change (black line) as ecosystems are exposed over time to chronic resource alterations associated with global changes (e.g., elevated CO₂, nitrogen deposition, and climate shifts). Fairly modest initial ecosystem responses may reflect relatively rapid individual-level responses (A), with the magnitude and extent of these initial responses limited by traits of the resident species. Larger shifts in ecosystem response are expected with reordering of species (B) in the community (e.g., shifts in relative abundance). The timing and duration of this phase may vary depending on variation in traits and the rate of population turnover or may be attenuated depending on internal interactions. Finally, immigration of new species better suited for altered resource levels may result in further change in ecosystem response (C). Timing may depend on the regional species pool and dispersal limitation. Other responses to chronically altered resources are possible, including gradual linear change (thin grey line) if the magnitude and rate of change were similar for all three mechanisms (A, B, and C). The HRM has potential exceptions. For example, ecosystems dominated by very long lived species with slow turnover rates, such as forests, may appear to be resistant to change (D) as resources accumulate over time. Conversely, ecosystems that become susceptible to invasion by exotic species or pests and pathogens due to resource alterations may bypass changes driven by individual-level responses or community reordering and could experience large shifts in structure and function in a relatively short period of time (E). [Source: Figure modified from Smith, M. D., A. K. Knapp, and S. L. Collins. "A Framework for Assessing Ecosystem Dynamics in Response to Chronic Resource Alterations Induced by Global Change," *Ecology*, in review.]



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Key Research Questions

1. Which phenotypic trait or suites of traits are most important in determining ecosystem response to change? What are the relevant genomic markers for phenotype?
 - a. What is the relative importance of phenotypic-trait variation within populations (i.e., genetic level) versus among species (i.e., species level) in determining ecosystem response to change?
 - b. What is the relative importance of ecosystems' physiological versus transformational responses in determining productivity, carbon biosequestration, and carbon-pool stability?

alterations are expected to be driven, in part, by plant and associated symbionts' responses determined by phenotypic-trait variation and occurring at different hierarchical scales.

The primary and most rapid response to chronic resource alteration is expected to occur at the individual level (see Fig. 5.3, A, p. 73). This response is driven by traits related, for example, to physiology, metabolism, growth, and stress tolerance that in turn are expected to affect NPP, carbon biosequestration, and other processes over the short term. The impacts of altered resources could be either positive or negative depending on the suite of traits represented in a community and the effects of these traits on NPP and carbon biosequestration. As resources continue to shift and in some cases accumulate over time, some species or populations are expected to increase in abundance as a consequence of possessing traits favorable to the new environmental conditions. Meanwhile, those less suited for such conditions are expected to decline. This species- or population-reordering phase of response (see Fig. 5.3, B, p. 73) also likely will affect NPP and carbon biosequestration, with the impact expected to be nonlinear and large as a consequence of rapid population growth and alterations in species or genotype interactions (May 1986; Frost et al. 1995; Blenckner 2005; Ives and Carpenter 2007). Finally, with continued resource alteration, new species or genotypes are expected to immigrate into the community. These species will possess novel suites of traits potentially favorable to the new conditions and contribute in different ways to NPP, biosequestration, and other ecosystem processes. As a result, the immigration phase (see Fig. 5.3, C, p. 73) is expected to elicit the greatest ecosystem response, increasing productivity nonlinearly due to rapid population growth from immigration of new species and subsequent alterations in species interactions (Hobbs et al. 2006; Ives and Carpenter 2007; Knapp et al. 2008).

An important challenge for researchers is determining the nature and relative importance of ecosystem physiological and transformational responses that control productivity, carbon biosequestration, and carbon-pool stability. If, in climate change scenarios, conditions such as resource alterations continue to evolve, then the processes of growth and alteration can be expected to continue, with stands transforming continually.

Variation in rates of change and durations of lag periods between the transitions depicted in Fig. 5.3, p. 73, will in part determine different ecosystems' vulnerability to change. This variation will depend not only on trait diversity at the population level and among ecosystems' plant species, but also on the ability of species to adapt to changing conditions. Other ecosystem attributes and phenomena also will influence the pace of change and the time between transitions. These factors include the magnitude, rates, and types of resource alterations; interactions with other environmental and anthropogenic changes such as atmospheric nitrogen deposition, altered land use, and habitat fragmentation; and shifts in disturbance regimes.

Interannual Variability: Episodic Stress

Carbon-flux data from long-term site studies are invaluable for detecting trends in terrestrial ecosystem responses to episodic phenomena such as interannual variability (e.g., El Niño and La Niña). Consequently, such data are increasingly valuable as sites operate longer and grow in number. Long-term data can be used

to detect scale-emergent processes operating at multiple temporal scales (Urbanski et al. 2007; Dunn et al. 2006) and to characterize complex and nonlinear behaviors as switches, pulses, lags, and hysteresis. For example, these data can provide insight into the dependency of light use efficiency on diffuse radiation; the role of growing-season length, stand age, and drought on net ecosystem exchange (NEE) of CO₂; and the impact of rain pulses on ecosystem respiration and interannual variation in NEE (NEE equals NEP plus CO₂ sources and sinks not involving conversion to or from organic carbon). Urbanski et al. (2007) found that 13 years of data allowed them to identify disturbance-related anomalies and their legacies and to measure underlying ecosystem trends toward greater rates of net carbon uptake, increased photosynthetic capacity, and higher rates of respiration—unexpected findings considering the age of the forest studied. The researchers demonstrated that long-term ecosystem flux measurements are absolutely essential for detecting interannual and decadal trends in response to climate and disturbance. They also showed how short-term data can lead to misinterpretation of results, even the trajectory of a particular ecosystem response. In contrast, alternative approaches producing carbon-flux estimates from remote sensing and models are inferential and do not capture the anomalies and trends of the features of complex systems. While these alternative approaches have merit for conducting desired continental-scale integration, remote sensing–derived products and data-assimilation approaches *must* be anchored with flux measurements, and model parameters should be shaped by continuous and long-term carbon-flux data across a spectrum of sites.

Disturbance and the Dynamics of Carbon Cycling and Biosequestration

Background

Variability of terrestrial net carbon flux at decadal and multidecadal time scales is strongly influenced by the frequency and intensity of disturbance (Irvine, Law, and Hibbard 2007; Bond-Lamberty, Wang, and Gower 2003; Law et al. 2003; Thornton et al. 2002). A common carbon-flux pattern emerges from both measurement and modeling studies investigating ecosystem response to disturbance. First, following a large carbon source associated directly with the disturbance process, an initial period of ecosystem recovery occurs during which source strength diminishes. This recovery is then followed by a period of increasing sink strength as vegetation structure is re-established. Next is a long “tail” phase during which sink strength declines gradually toward a neutral carbon flux; however, a new episodic disturbance can interrupt and reinitiate the pattern at any time. Thus over a long period of time, the emerging climatological mean of disturbance frequency and intensity plays a central role in establishing the mean carbon and nutrient stocks in vegetation, litter, and soil organic matter.

The carbon-flux response of a particular ecosystem to an individual disturbance event depends on a multitude of factors, including long-term mean carbon state, climate, existing community structure and its alteration during recovery, time since previous disturbance, physical properties such as topography and soil structure, disturbance type and magnitude, and climate variability during the postdisturbance period. Basic research needs are associated with each of these aspects of carbon cycle response to disturbance, and additional research requirements emerge when

Key Research Questions

Place-based observations have the potential to answer the following:

1. What are the magnitudes of carbon storage and the exchanges of energy, CO₂, and water vapor in terrestrial systems? What are the spatial and temporal variabilities of these processes?
2. How are these variabilities influenced by vegetation type, phenology, soils and microbial populations, changes in land use and management, and disturbance history, and what is the relative effect of these factors?
3. What is the causal link between climate and the exchanges of energy, CO₂, and water vapor for major vegetation types? How do seasonal and interannual climate variabilities and anomalies influence fluxes by their effects on plants and associated microbial symbionts?
4. How do boundary-layer CO₂ concentrations vary spatially and temporally, and how do these levels vary with topography, climatic zone, and vegetation?

Box 5.1

Partial List of Disturbance Types

Classifying disturbances as related either to climatic or anthropogenic factors is useful. The fact that these categories overlap underscores an area of pressing importance for new research and understanding.

Climate-Driven Disturbance

- Wildland fire
- Extreme events or severe weather (e.g, hurricanes and floods)
- Insects and disease
- Drought

Anthropogenic Disturbance

- Conversion of forest and grassland to agriculture
- Burning of agricultural waste products
- Implementation of biofuel or carbon biosequestration strategies
- Wood harvesting (e.g., for products or fuels)
- Urbanization
- Human-modulated burning of forest and grassland for establishment of new agriculture and grazing (Such activity is an important overlap with climate-driven fire disturbance.)

Key Research Questions

1. **What are the vulnerabilities of carbon sinks to natural and anthropogenic episodic disturbances?**
2. **How will these vulnerabilities change if disturbance frequency and intensity change?**
3. **How does ecosystem recovery following disturbance depend on atmospheric and climatic change (e.g., rising atmospheric pCO₂, warming, and nitrogen deposition)?**
4. **How do climate and carbon–nutrient cycle feedbacks impact potential carbon biosequestration strategies?**

considering the interactions of disturbance dynamics and carbon biosequestration strategies and practices (see Table 5.1. Research Needs for Carbon Cycle Consequences of Disturbance, p. 77). For example, details of stand structure, such as variation in tree spacing, were important determinants of Hurricane Katrina impacts on carbon stocks in Gulf Coast forests (Chambers et al. 2007).

Trajectories of change in net biome productivity and carbon stocks can vary greatly depending on severity, frequency, and type of disturbance. Prognostic models thus require *a priori* knowledge of carbon transformations (e.g., amounts moving from live to dead pools) and combustion efficiencies of different carbon pools (i.e., effects of various fire intensities and vegetation types). Such knowledge is critical for determining how much carbon is combusted in wildfires and how much remains to decompose over years to decades (Campbell et al. 2007). Data on such transformations are lacking, however, and related defaults used in some models result in gross overestimates of carbon combustion and respiration after fire. Also lacking are carbon-budget observations at different stages after disturbance—measurements critical for evaluating and improving models. Thus, more field observations are needed to inform models and develop remote-sensing techniques for mapping carbon pools and fluxes after disturbances (see Box 5.1, Partial List of Disturbance Types, this page). Table 5.1, p. 77, and Box 5.2, Observation Strategy for Long-Term Data to Improve, Modify, Parameterize, and Test Models of Terrestrial Carbon Processes, p. 78, list types of disturbances and outline research needed to understand their effects on carbon cycling.

Table 5.1. Research Needs for Carbon Cycle Consequences of Disturbance

Topic	Research Needs
Historical patterns of disturbance	<ul style="list-style-type: none"> • Represent current carbon stocks consistent with historical patterns of disturbance intensity and frequency.
Climate change impacts on frequency and intensity	<ul style="list-style-type: none"> • Progress from diagnostic to mechanistic to prognostic capabilities of disturbance patterns.
Multiple spatial and temporal scales	<ul style="list-style-type: none"> • Characterize disturbances by episodic nature in space and time. • Relate statistical mean, variability, and high-order moments of disturbances and carbon stocks. • Use variability as a scale-of-analysis function. Relate properties on coarse climate grids.
Fire	<ul style="list-style-type: none"> • Develop a globally gridded representation of current natural and anthropogenic spatial and temporal fire patterns. • Determine combustion efficiencies, total emissions, and speciated emissions of CO₂, CO, black carbon, aerosols, and reactive nitrogen. • Gain a mechanistic understanding of the relationships among climate drivers, vegetation community structure, and human influence. • Base predictions on climate and ecosystem-level drivers as well as interactions with human populations, land-use practices, and changing land cover. • Determine timing of energy balance. Study partitioning at site and pyrogenic (soot) deposition on snow. • Understand carbon cycle consequences of fire recovery and associated mechanics of climate and nutrient impacts. • Conduct on-site assessments of remaining carbon and fire effects on heterotrophic respiration and nutrient dynamics during recovery.
Insects and disease	<ul style="list-style-type: none"> • Understand the mechanistic relationships among climate, insect and disease outbreaks, and the carbon cycle. • Determine the consequences for carbon, nutrient, water, and energy cycling. • Increase predictive capability for insects and disease under future climate change scenarios. • Develop carbon biosequestration strategies to improve resilience. • Study historical examples of recovery dynamics and carbon cycle consequences.
Drought	<ul style="list-style-type: none"> • Determine controls of drought-induced carbon fluxes at the level of plant physiology and soil microbial functioning. • Understand impacts of climate and ecosystems on resilience factors. • Understand carbon cycle consequences of changed communities and behaviors within them.
Extreme weather (e.g., hurricanes, floods, and freeze-thaw dynamics)	<ul style="list-style-type: none"> • Conduct long-term studies on spatial and temporal patterns and vulnerabilities relative to carbon biosequestration. • Assess effects of climate change and related factors (e.g., CO₂, methane, flooding and N₂O, and freeze-thaw dynamics).
Changing allocation patterns	<ul style="list-style-type: none"> • Understand the influence of disturbance over time and its impacts on carbon pools. • Investigate carbon flux and partitioning of GPP to plant components within and among plant functional types under a range of climatic conditions and following disturbances.
Threshold behavior in climate change trends	<ul style="list-style-type: none"> • Elucidate mechanisms whereby ecosystems cross vulnerability thresholds as they develop.
Carbon cycle consequences of anthropogenic nitrogen deposition	<ul style="list-style-type: none"> • Quantify effects of a range of modest levels of nitrogen deposition on canopy and soil processes across various biomes, forest ages, and water availabilities. Also assess effects of such deposition on carbon pools, respiration, and nitrogen balance.
Disturbance–climate system feedbacks	<ul style="list-style-type: none"> • Understand carbon loss followed by carbon uptake. Determine ecosystem transformations resulting from climate and albedo shifts.
Technologies, theories, experiments, and observations	<ul style="list-style-type: none"> • Develop approaches for chronosequences and quantification of variables, carbon budgets and allocations, respiration, nutrients and water, and new agent-based dynamic vegetation models linking biogeochemistry and vegetation change.

Observation Strategy for Long-Term Data to Improve, Modify, Parameterize, and Test Models of Terrestrial Carbon Processes

(Examples: Dynamic Global Vegetation Models and Coupled Climate–Carbon Cycle Models)

- Long-term observations are needed to better understand fundamental controls on terrestrial carbon accumulation rates and effects of climate and disturbance variations on carbon, nutrient, water, and energy exchange with the atmosphere. Uniformly and appropriately applying a range of new tools (e.g., isotopic methods coupled with genomics and molecular markers) will enable analysis of such controls and variations at all spatial and temporal scales.
- Momentum is building for future studies aimed at continental integration of carbon cycling research via data assimilation. As one component of an integrated North American carbon cycle research program, data assimilation will enhance this initiative's diagnostic, explanatory, and predictive capabilities. Success of assimilation depends on a continuous flow of high-quality carbon-flux measurements and meteorological, ecological, soil, and physiological data from a wide spectrum of climate zones, biomes, and disturbance classes. For accurate regional and continental analyses, the modeling community has stressed the value of data from AmeriFlux—a network providing continuous ecosystem-level measurements of, for example, CO₂, water, and energy exchanges from sites in North, Central, and South America. The importance of such observations has pushed the network to deliver high-quality data to a public archive at an unprecedented rate.
- Carbon-flux data from long-term site studies are invaluable for detecting trends in terrestrial ecosystem responses. Consequently, such data are becoming increasingly valuable as sites operate longer and increase in number and density (see section, Interannual Variability: Episodic Stress, p. 74).
- Maintaining carbon-flux data from long-term sites is imperative as the transition period from historic climate norms to perturbed and warming conditions continues. Ongoing measurements could help produce within the next 10 to 20 years an observation record by which society will be able to assess global warming's effect on the health and function of the biosphere. Ecosystem flux data will be crucial in developing coupled climate–carbon cycle models to interpret and predict the impact of future fossil fuel–consumption scenarios.
- Coordinated design and implementation of long-term observation strategies and methods will be critical to understanding short- and long-term terrestrial carbon processes and feedbacks to climate. Observationalists, experimentalists, and theoreticians working together can improve fundamental understanding of the controls on carbon stocks, fluxes, and terrestrial feedbacks to climate and can devise ways to implement this knowledge in a new generation of models. Achieving this goal will require careful and coordinated site selection, measurement, and analysis. For example, model-data integration could be applied to examine how disturbance affects carbon stocks and fluxes across chronosequences of sites in major biomes and climate zones or to assess how interannual variation in precipitation or long-term drought impacts carbon fluxes in different biomes.