16. Remembrance of Weather Past: Ecosystem Responses to Climate Variability

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> . . . the biosphere is . . . a highly complex system with ten million to thirty million different kinds of working parts and myriad feedback systems positive and negative, each with its own lag time, of which we have little ken.
>
> —Thomas E. Lovejoy 1992

16.1 Introduction

The future of the carbon cycle is one of the great uncertainties in projecting the future of climate. The response of terrestrial ecosystems remains largely unknown, and qualitative disagreement persists regarding the influence of climate change on ecosystem carbon storage. There has been a sustained effort to understand how ecosystems respond to climate and carbon dioxide (Prentice et al. 2001) using observations, experiments, models, and the paleorecord. Despite this massive research effort, and considerable effort to synthesize its results, considerable uncertainty remains. We do not have a clear paradigm for interpreting observations of ecosystem climate responses in time and space and for translating that paradigm into predictive models. Many of the disagreements occur because it is difficult to separate the effects of processes operating on different timescales. For example, low cloud cover, high solar radiation, and consequent high temperatures may increase photosynthesis (A) in the short term. On slightly longer timescales, these conditions may favor allocation of new photosynthate to roots, reducing leaf area relative to a cooler year. The *flux* in units of mass per area depends on both the specific rate of photosynthesis (mass per unit Leaf Area Index (LAI)) and the LAI, multiplicatively. The ecosystem-level change can be predicted only by knowing the impact of physical variables on a range of parameters, some of which respond in seconds (for example, A) and others that respond over days to months (e.g., allocation to leaf area).

This type of complexity pervades the terrestrial carbon cycle, in which fluxes depend on both rate constants (e.g., water, temperature, or light dependence) and substrate (e.g., leaf area or detrital carbon) in a first-order (multiplicative) fashion. Biogeochemists have tended to extrapolate the consequences of environmental change from the direction and relative magnitude of the immediate rate constants (e.g., photosynthesis vs. respiration), since we have much less direct information about the "slower" physiological rate constants, such as those controlling allocation of photosynthate to leaves and litter quality and microbial processes controlling soil carbon. These slower processes tend to affect the state variable component of first-order regulation of fluxes and so transmit the integrated history of influences on the ecosystem to the short-term responses.

The growing attention paid to slower processes partly reflects developments in methodology. Early efforts to model whole-ecosystem carbon exchange (Detling, Parton, and Hunt 1978) were based on scaling-up leaf-level of chamber measurements, with fluxes measured in area-specific rates, multiplied by estimates of the relevant substrate (leaf area). Currently, eddy covariance provides a measure of the flux on a true area basis, but the specific rates and relevant substrate (leaf area, litter, etc.) amounts are more difficult to ascertain because of the high heterogeneity in vegetation and soil properties within the footprint of flux towers. This poses new challenges for modeling (Thornton et al. 2002). Existing observational time series intrinsically capture the higher frequencies best, but eddy covariance time series are now long enough that the role of interannual changes to state variables, such as LAI, litter mass, or soil water amount, should be evident.

Developing an observational basis for understanding long-term carbon dynamics from flux observations is challenging. The problem can be described as detecting the signal of slow processes through the "noise" of daily and seasonal changes. Fluxes vary strongly and predictably with physical forcing. Interannual changes to carbon uptake may be driven by climate but do not scale simply with the integral or average of short-term forcing (Vukicevic, Braswell, and Schimel 2001; Wofsy personal communication). In this paper, we use a model to simulate observations of ecosystem flux and state variables and analyze the interaction between short-term climate effects and slower state variable responses, as reflected in both "fast fluxes" and slow pools. We do not address the longer timescales of sand and soil development.

The existence of processes operating on different timescales in the carbon system is well known. Both formal and empirical approaches to unraveling the dynamics of multiscales processes are just beginning to be applied in biogeochemistry (Katul et al. 2001a), although mathematical scaling has long been the subject of formal analysis in atmospheric science and hydrology (Famiglietti and Wood 1994). While current models simulate dynamics on various timescales (Collatz et al. 1991; Rosenbloom, Doney, and Schimel 2001), observations and experiments intrinsically provide more information about "fast" than "slow" processes, although as time series of observations in flux networks and long-term ecological studies lengthen, long-term dynamics become more apparent

(Goulden et al. 1996; Thornton et al. 2002). Creative use of long operational time series (Caspersen et al. 2000) and isotopic measurements (Gaudinski et al. 2000) also provide insight into long-term processes.

In the past decade, the amount and sophistication of terrestrial biogeochemical data has increased dramatically (Canadell et al. 2000). At the same time, ecosystem models have generally increased in complexity and in their ability to accurately predict observations (Jenkins, Birdsey, and Pan 2001; Schimel et al. 1997). Furthermore, the number of measured variables available for comparison to simulated quantities has expanded greatly, even from the 1990s (Parton et al. 1993) to the present (Kelly et al. 2000). However, validation of the time-dependence of many modeled processes remains elusive, and it is still not clear why terrestrial models do not show closer agreement with each other (McGuire et al. 2001; Schimel et al. 2001). The abundance of data and the increasing sophistication of models therefore pose operational problems for the biogeochemical community. How can models be evaluated against observations of multiple timescales simultaneously and objectively? We address this through a simple and instructive model experiment.

16.2 Methods

16.2.1 Model

We used the model Biome-BGC to simulate flux and process observations. Biome-BGC has been extensively described in the literature (Running et al. 1994) and is a comprehensive model of ecosystem physiology. A detailed and recent comparison of Biome-BGC to eddy covariance measurements of Net Ecosystem Exchange (NEE) is found in Thornton et al. (2002), along with a description of the model. In short, the Biome-BGC model simulates daily photosynthesis and respiration as a function of physical variables and nutrient availability, and decomposition as a function of soil microclimate and nutrient dynamics. Plant growth and allocation to leaves, roots, and wood are simulated at the whole-plant level and respond dynamically to the environment. In Biome-BGC as in other state-of-the-art ecosystem models water and nitrogen couple autotrophic and heterotrophic processes together (Schimel et al. 1997). Biome-BGC was chosen for this study because of its relatively mechanistic canopy model, and because it has been extensively compared to flux measurements.

16.2.2 Experimental Design

An ensemble of experiments was performed with Biome-BGC and is referred to as the *ecosystem memory* experiment. In the ecosystem memory experiment, parallel simulations were run to create an ensemble. The simulations were integrated using long-term weather until the systems were a statistical steady state (year-to-year carbon fluxes varied with the weather, but decadal fluxes were stable). This results in systems with relatively low Net Ecosystem Exchange and

Net Primary Productivity. We chose this state because it makes the sensitivity of disparate systems comparable, and to maximize sensitivity of the analysis. The experiments were identical in every respect until 1975, which we chose arbitrarily as the base year. Note that the base year includes daily, seasonal, and interannual variability although most figures show annual results (Fig. 16.1). Simulations were integrated in which the weather from each of the 10 years prior to and including 1975 were substituted for 1975 (Table 16.1). After 1975, the inputs to all runs were once again identical. Table 16.1 shows the differences in annual meteorological parameters between the long-term mean, the base year of 1975, and each year substituted for 1975 to create the ensemble. The simu-

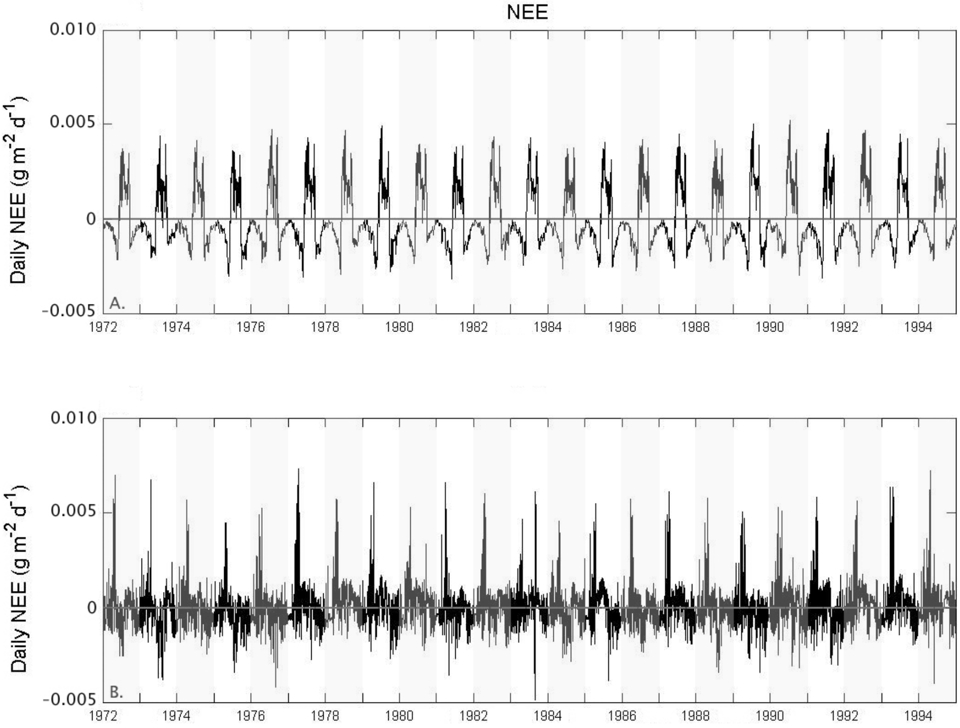

Figure 16.1. Simulated daily NEE for the Harvard Forest stand base cases. This figure illustrates the amount of variability on all timescales inherent in the simulations and the significant differences in the character of fluxes between growth forms. The Harvard Forest is shown to visualize the amount and scales of variability. Hyytiala's simulations have comparable daily, seasonal and interannual variability in fluxes. To produce Figs. 16.2 through 16.7, the annual values of the perturbed simulations were subtracted from the annual values derived from the base simulation to visualize the relative change introduced by direct and delayed effects. **(A)** Harvard Deciduous; **(B)** Harvard Coniferous. Subsequent plots are based on annual rather than daily values.

Table 16.1. Location and meteorology for the Harvard Forest and Hyytiala sites. Annual meterological parameters are shown for the mean, the base year of 1975, and the years substituted for 1975 to create the ensemble. Note that the model is run using daily weather files and these are computed average values.

Year	Mean T°	**SD**	**Mean annual precip.**	**SD**	**Mean vapor pressure deficit**	**SD**	**Mean Incident shortwave**	**SD**
Hyvitiala, Finland, 61° 51' N								
1965–1994 (annual)	4.67	1.0	70.52	10.7	414.55	32.70	162.27	5.05
1965	4.17	9.8	65.53	—	413.5	396.4	163.0	135.6
1966	3.27	11.8	68.43	—	415.7	463.3	161.17	140.2
1967	4.83	11.0	83.4	—	400.7	391.9	157.2	135.9
1968	3.9	10.8	61.78	—	411.9	421.3	161.5	137.0
1969	3.89	11.3	61.18	—	461.99	471.3	171.8	143.9
1970	4.09	10.7	67.24	—	411.14	436.6	159.6	139.4
1971	4.63	9.93	60.32	—	479.2	513.2	168.69	141.0
1972	5.77	10.0	75.5	—	417.4	432.2	160.7	136.6
1973	4.92	10.3	59.24	—	442.91	462.4	162.17	135.2
1974	6.03	7.7	97.85	—	389.26	375.5	158.5	136.3
1975 (Base)	6.4	8.7	60.09	—	468.4	445.1	167.32	141.2
Havard Forest USA, 42° 30' N								
1965–1994 (annual mean)	9.8	0.7	111.7	19.4	639.4	36.5	316.33	8.2
1965	9.1	10.9	62.5	—	647	474.2	321.5	124.2
1966	9.78	10.2	80.88	—	684.59	489.1	320.52	121.6
1967	9.0	10.5	112.1	—	606.5	426.9	324.28	121
1968	9.41	11.2	87.06	—	648.44	454.6	324	122.2
1969	9.56	10.5	103.01	—	610.47	424.9	314.67	123.6
1970	9.26	11.4	86.33	—	629.83	454	327.04	119.8
1971	9.51	10.9	99.84	—	635.21	451.3	325.24	127.4
1972	8.77	10.3	122.84	—	550.73	395	308.94	123.9
1973	10.7	10.1	123.59	—	635.93	412.3	313.65	112.5
1974	9.51	10	107.93	—	604.46	419.1	320.74	118.5
1975 (Base)	10.0	10.4	135.7	—	622.27	437.9	309.63	128.7

lations of 1965 to 1994 differed only during simulated 1975. By comparing the perturbed runs to the base case (1975 weather was the actual weather for that year), we could assess how long ecosystem pools and fluxes would be influenced by past weather conditions.

We substituted natural variability in climate forcing as an alternative to a systematic factorial sensitivity analysis in order to (1) probe realistic levels of ecosystem response to the degree of natural variability experienced at each site, and (2) because, as a practical matter, it is difficult to distribute a systematic perturbation over a daily weather year, while maintaining realistic autocorrelation, correlations between climate variables, event structures, and other characteristics of the weather that affect ecosystems. As Knapp and Smith (2001) show, ecosystem characteristics are closely adapted to both the local mean and natural variability of the site. Our ensemble approach produces a model estimate of responses scaled to representative behavior at each site. A systematic sensitivity experiment may produce exaggerated results in some cases, while underestimating the response in others, depending on the relationship of the perturbations applied to a site's natural variability.

16.2.3 Sites

Two sites were used for the ecosystem memory experiment: Hyytiala, Finland, and Harvard Forest, United States. At each site, defined in the model by latitude, climate (see Table 16.1), and soils, deciduous and coniferous stands were simulated. Meteorological data were derived from local weather station records, as both sites had available daily meteorological data. Both deciduous and coniferous growth forms were simulated: first, because the two regions contain both growth forms (the Hyytiala region contains birch and deciduous understory vegetation, although the flux site footprint is pine); and second, to examine the effect of differences between growth forms in leaf turnover time and foliar chemistry. Note that for the Harvard Forest site, by chance, 1975 was the wettest and one of the warmest years in the period from 1965 to 1975. As a consequence, at that site, the ensemble members differ monotonically and systematically from the base case.

16.3 Results and Discussion

16.3.1 Responses of Net Ecosystem Exchange

We analyzed the initial and long-term responses of multiple ecosystem variables. Plotting the difference between the base case and perturbed ensemble members allows visualization of how long weather effects in a single year cause indirect ecosystem responses. Fig. 16.2 shows the difference in NEE resulting from a single year's perturbation. NEE fluxes are significantly affected by weather in prior years. The effect is large for several years and can continue for periods of decades.

The differences in NEE were often larger in the year after the perturbed year (1975), even though the weather for that subsequent year was identical for all simulations. NEE slowly returned to the base case and generally approached the baseline after 3 to 5 years. The rates and pattern of this "relaxation" were ecosystem specific. Note that because these experiments were analyzed while systems were at a mature NEE/NPP state, the sensitivity expressed as a fractional change is amplified relative to systems rapidly accumulating carbon. Experience

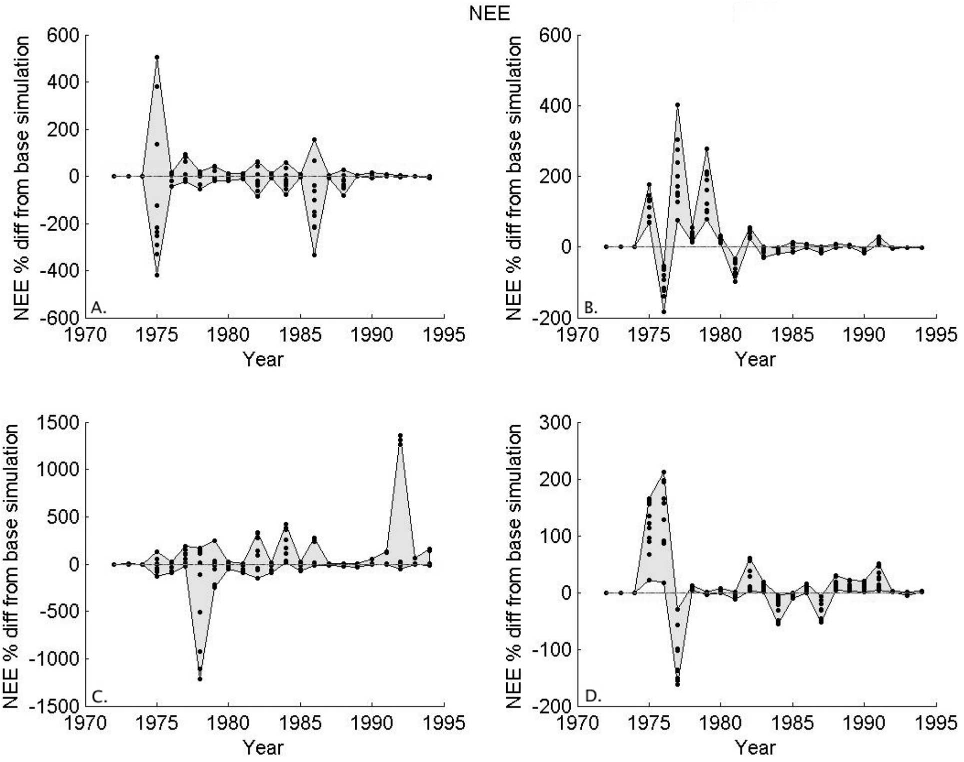

Figure 16.2. Net ecosystem exchange for the model ensemble. All results are shown as annual % difference from the base case. The shaded envelope brackets the ensemble of results; individual ensemble results are shows as points within the envelope. **(A)** the Hyytiala site coniferous stand; **(B)** the Harvard Forest coniferous stand; **(C)** Hyytiala decidous; and **(D)** Harvard Forest deciduous stand.

with this model suggests that the various effects described below remain significant and are on the order of 10% to 50% of the mean NEE flux in accumulating stands (Thornton et al. 2002).

The effects on NEE do not decay away smoothly but decline and recur, depending on the subsequent year's weather and variations in litter carbon and leaf area. Ecosystem sensitivity to climate variability in one year is contingent on responses to the weather in previous years. Since fluxes per se have no memory in the model, these lags arise because of changes to model state variables, including carbon, nitrogen, or water pools. Responses to weather in one year can predispose ecosystem component fluxes to respond more or less strongly to weather in subsequent years. This type of contingency, though expected from ecosystem theory, is rarely accounted for in analyses of biogeochemical flux time series (Goulden et al. 1996; Kelly et al. 2000).

16.3.2 State Variable Dynamics

Plotting state variable changes over time provides insights into the mechanisms causing lagged responses in NEE (Fig. 16.3). The responses of maximum leaf area, soil water, soil nitrogen, and litter mass are shown for the Harvard Forest Coniferous simulation; other sites and growth forms show qualitatively similar results. Foliage, soil water, and nitrogen cycles were all affected by the weather perturbation and then recovered on different timescales. Soil water generally responds quickly (1–2 years) and quickly returns to the base case, which is expected since the modeled turnover time for soil water is a little less than a year. Leaf area also has a short turnover time (depending on coniferous or deciduous growth habit) but is affected through water and nitrogen effects on productivity for many years. Since the nitrogen cycling response is controlled by decomposition, it responds slowly, as does litter carbon. Litter responds to

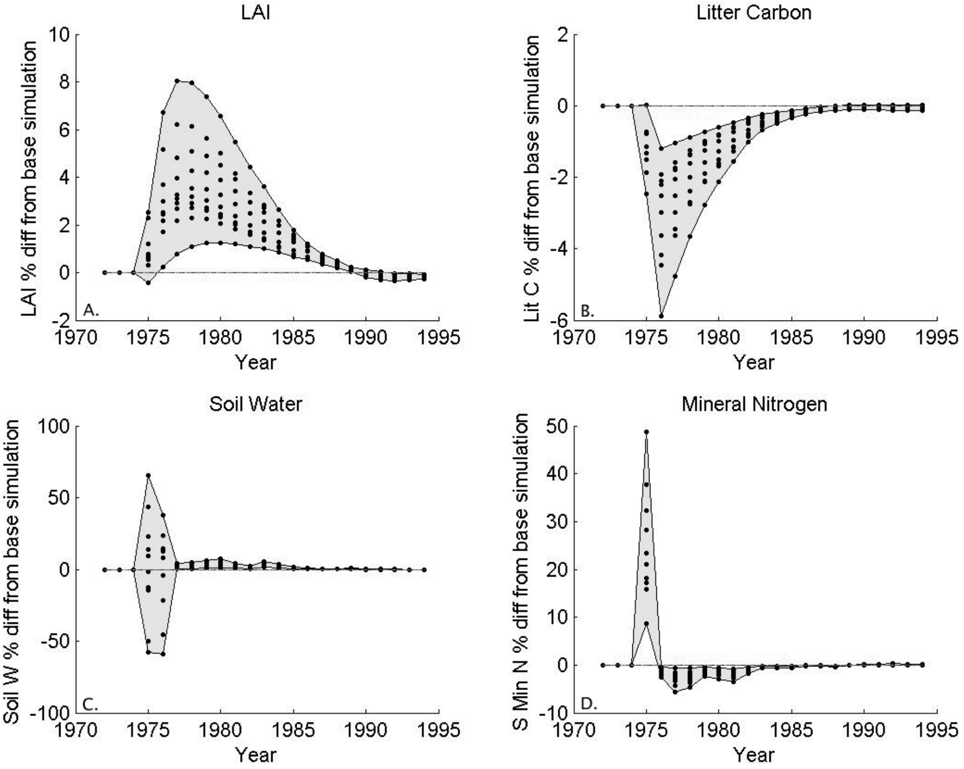

Figure 16.3. Effects on key state variables. All results are shown as annual % difference from the base case. Example results are shown for the Harvard Forest Coniferous stand. **(A)** Maximum leaf area index; **(B)** Litter carbon; **(C)** Soil water; and **(D)** soil mineral nitrogen (plant available N).

altered NPP and then returns to quasi-equilibrium slowly with a rate determined by litter decomposition rates and changes to inputs from NPP. Nitrogen plays a key role in coupling plant and soil time scales together. Rates of N cycling are modified by the initial water and litter C perturbations. Altered N cycling then affects productivity, litter production, and so feeds back again to N cycling and so on.

Plant growth forms affect response times of state variables. The magnitude of effects arising from growth forms is at least as large as the differences between latitudes, based on this limited comparison. Fig. 16.4 shows a comparison of leaf area responses between growth forms at the two sites. Sites and growth forms differ significantly in their responses. The difference in peak proportional response between the deciduous and coniferous responses is large (6 vs. 18% for the northern site) compared to the mean site-to-site differences (9 vs. 12%).

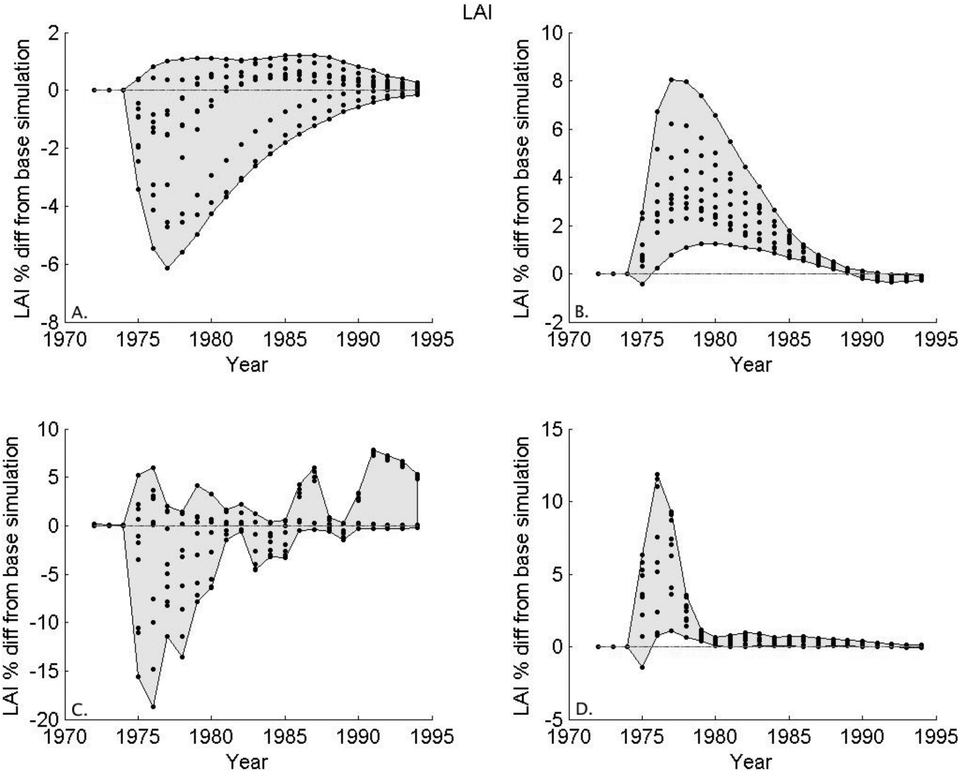

Figure 16.4. Effect of growth form and site on state variables: maximum leaf area index. All results are shown as annual % difference from the base case. This figure compares leaf area index responses of coniferous and deciduous stands at the two sites. **(A)** Hyytiala Coniferous; **(B)** Harvard Coniferous; **(C)** Harvard Deciduous; and **(D)** Hyytiala Deciduous.

For three of the simulations, the timescale of the LAI perturbation is about 15 years, while at the Harvard Forest deciduous site, the timescale is only about 4 years. In the case of the northern deciduous simulation, the extremely long timescale appears to result from the long-lived perturbation to the nitrogen cycle, which in this cold forest is controlled by slow decomposition rates. The differences are indicative of the additional parameterization and validation needed to accurately model "slow" responses globally.

16.3.3 GPP and Ecosystem Respiration Responses

Ecosystem state variables have direct effects on the component fluxes Gross Primary Production and Ecosystem Respiration (ER = microbial respiration + plant growth and maintenance respiration). Fig. 16.5 shows proportional changes in GPP and ER for the coniferous sites. The proportional changes in GPP and ER are larger than those in the state variables, although much smaller than the

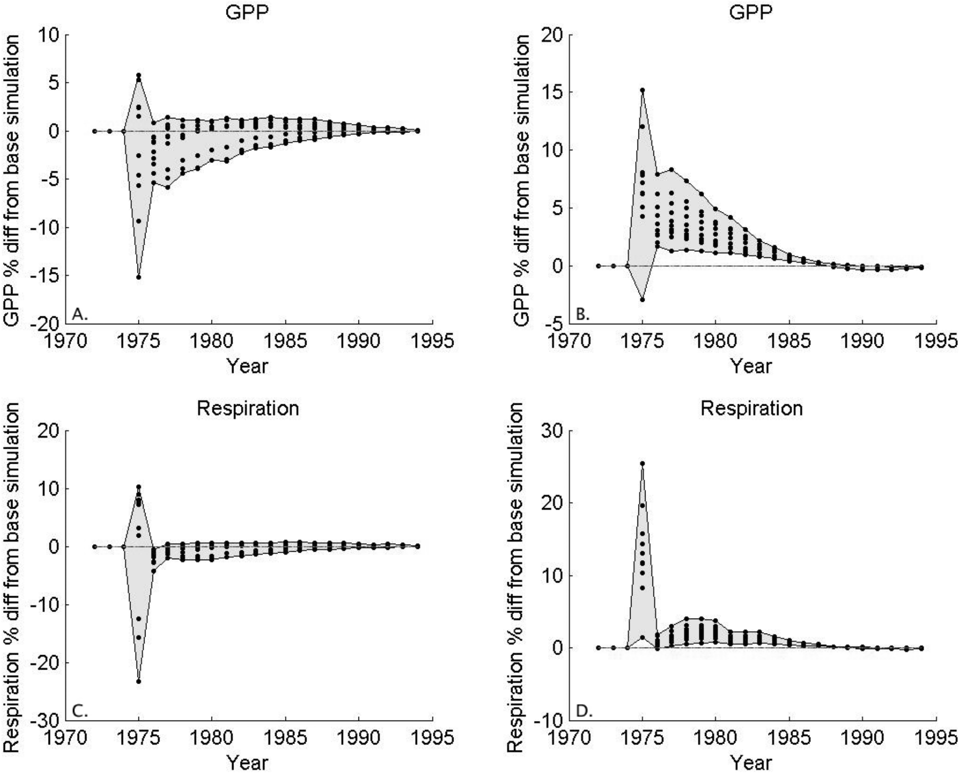

Figure 16.5. GPP and Ecosystem respiration for the coniferous sites. Results are annual % difference from the base case. **(A)** Hyytiala GPP; **(B)** Harvard GPP; **(C)** Hyytiala Respiration; and **(D)** Harvard Respiration.

changes in NEE (see Fig. 16.2). The initial responses and recovery of GPP and ER are smoother than those of NEE. The highly discontinuous responses of NEE occur because GPP and ER change out of phase with one another, on slightly different timescales, causing the difference to vary nonlinearly. Growth form also affects the responses of GPP and ER. Fig. 16.6 compares the GPP perturbations for the Harvard Forest coniferous and deciduous simulations. The GPP effects are longer lasting in the coniferous stand, due mainly to the multi-year needle retention time, and secondarily to coupled effects resulting from slower decomposition rates.

NEE is more sensitive to lagged effects than are GPP and ER separately. Large effects on NEE occur when GPP and ER responses are uncorrelated in time. A variety of ecosystem processes can cause uncorrelated changes in ER and GPP. For example, the production of a large litter cohort in one year may

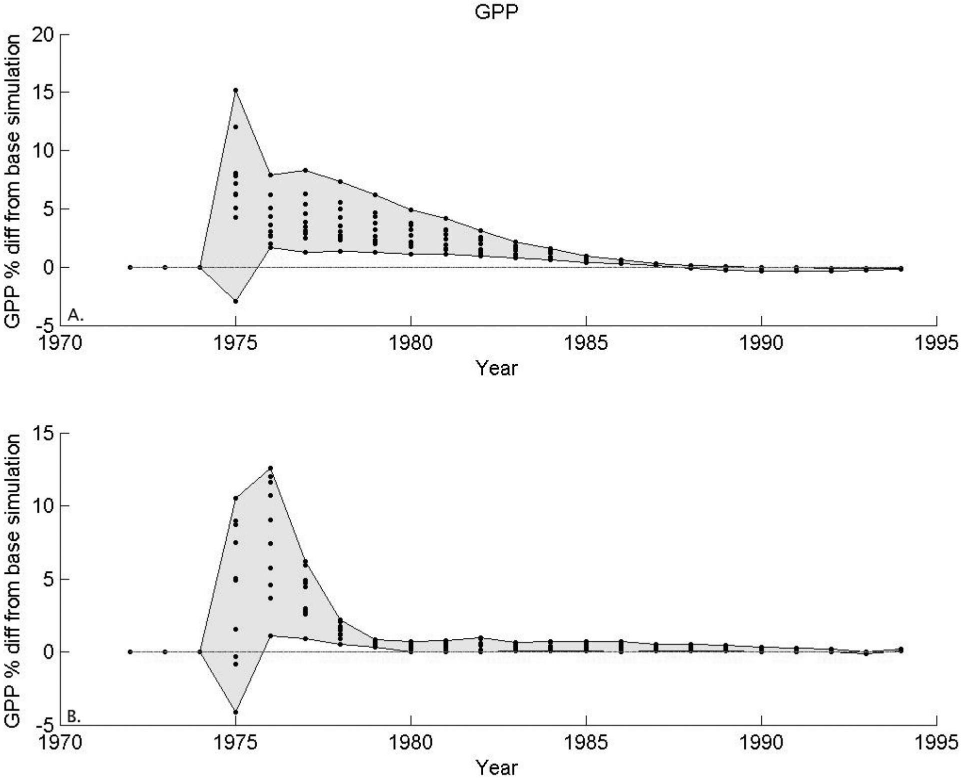

Figure 16.6. GPP perturbations (annual % difference from the base case) for the Harvard Forest coniferous and deciduous simulations, showing the effects of growth form on a component flux response. Note that ER in the model is computed from the sum of plant growth respiration maintenance respiration and heterotrophic respiration, all of which are computed separately. **(A)** Coniferous; **(B)** Deciduous.

increase ER the next year without a corresponding impact on state variables affecting photosynthesis. Changes in nitrogen availability driven by changes in litter mass and heterotrophic activity may also affect GPP. The effects of climate perturbations tend to be largest the year after the perturbation. During the anomalous year, changes to temperature and moisture affect both autotrophic and heterotrophic processes. The effects on GPP and ER are largest initially but may cancel each other out. In subsequent years, the anomalies in GPP and ER are smaller but uncorrelated, leading to larger effects on NEE than in the year when GPP and ER respond the most.

16.3.4 Multiple Steady States in Total Carbon Storage

State variables are important controls in ecosystem models because of the strong first-order dependence of most fluxes. Because the state variables change slowly relative to fluxes and change as a consequence of integrated fluxes, they contribute low-frequency behavior to the model. Differences in the values of state variables that are small relative to measurement error, and too small to simulate accurately, will affect model solutions. This is a precondition for complex responses or even chaotic behavior (May 2001). Fig. 16.7 shows that the model, examined in terms of total carbon storage, has multiple steady states, at least on decadal timescales. Each realization of the model equilibrates at a slightly different level of total carbon. Initially, the total carbon responses diverge, a precondition for chaotic behavior. For the model to be chaotic, these responses would have to diverge exponentially as a function of an initial infinitesimal perturbation. The plots show modest quantitative differences between model states, but given that the variable plotted is total carbon, these small differences are significant. Given the timescale of the perturbation, the differences would be entirely between much smaller active pools (e.g., litter, microbial C, leaf area) and so significant for fluxes. These small differences in state can “precondition” the system for later, altered sensitivity as can be seen 5 to 15 years after the perturbation for some site/growth form combinations.

16.3.5 Significance of Lagged Effects

Ecosystem responses to the environment are a complex mixture of immediate responses to environmental variability and indirect effects mediated through biological processes. Ecosystems therefore respond to any given forcing (e.g., weather) on multiple timescales. This is a characteristic of systems that contain components that respond with different time-constants. The carbon cycle literature has long identified multiple timescales of response as a key aspect of ecosystem behavior (Moore and Braswell 1994; Schimel et al. 1997). Recent papers have begun to address this question as well, as time series grow longer (Katul et al. 2001a,b; Baldocchi, Falge, and Wilson 2001). Ecosystem memory—the effects of prior disturbance and weather forcing of ecosystem responses—exerts a significant effect on net carbon exchange (Vukicevic, Braswell, and Schimel 2001).

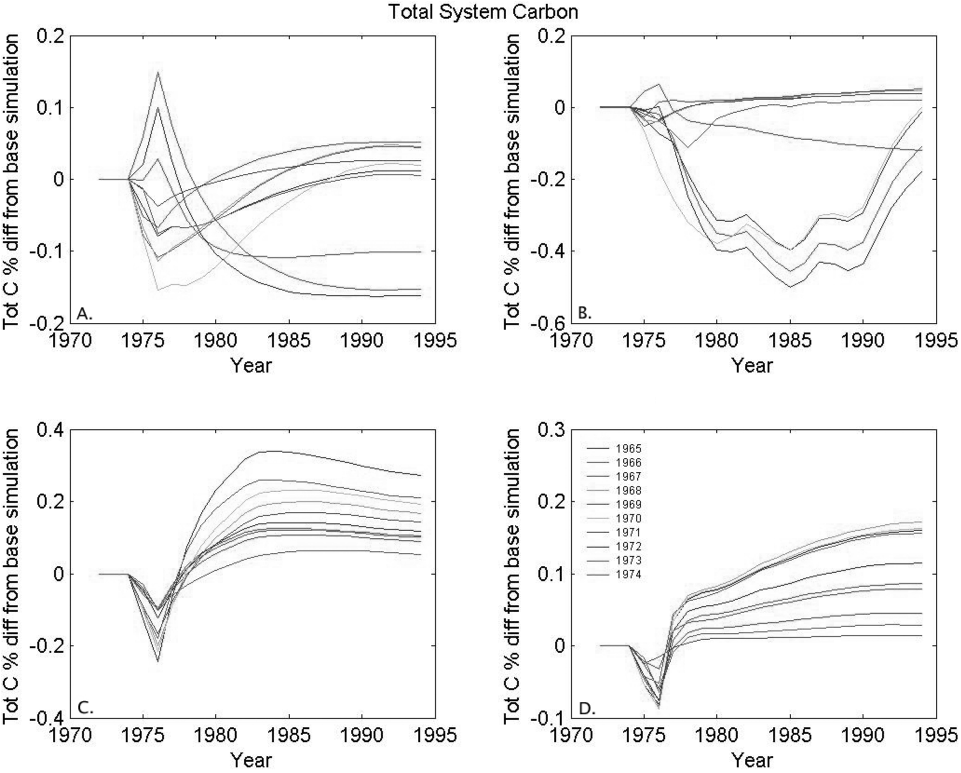

Figure 16.7. Total ecosystem carbon (plant plus soil stocks) for both sites and growth forms, shown as annual % difference from the base case. Each individual ensemble member is shown as a separate trajectory and is color-coded. To create the ensemble members, a year previous to 1975, chosen from 1965 to 1974, is substituted in place of 1975; the substituted year is indicated in the legend in Panel C. Note the variety of dynamical responses of total C illustrated by the NEE trajectories. All simulations show parallel behavior of ensemble members as they approach new steady states (possibly converging on very long timescales). **(A)** the Hyytiala site coniferous stand; **(B)** the Harvard Forest coniferous stand; **(C)** Hyytiala deciduous; and **(D)** Harvard Forest deciduous stand.

Braswell et al. (1997) and Vukicevic, Braswell, and Schimel (2001) argue that the atmospheric carbon dioxide response to temperature variability suggests that ecosystems respond initially to increased temperature by releasing carbon, but that a delayed increase in uptake occurs on average 1 to 3 years after the initial release. They hypothesized that this occurs because increased respiration in the initial year causes increased nutrient availability, and hence increased productivity in subsequent years, without a balancing increase in respiration. There is some evidence for this pattern in the ecosystem memory experiment, as this is the pattern shown in the Harvard Forest deciduous simulation. Other sites and forest types show other responses. As in Schimel et al. (1996) and Braswell et al. (1997), Biome-BGC suggests that ecosystem characteristics significantly influence the response to climate variability. Large responses in the atmosphere must result when spatially coherent climate anomalies trigger responses across ecosystems that respond in similar ways. Vukicevic, Braswell, and Schimel (2001) show that a dominant mode of temperature variability on land occurs in the Northern Hemisphere mid-latitudes, a region that contains most temperate deciduous forests. Because effects of weather in prior years can significantly alter NEE, GPP, and ER from average values, we caution that space-for-time analyses where short flux records are plotted against mean or current year's climate (Valentini et al. 2000) may be significantly affected by lagged effects. As a result, space for time substitution can give extremely misleading results for environmental controls over fluxes.

16.3.6 The Response Hierarchy and State Space Estimation

We observed a hierarchy in the impact of indirect effects from state variables to component fluxes to the integrated (NEE) flux. The ecosystem memory experiment shows that lagged effects are discernible in ecosystem state variables such as leaf area, soil water, soil mineral nitrogen, and litter mass. The magnitude of these effects is of the order 1% to 18% difference from the base case, depending on variable and time since disturbance. The effects persist for 3 to 15 years. The ecosystem component fluxes (GPP and ER) likewise show lagged effects and have delayed responses of up to 25% to 50%. The component fluxes show their largest responses soon after the initiation of the ensemble and decay away smoothly. Delayed differences relative to the base case arise from lags in the ecosystem state variables, because, unlike fluxes, they are able to carry information from one time step to the next. NEE is the difference between GPP and ER and is, therefore, typically a small fraction of either flux. Small changes in either GPP or ER can cause large changes in NEE. The magnitude of the differences between ensemble members in NEE is of the order 50% to 1500%, far larger than the proportional differences in state variables or the component fluxes. At each level of control, the effects of the perturbation are amplified. Accurate simulation of NEE on the interannual timescale depends on highly accurate simulation of state variables and component fluxes of GPP and ER.

Note that the sensitivity of modeled fluxes to key control variables, such as leaf area and litter fall, has profound implications for measurement strategies. It has long been known that errors in GPP scales nearly linearly with errors in leaf area, and as a result major efforts have gone into developing in situ and satellite estimates of leaf area (Running et al. 1994). The current state of the art allows for precision in LAI measurements at the stand scale of 10% to 25% of the mean. Model predictions of leaf area can typically be verified to within about 10% to 25% of the true value. This may result in acceptable errors in GPP and NPP, which are also typically known to within about 25% (Parton et al. 1993) but can result in very large errors in NEE (including a possible sign change). Similar scaling applies to errors in ecosystem respiration, which, however, is rarely measured with comparable accuracy and precision to NPP or GPP.

Until the relatively recent advent of long, quality-controlled NEE time series from eddy covariance, model verification was usually based on comparison to state variables, and NPP, estimated from state variables. Accurate simulation of NEE will require models whose simulation of key state variables is optimized as carefully as are parameter values. While correct model structure and accurate parameters will help with simulation of state variables, other techniques may also be applied. State space estimation, or adjustment of initial and simulated state variable values to minimize the difference between observed and simulated fluxes, while accounting for uncertainties in all variables, is a clear alternative to estimation and tuning or model parameters. This approach is widely used in geophysical models and in weather forecasting and is well justified in systems where model evolution depends sensitively on poorly known state variables (Kalnay, in press).

The sensitivity of NEE to small changes in state variables may explain some of the discrepancies among ecosystem models (Melillo et al. 1995). Ecosystem models with similar structures and parameterizations generally perform similarly under today's climate and compare similarly against NPP data (Schimel et al. 2000; Jenkins, Birdsey, and Pan 2001). However, these same models tend to diverge when simulating climate change (Melillo et al. 1995). Given the sensitivity of NEE to small differences in LAI and other state variables, model biases too small to detect with today's data can have large impacts on modeled NEE. This provides an alternate perspective on model-model disagreements and suggests that far more detailed model intercomparisons will be required to diagnose the cause of differences, such as detailed diagnoses of interannual variability. Models validated against state variable measurements can have major errors in NEE, and equally "valid" models can differ substantially in predictions. Small errors, undetectable with current measurements, in allocation, litter chemistry, soil water, and other key states can accumulate and produce large errors in the long-term carbon balance. This is especially true when models represent aggregated properties (stands or pixels) and average parameter values must be estimated. Long-term modeling of NEE can easily require more accuracy than sampling error permits! Correct models may not even be identifiable with current process study techniques. The solution to this dilemma is not purely reductionist, but rather through the use of novel estimation strategies, as discussed above.

16.3.7 Complex Dynamics in the Carbon System

It is well known that model systems can exhibit stable or chaotic behavior, depending on parameter values (May 2001). In the state and parameter domain examined in this study, Biome-BGC exhibits multiple steady states but not chaotic dynamics. As ecosystem models and data are analyzed under more and more conditions, we should pay close attention to appropriate diagnostics to identify whether systems are entering chaotic domains. The existence of chaotic behavior in biogeochemical systems would have a major impact on both observing system design and modeling strategy. Currently, monitoring and analysis systems for chaotic systems (e.g., the atmosphere, some animal populations) exist, but most biogeochemical observations have tacitly assumed a high degree of linearity between forcing and response (Schimel et al. 1997). If this were to change with alterations in either the biota or the climate system, management of carbon, water quality, and other ecological goods and services would become even more challenging.

Katul et al. (2001b) suggested that ecosystems were dissipative systems, creating some degree of order from chaotic atmospheric forcing (this amounts to an operational definition of life, couched in terms of fluxes). That hypothesis remains tenable. Our results suggest that one mechanism of dissipation is to "rectify" chaotic forcing from the atmosphere into longer timescales. These model results show that interannual variability in climate forcing of ecosystems has impacts on timescales up to decadal. Ecosystem responses may be proportional in the integral to the chaotic portion of forcing but spread over a long period of time, thus limiting the change to average or instantaneous rates. Because NEE is a small difference between large opposing fluxes, its dynamical characteristics are different from the variables ecosystem modelers have focused on for decades (NPP, biomass, and other state variables). Our study addresses intermediate timescales just reached in the short time series that Katul et al. (2001b) analyzed, but it has implications for behavior over a longer term. Ecosystems may either damp or amplify high-frequency chaotic forcing into chaotic fluxes on longer timescales, depending on whether ecosystems are chaotic systems themselves. Models and data about the dynamical characteristics of biogeochemical systems have just reached the point where questions about complexity, nonlinearity, and predictability can be concretely addressed.

16.4 Summary

Understanding the contribution to ecosystem change from processes with different time constants is extremely difficult using short observational time series. We used a model to simulate observations of ecosystem flux and state variables and then linked behavior in the simulated observations to underlying mechanisms and timescales as a model for developing new strategies for observing and analyzing ecosystems. We performed a simple model experiment, using a widely used and well-tested ecological mode, Biome-BGC. We ran many parallel multidecadal simulations, which differed only in the weather during one year (simulated 1975). One simulation used 1975 weather during 1975 while the others had different weather years substituted in that year. Following the 1975 perturbation, the inputs were again identical. This allowed us to analyze both the rate of recovery of ecosystem variables after a one-year perturbation and the mechanisms that caused delayed responses. We observed a hierarchy in the impact of indirect effects arising from state variables and component fluxes upon the integrated (NEE) flux. State variables such as leaf area, soil water, and litter mass were affected by 1% to 15% difference from the base case. The effects persisted for 3 to 15 years. The ecosystem component fluxes (GPP and ecosystem respiration) had responses of up to 25% to 50%, which persisted for 3 to 5 years. The component fluxes show their largest responses soon after the initiation of the ensemble and decay away smoothly. Net Ecosystem Exchange was altered by 50% to 1500% with lagged effects persisting for many years. The fluxes themselves have no memory per se and so lagged differences from the base case arise from anomalies in the ecosystem state variables. The model suggests that a large fraction of interannual variation in NEE occurs when subtle lagged changes in GPP and Ecosystem Respiration occur out of phase with each other. The sensitivity of NEE to small changes in state variables may explain some of the discrepancies amongst ecosystem models. Model biases too small to detect with today's data can have large impacts on modeled NEE. Models validated against state variable measurements can have major errors in NEE, and equally "valid" models can differ substantially in predictions. Aggregated state variables (ecosystem carbon storage) showed multiple steady states but not chaotic dynamics. Biogeochemical systems may be, however, on the "edge" of chaos and future observations, and models should consider the possibility of highly nonlinear and chaotic dynamics arising as novel climate and ecological changes occur.

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References

Baldocchi, D., E. Falge, and K. Wilson. 2001. A spectral analysis of biosphere-atmosphere trace gas flux densities and meteorological variables across hour to multiyear time scales. *Agricultural and Forest Meteorology* 107:1–27.

Braswell B.H., Schimel D.S., Linder E, Moore B. 1997. Science 278 (5339): 870–872.

Canadell, J.G., H.A. Mooney, D.D. Baldocchi, J.A. Berry, J.R. Ehleringer, C.B. Field, S.T. Gower, D.Y. Hollinger, J.E. Hunt, R.B. Jackson, S.W. Running, G.R. Shaver, W. Steffen, S.E. Trumbore, R. Valentini, and B.Y. Bond. 2000. Carbon metabolism of the terrestrial biosphere: A multitechnique approach for improved understanding. *Ecosystems* 3:115–30.

Caspersen, J.P., S.W. Pacala, J.C. Jenkins, G.C. Hurtt, P.R. Moorcroft, and R.A. Birdsey. 2000. Contributions of land-use history to carbon accumulation in US forests. *Science* 290:1148–51.

Collatz, G.J., J.T. Ball, C. Grivet, and J.A. Berry. 1991. Physiological and environmental regulation of stomatal conductance, photosynthesis, and transpiration: A model that includes a laminar boundary-layer. *Agricultural and Forest Meteorology* 54:107–36.

Detling, J.K., W.J. Parton, and H.W. Hunt. 1978. An empirical model for estimating CO_2 exchange of *Bouteloua gracilis* (H.B.K.) Lag. in the shortgrass prairie. *Oecologia* 33: 137–47.

Famiglietti, J.S., and E.F. Wood. 1994. Multiscale modeling of spatially variable water and energy-balance processes. *Water Resources Research* 30:3061–78.

Gaudinski, J.B., S.E. Trumbore, E.A. Davidson, and S.H. Zheng. 2001. Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates, and partitioning of fluxes. *Biogeochemistry* 52:113–14.

Goulden, M.L, J.W. Munger, S.M. Fan, B.C. Daube, and S.C. Wofsy. 1996. Exchange of carbon dioxide by a deciduous forest: Response to interannual climate variability. *Science* 271:1576–78.

Jenkins, J.C., R.A. Birdsey, and Y. Pan. 2001. Biomass and NPP estimation for the mid-Atlantic region (USA) using plot-level forest inventory data. *Ecological Applications* 11:1174–93.

Kalnay, E. [*in press*] Atmospheric modeling, data assimilation, and predictability. Cambridge: Cambridge University Press.

Katul, G.G., C.T. Lai, J.D. Albertson, B. Vidakovic, K.V.R. Schafer, C.I. Hsieh, and R. Oren. 2001b. Quantifying the complexity in mapping energy inputs and hydrologic state variables into land-surface fluxes. *Geophysical Research Letters* 28:3305–3307.

Katul, G., C.T. Lai, K. Schafer, B. Vidakovic, J. Albertson, D. Ellsworth, and R. Oren. 2001a. Multiscale analysis of vegetation surface fluxes: From seconds to years. *Advances in Water Resources* 24:1119–32.

Kelly, R.H., W.J. Parton, M.D. Hartman, L.K. Stretch, D.S. Ojima, and D.S. Schimel. 2000. Intra-annual and interannual variability of ecosystem processes in shortgrass steppe. *Journal of Geophysical Research-Atmospheres* 105:20093–20100.

Knapp, A.K., and M.D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291:481–84.

Lovejoy, T. 1992. Preface. In *Global warming and biological diversity,* ed. R.L. Peters and T.E. Lovejoy. New Haven: Yale University Press.

May, R.M. 2001. *Stability and complexity in model ecosystems.* Princeton, New Jersey: Princeton University Press.

McGuire, A.D., S. Sitch, J.S. Clein, R. Dargaville, G. Esser, J. Foley, M. Heimann, F. Joos, J. Kaplan, D.W. Kicklighter, R.A. Meier, J.M. Melillo, B. Moore, I.C. Prentice, N. Ramankutty, T. Reichenau, A. Schloss, H. Tian, L.J. Williams, and U. Wittenberg. 2001. Carbon balance of the terrestrial biosphere in the twentieth century: Analyses of CO_2, climate and land use effects with four process-based ecosystem models. *Global Biogeochemical Cycles* 15:183–206.

Melillo, J.M. J. Borchers, J. Chaney, H. Fisher, S. Fox,A. Haxeltine, A. Janetos, D.W. Kicklighter, T.G.F. Kittel, A.D. McGuire, R. McKeown, R. Neilson, R. Nemani, D.S. Ojima, T. Painter, Y. Pan, W.J. Parton, L. Pierce, L. Pitelka, C. Prentice, B. Rizzo, N.A. Rosenbloom, S. Running, D.S. Schimel, S. Sitch, T. Smith, I. Woodward. 1995. Vegetation/Ecosystem Modeling and Analysis Project (VEMAP): continental-scale study of terrestrial ecosystem responses to climate change and CO_2 doubling. Global Biogeochemical Cycles 9(4): 407–437.

Moore, B., and B.H. Braswell. 1994. The lifetime of excess atmospheric carbon-dioxide *Global Biogeochemical Cycles* 8:23–38.

Parton, W.J., J.M. O. Scurlock, D.S. Ojima, T.G. Gilmanov, R.J. Scholes, D.S. Schimel, T. Kirchner, J.C. Menaut, T. Seastedt, E.G. Moya, A. Kamnalrut, J.I. Kinyamario. 1993. Observations and modeling of biomass and soil organic-matter dynamics for the grassland biome worldwide. *Global Biogeochemical Cycles* 7:785–809.

Prentice, I.C., G.D. Farquhar, M.J.R. Fasham, M.L. Goulden, M. Heimann, V.J. Jaramillo, H.S. Kheshgi, C. Le Quere, R.J. Scholes and D.W.R. Wallace. In: J.T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell, C.A. Johnson (eds) Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, U.S.A. pp. 183–237.

Rosenbloom, N.A., S.C. Doney, and D.S. Schimel. 2001. Geomorphic evolution of soil texture and organic matter in eroding landscapes. *Global Biogeochemical Cycles* 15: 365–81.

Running, S.W., C.O. Justice, V. Salomonson, D. Hall, J. Barker, Y.J. Kaufmann, A.H. Strahler, A.R. Huete, J.P. Muller, V. Vanderbilt, Z.M. Wan, P. Teillet, and D. Carneggie. 1994. Terrestrial remote-sensing science and algorithms planned for EOS MODIS. *International Journal of Remote Sensing* 15:3587–3620.

Schimel, D.S., B.H. Braswell, R. McKeown, D.S. Ojima, W.J. Parton, and W. Pulliam. 1996. Climate and nitrogen controls on the geography and timescales of terrestrial biogeochemical cycling. *Global Biogeochemical Cycles* 10:677–92.

Schimel, D.S., W. Emanuel, B. Rizzo, T. Smith, F.I. Woodward, H. Fisher, T.G.F. Kittel, R. McKeown, T. Painter,N. Rosenbloom, D.S. Ojima, W.J. Parton, D.W. Kicklighter, A.D. McGuire, J.M. Melillo, Y. Pan, A. Haxeltine, C. Prentice, S. Sitch, K. Hibbard, R. Nemani, L. Pierce, S. Running, J. Borchers, J. Chaney, R. Neilson, and B.H. Braswell. 1997. Continental scale variability in ecosystem processes: Models, data, and the role of disturbance. *Ecological Monographs* 67:251–71.

Schimel D.S., J.I. House, K.A. Hibbard, P. Bousquet, P. Ciais, P. Peylin, B.H. Braswell, M.J. Apps, D. Baker, A. Bondeau, J. Canadell, G. Churkina, W. Cramer, A.S. Denning, C.B. Field, P. Friedlingstein, C. Goodale, M. Heimann, R.A. Houghton, J.M. Melillo, B. Moore, D. Murdiyarso, I. Noble, S.W. Pacala, I.C. Prentice, M.R. Raupach, P.J. Rayner, R.J. Scholes, W.L. Steffen, C. Wirth. 2001. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature* 414 (6860): 169–172

Thornton, P.E., B.E. Law, H.L. Gholz, K.L. Clark, E. Falge, D.S. Ellsworth, A.H. Goldstein, R.K. Monson, D. Hollinger, M. Falk, J. Chen, and J.P. Sparks. 2002. Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agricultural and Forest Meteorology* 113:185–222.

Valentini, R., G. Matteucci, A.J. Dolman, E.D. Schulze, C. Rebmann, E.J. Moors, A. Granier, P. Gross, N.O. Jensen, K. Pilegaard, A. Lindroth, A. Grelle, C. Bernhofer, T. Grunwald, M. Aubinet, R. Ceulemans, A.S. Kowalski, T. Vesala, U. Rannik, P. Berbigier, D. Loustau, J. Guomundsson, H. Thorgeirsson, A. Ibrom, K. Morgenstern, R. Clement, J. Moncrieff, L. Montagnani, S. Minerbi, P.G. Jarvis. 2000. Respiration as the main determinant of carbon balance in European forests. *Nature* 404:861–65.

Vukicevic, T., B.H. Braswell, and D. Schimel. 2001. A diagnostic study of temperature controls on global terrestrial carbon exchange. *Tellus* B53:150–70.