CHAPTER 19

The Harvard Forest and Understanding the Global Carbon Budget

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Why Make CO₂ Flux Measurements at Harvard Forest?

Harvard Forest today is very different from the forest that existed before European settlement; trees are smaller and younger, and the forest is composed of different species. There are more red oak, red maple, and paper birch (and other species typical on disturbed lands) and fewer hemlock, beech, yellow birch, and spruce. Chestnut have been eliminated by introduced disease. Harvard Forest today is more similar to the forests of the Middle Atlantic region and less like forests of colder climates in northern New England, as compared with the seventeenth century.

The evidence collected in previous chapters indicates that several hundred years would be required for Harvard Forest to attain the status of “old growth,” and this is true for similar tracts throughout New England. We can imagine that if the forest remained undisturbed for such a long period, the processes of growth and decay, recruitment of seedlings, and death of old trees would attain an approximate balance. A large area might have to be considered, however, in order to find this “steady state,” since we must encompass an ensemble of patches of different ages and disturbance history.

Only 100 to 150 years have passed since the agricultural era and not yet 70 years since the devastating hurricane of 1938. The climate today is warmer than the climate during the sixteenth century. Forested lands are virtually all manipulated and harvested in various ways to realize and enhance economic value. Cycles of repeated disturbance and succession, creating even-aged stands 50 to 100 years old, are typical of vast areas of forests in the United States today. “Equilibrium” forests, if they ever existed here, are unlikely to be seen again on any broad scale in central Massachusetts, or in most regions of North America.

Recent evidence indicates that the large areas of young and mid-successional forests in North America may represent a significant sink in
the global budget for atmospheric CO₂. Atmospheric measurements of CO₂ consistently show an imbalance between global inputs of CO₂, from combustion of fossil fuel, and the accumulation of CO₂ in the atmosphere. For example, in the decade 1980–90, the “missing” (unaccounted) uptake of CO₂ amounted to approximately 1.5 gigatons of carbon per year (1 gigaton = 1 billion metric tons, or 10^12 kilograms), equivalent to about 30 percent of the input from fossil fuel (Table 19.1). Even larger amounts are “missing” in the 1990s. Other data show that this uptake of CO₂ is associated with release of oxygen and with increase of the ^13C/^12C isotopic ratio in CO₂, both indicating that “missing” carbon has been converted into organic matter. From one year to the next, the unaccounted uptake varies by a factor of three or more, implying sensitivity to El Niño and other climatic fluctuations. Were sequestration of CO₂ by forests and other vegetation to cease, the annual increase of atmospheric CO₂ would be 50 to 100 percent greater than observed in recent decades.

**Motivating Questions**

Do the forests of the northeastern United States contribute significantly to sequestering atmospheric CO₂? The spatial patterns of CO₂ concentrations in the atmosphere suggest substantial areas of uptake in northern middle latitudes, with one study pointing toward the temperate forests of North America in particular. We would like to know whether this region is indeed a significant sink and to understand the factors regulating the amount taken up. Therefore, one objective of the studies at the Harvard Forest is to assess how long sequestration might continue, how much carbon might be stored, and for how long it may persist as organic matter. A related goal is to learn how to manage forests to optimize economic, aesthetic, and environmental benefits.

This interest provided strong motivation for initiating the long-term study of carbon fluxes at the Harvard Forest described in Chapter 10. We

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**Table 19.1. Global CO₂ Budget (Pg C yr⁻¹), 1980–1990**

<table>
<thead>
<tr>
<th>Sources</th>
<th>1980–1990</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fossil fuel + cement</td>
<td>5.3</td>
</tr>
<tr>
<td>Tropical deforestation</td>
<td>1.2</td>
</tr>
<tr>
<td>Total</td>
<td>6.5–7.3</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Sinks</th>
<th>1980–1990</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atmospheric accumulation</td>
<td>3.2</td>
</tr>
<tr>
<td>Ocean uptake</td>
<td>2.1</td>
</tr>
<tr>
<td>“Missing sink”</td>
<td>1.2</td>
</tr>
<tr>
<td>Total</td>
<td>6.5–7.3</td>
</tr>
</tbody>
</table>

*Note: 2.1 Pg C = 1 ppm atmospheric CO₂ (Ciais et al. 1995).*
wanted to know whether the Harvard Forest is storing carbon at rates large enough to be consistent with the sink inferred in global carbon budgets. Would factors found to regulate carbon uptake at the Harvard Forest help elucidate causes of year-to-year variations observed in the global budget? Would we find that the ecosystem responds to environmental variations as predicted by models based on process studies (such as described in Chapter 17)?

**Approach**

New types of observations and a new strategy for long-term measurements were developed to answer these questions. The carbon budget for the entire ecosystem was measured accurately, for many years. The factors that regulate net carbon uptake had to be determined quantitatively. We needed additional information beyond that available from the two principal methods used before 1990 to estimate carbon sequestration:

- **Biometric surveys**, such as carried out in the U.S. Forest Service Forest Inventory Analysis (FIA), estimate net changes in aboveground wood volume by measuring the diameters of tree boles at thousands of locations across the United States. Long intervals (years to decades) between samples are required to allow time for significant change in volume, making it impossible to resolve responses of the ecosystem to seasonal or annual climatic anomalies. Changes in soil organic matter are not measured. The FIA is intended to assess current harvestable stocks of wood and therefore does not give the amount of timber removed over time from the stands nor account for reclassification of land to nonforest uses. Complex calculations are required to estimate carbon fluxes from the observed wood volumes, and the results are very difficult to check. Nevertheless, the FIA provides important regional and national information and a critical constraint on carbon fluxes and budgets in forests.

- **Ecological process studies**, such as measurements of rates for leaf photosynthesis or soil respiration, record the response of components of the forest system to environmental conditions over short time intervals. To assess net carbon exchanges, we have constructed computer models to aggregate these observations to the relevant spatial scales (whole ecosystems, landscapes) and time intervals (seasons, years). Before the eddy flux studies, there were no data to test these models on timescales from hours to years. Our observations test critical aspects of these models, providing a quantitative measure of effects of factors that influence net carbon balance on long timescales, such as climate change and forest succession.

Harvard Forest proved to be the ideal setting for the first long-term study using continuous direct flux measurements. The infrastructure and long-term ecological data base provided the means for us to develop new instrumentation and methods. The ongoing collection of ecological data and coordinated manipulations and demonstrations is an important tool for understanding the processes that control carbon exchange.

The first step was to adapt the flux-tower covariance method for measuring carbon exchange (see Chapter 10). We wished to conduct long-term process studies by aggerating many years. The next step was to obtain the observed and estimated values of net carbon exchange in terms of time of year, day of year, and weather, establishing rigorous data collection and management procedures. We used these data to test the hypothesis that the ecosystem is capable of adapting to changes in climate, including those resulting from global warming. This analysis established the potential for ecosystem adaptation to climate change, demonstrating the importance of key carbon exchange processes in regulating carbon storage and fluxes across the landscape.

These papers provided the inspiration for a new network of tower flux sites in the United States, Canada, and several other countries, including those in the southern hemisphere. The Harvard Forest ecosystem flux tower became a key site in this network, providing a unique opportunity to study the role of forests in the global carbon cycle.

**A New Way of Seeing**

The long-term flux data provide a new way of seeing the ecosystem processes at work. The data span timescales from extremely fine, such as daily monitoring of carbon exchange, to interannual, with the focus remaining on the local ecosystem. The data also provide a new way of seeing the landscape, connecting local processes to the larger scale.

Figure 19.1 shows the average carbon exchange for eight years of data, October to November, each hour and day of a mean of 3 days. The data show the response of the ecosystem to fluctuations in solar input and temperature. The data can be used to identify periods of high and low carbon exchange, as well as periods of high and low carbon storage. The data also show the response of the ecosystem to seasonal changes in climate, such as the increase in carbon exchange during the growing season.

Uptake of CO₂ appears dramatic during the growing season, but the data also show that the ecosystem continues to exchange carbon during the winter months. The data provide a new way of seeing the ecosystem, highlighting the importance of seasonal and interannual variations in carbon exchange.

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The first step was to adapt for long-term, automated studies the eddy covariance method for measuring fluxes at the ecosystem scale (see Chapter 10). We wished to apply this technique, developed for shorter-term process studies by agricultural scientists, to studies in forests spanning many years. The next step was to show that the observations obtained using this technique could be aggregated to long time periods accurately; that is, that systematic errors could be controlled sufficiently to resolve the important features of ecosystem carbon sequestration. A series of papers published between 1993 and 1996 provided these demonstrations. We used the vast numbers of measurements and the repeated patterns of diurnal and seasonal variations to test and dissect the data set, establishing rigorous quantitative bounds for errors and biases. This analysis established the capability of eddy flux data to record rates of key carbon exchange processes for time intervals as long as a decade. These papers provided the impetus and conceptual foundation for several networks of tower flux measurement sites established in North America, Europe, and Japan since 1995. In 2001, there were more than fifty long-term flux sites in operation.

**A New Way of Seeing the Forest**

The long-term flux data set provides an extraordinarily rich view of ecosystem processes, with quantitative resolution spanning timescales from extremely fine grained (thirty minutes) to decadal. Examining these data is like looking at a huge photograph of a city, in which the focus remains sharp whether viewed from a great distance, taking in the whole landscape, or from very close, looking at the salad at the local pizza parlor.

Figure 19.1 shows the average rates of CO₂ sequestration and release for eight years of data, October 1991 to September 1999, representing each hour and day of a mean year. We have measured over and over again the response of the forest to environmental changes: daily variations of solar input and temperature, precipitation events, synoptic weather changes, and seasonal variations of temperature and day length. The waxing and waning of rates for respiration, associated with seasonal warming and cooling and wetting and drying, are clearly defined by data from thousands of nighttime observations. The data define both the mean conditions shown in the figure and the deviations from the mean caused by environmental variance.

Uptake of CO₂ appears dramatically in May, when the forest canopy develops. The date when this happens varies, with shifts of up to two weeks in the timing of leaf-out and the onset of photosynthesis. Varia-
Figure 19.1. Three-dimensional view depicting net carbon exchange at the Harvard Forest versus time of day and day of year, averaged over eight years of observations (October 1991–September 1999). Top: Seasonal and diurnal variations of ecosystem respiration (summer, nights; winter, all hours) viewed from “above.” Bottom: Another perspective from “below,” showing the average year of net uptake of CO$_2$ at the Harvard Forest, providing perspective on the seasonal onset and decline of carbon sequestration.

Tation in the timing of the onset of spring can have a major effect on forest processes, as up to 1 additional ton of carbon per hectare per year can be fixed as a consequence of early canopy development. Maximum daily rates of uptake of CO$_2$ are observed in July, with gradual declines through August and September. The date for the end of the growing season, in early October, generally varies less, and its effect on carbon fixation is even smaller (only about 0.2 tons carbon per hectare) because there is much less incident sunlight on the forest in October than in May, and leaves have lost much of their capacity for photosynthesis.
The Short and the Long: Instantaneous Response versus Emergent Properties

The data show dramatically that the very nature of the interaction between the forest and the environment depends on the time interval of interest. The environmental parameters important for controlling CO$_2$ uptake at short timescales are different variables from those important at longer timescales. At first this may seem odd. Isn’t growth and decay of the forest over a year just the sum of net CO$_2$ exchange over each hour?

Let’s consider a simple analogy to illustrate why different factors come into play when we average results over different time intervals. Suppose I ride an escalator that is moving very slowly, so that it takes all day to ascend to the next floor. It’s boring, so I practice throwing and retrieving a yo-yo. When an observer measures the motion of the yo-yo for short times, s/he sees my throwing and retrieving. Slow progress on the escalator appears as a slight bias in the trajectory of the yo-yo, each throw on average being a little farther along than the last one. But I don’t throw the yo-yo the same each time, so the yo-yo doesn’t go up uniformly. Upward progress can be detected only if the observer carefully averages the results of many throws or compares accurately positions at the start and end. The yo-yo motion over short timescales, rapid with large amplitude, tells the observer how fast I throw, perhaps how tall I am, or that I am left-handed. Gradual movement over the day provides completely different information: slope, rate, and length of the escalator.

Hour-to-hour variations of net carbon exchange reflect ecosystem response to temperature and incident sunlight, the basic driving variables that control the metabolism of trees and microbes. The living biomass of vegetation and soils must respire to sustain life. Trees convert CO$_2$ to organic matter if roots have water and nutrients and the trees have leaves and sunlight. The rate of respiration increases with temperature, and the rate of photosynthesis increases with the quantity of sunlight, almost instantly. We use as an index of the temperature of the whole forest the temperature right near the surface of the soil, denoted $T_s$. The amount of sunlight for photosynthesis is denoted photosynthetically active radiation (PAR). Our measurements accurately capture the variations of these key variables, hourly and through the year (Figure 19.1), as well as the response of the forest ecosystem in terms of respiration, $R$; photosynthesis, GEE (gross ecosystem exchange); and net ecosystem exchange, NEE (see also Chapters 3 and 10). These variations in forest metabolism of CO$_2$ are similar to the throwing and retrieving of the yo-yo in our analogy, short-term and large amplitude. These are the instantaneous properties of the ecosystem.

Long-term averages of rates for respiration or photosynthesis by the forest as a whole evidently depend on many factors other than PAR and
\( T_e \). The total amount of living biomass, the quantity of detritus and its susceptibility to decomposition, and the available reservoir of plant nutrients are key factors. The inventories of nutrients and of living and dead organic matter require decades or centuries to accumulate. Water and nutrients in the soil, needed to nourish plants and microbes alike, play key roles in regulating rates for both respiration and photosynthesis. Trees must have leaves to conduct photosynthesis. Soil moisture and the forest canopy develop over seasonal timescales. These factors do not change hour by hour. Their influence shows up only as subtle shifts in the relationships between \( R, GEE, \) and \( NEE \) with \( PAR \) and \( T_e \).

The long-term average behavior and slowly changing drifts are the emergent properties of the ecosystem, analogous to the properties of the escalator in the yo-yo analogy.

More than 90 percent of the hourly variations observed in eight years of data can be reproduced by a very simple function of \( PAR \) and \( T_e \),

\[
NEE = a_1 + a_2 T_e + \frac{a_3 PAR}{a_4 + PAR}
\]

(1)

as illustrated in Figure 19.2. The magnitudes of the parameters \( \{a_1, a_2, a_3, a_4\} \) derived from our observations are important, quantitative measures of ecosystem metabolism and of the instantaneous response of the ecosystem. Once we have obtained \( \{a_1, a_2, a_3, a_4\} \), we can analyze the data set to obtain the emergent properties, hitherto difficult to measure using the same methods as used for the instantaneous properties. We can then discover the extent to which net uptake of \( \text{CO}_2 \) by the forest is regulated by long-term changes in fundamental forcing variables \( (PAR, T_e) \) versus regulation by long-term changes in the ecosystem itself. Have climatic changes (annual trends or variations in cloudiness or temperature) affected \( PAR \) and \( T_e \), and do these trends measurably affect long-term uptake of \( \text{CO}_2 \)?

To answer these questions we examine the deviations from average fluxes observed each year and compare these with climatic anomalies. Some of the changes in \( NEE \) from month to month and year to year directly reflect variations in \( PAR \) and \( T_e \), and the ecosystem response can be computed from our simple “instantaneous” equation (Figure 19.2). Mostly this is not true, however, and the emergent properties are controlled by different factors.

Compare, for example, the drought year of 1995 with other years (Figure 19.2; see Chapter 10). There was more sunlight than average during July and August 1995 and thus more photosynthesis. The large trees mined deep soil moisture and happily continued to fix \( \text{CO}_2 \), more, in fact, than during an average summer. However, Equation 1, driven by \( PAR \) and \( T_e \), failed to capture important effects. The efficiency of the forest in using light was lower because ferns and shrubs on the forest floor and understory and small trees and seedlings understory were lower than average, and the decline of herbs and shrubs in composition by soil fungi and...
the quantity of detritus and its available reservoir of plant nutrients and of living and dead plant material, centuries to accumulate. Water availability, temperature, and light, respiration and photosynthesis are the most important factors. Soil moisture availability on a daily basis, and light availability also change with PAR and T (Equation 1), so that both variables are important in determining the properties of the ecosystem. The diurnal variation in observed (black) and calculated (gray) net ecosystem exchange based on hourly values using the simple function of Equation 1 (see text). Each “day” shown in the figure represents the composite of five days; that is, we have averaged the data for each hour of August 1–5, 6–10, etc., in order to display the results compactly for each of the eight years of data. Note the remarkable fidelity of the calculations to variations in the rates of both photosynthesis (daytime, negative values) and respiration (nighttime, positive values).

Figure 19.2. Diurnal variation in observed (black) and calculated (gray) net ecosystem exchange based on hourly values using the simple function of Equation 1 (see text). Each “day” shown in the figure represents the composite of five days; that is, we have averaged the data for each hour of August 1–5, 6–10, etc., in order to display the results compactly for each of the eight years of data. Note the remarkable fidelity of the calculations to variations in the rates of both photosynthesis (daytime, negative values) and respiration (nighttime, positive values).

est in using light was lower than average by approximately 10 percent because ferns and shrubs on the forest floor dried out and shriveled up and understory and small trees were also water stressed. Rates for respiration were lower than average despite warmer temperatures, reflecting the decline of herbs and shrubs and the lack of moisture to sustain decomposition by soil fungi and bacteria to process surface leaf litter from

\[ \text{Net Ecosystem Exchange (\mu m^2 \text{m}^{-2} \text{sec}^{-1})} = \frac{a_1}{a_2 + \text{PAR}} \]

The values of the parameters \(a_1\), \(a_2\), \(a_3\), \(a_4\), \(a_5\), and \(a_6\) are important, quantitatively measuring instantaneous response of the ecosystem to changes in climatic conditions. The hitherto difficult to measure and estimate fluxes of \(a_1\) and \(a_2\) are measurable properties. We can thus measure the rate of \(a_1\) and \(a_2\) by the forest is regulated by the climatic forcing variables (PAR, T) and \(a_3\) is the ecosystem itself. Have climate properties in cloudiness and temperature that measurably affect long-term trends and the deviations from average long-term climatic responses with climatic anomalies. These seasonal and annual variations in the ecosystem response can be modeled using a “composite” equation (Figure 19.2). Variation in emergent properties are considered in the evaluation of the model of 1995 with other years. On average, the trees received more sunlight than average during the growing season. The large trees continued to fix \(a_1\), more, in this period. However, Equation 1, driven by climatic conditions, explains the efficiency of the forest's carbon uptake and storage.
the previous fall, which dries readily. August 1995 showed greater-than-average net uptake of CO₂ (Figure 19.2), but the increase was less than predicted from Equation 1. Moreover, the “leftover” litter (undecomposed from this dry period) provided a positive anomaly in respiration later on, and there was tree mortality with little effect in 1995 but considerable significance for the future. On an annual basis (Figure 19.3), 1995 showed uptake stronger than predicted due to lots of sunshine in July before drying of the surface soil, but the summer anomaly favoring uptake was largely canceled out by anomalies at other times of year.

These observations reveal the quantitative effects of factors that control CO₂ uptake on timescales of a season, that is, soil moisture and the extent of persistence or removal of relatively fresh, easily decomposed detritus from the previous fall. It is not difficult to include soil moisture in an elementary model of the Harvard Forest (a small elaboration of our simple equation), and it is tractable, although somewhat trickier, to account for the carryover of short-lived organic matter such as leaves. We can readily account for the other major seasonal factors, the length of the growing season, and its effect on the timing of leaf-out and leaf senescence, using our data on PAR, Tₑ, and transmission of PAR through the canopy. When we do this, we attain quite respectable predictive capability for each month. But even a model accounting for soil moisture and carryover of litter does only a rough job of predicting year-to-year changes in CO₂ net uptake (Figure 19.3). We will need to account for tree maturation and mortality, production and decay of coarse woody debris, and succession of species in order to understand the longest-term trends in net CO₂ uptake for forests.

**New Knowledge about Northeastern Forests and New Questions**

The first major result from the study is confirmation that the Harvard Forest currently takes up significant CO₂ from the atmosphere, on average about 2 tons of carbon for each hectare per year. The total land area in North America and Europe with similar age structure and comparable (or more favorable) soils and climate is 200 to 400 million hectares. Hence, the data clearly show that the potential is there for forests such as these to take up a significant fraction of the “unaccounted” carbon, roughly 0.25 to 0.50 gigatons of carbon per year. Data from a single site cannot of course establish the global net exchange; data from many other sites are needed to determine a meaningful global estimate, along with a much better understanding of the age structures, vegetation assemblages, and management regimes for those 200 to 400 million hectares. Some early work along these lines in the AmeriFlux network of sites provides intriguing evidence that temperate forests worldwide are indeed important in restraining the long-term rise in CO₂.

Examination of monthly data provided many surprises (Table 1). The disturbance clearly provides a short-term boost in uptake, with net sequestration in May 1997 of 50 to 100 years predicted in current with continued rapid decline. The coordinate of the vegetation assessment is an earlier research at the Harvard Forest (Stephens’s historical reconstructions of the decline of earlier pioneer species). The longevity of the species (such as the warming depending on the lengthening of the growing period, but the large magnitude of the effect being dramatic and different than expected: the gestation of soil moisture content and greenhouse gases).
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but the increase was less than
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Western Forests

Study is confirmation that the
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worldwide are indeed important sinks for atmospheric CO₂ that help to
restrain the long-term rise in CO₂ concentrations.

Examination of monthly, seasonal, and interannual anomalies pro-
vided many surprises (Table 19.2). The legacies of prior land use and
disturbance clearly provide the long-term driving force for carbon up-
take, with net sequestration persisting well beyond the approximately
50 to 100 years predicted in some models. This driver is associated cur-
cently with continued rapid growth and maturation of the red oak com-
ponent of the vegetation assemblage, a phenomenon well-described in
earlier research at the Harvard Forest by Chad Oliver, using some of Earl
Stephens's historical reconstructive techniques. It also coincides with
the decline of earlier pioneer species with low wood density and rela-
tively short lifetimes (such as red maple and birches). Effects of climatic
warming depend on season but clearly favor net carbon uptake due to
lengthening of the growing period. This result by itself is hardly surpris-
ing, but the large magnitude of this factor was unexpected.

The influence of summertime droughts on net annual uptake is dra-
matically different than expected because of time lags and the hetero-
geneity of soil moisture content noted above. Drought summers were,
paradoxically, banner years for carbon sequestration at the Harvard For-

Figure 19.3. Annual net sequestration of carbon at the Harvard Forest, observed and predicted
using Equation 1 (see text). If predictions were perfect, all points would lie on the (1:1) line.
Variance of monthly and annual sums evidently is not reliably predicted by hourly data for PAR
and $T_e$. 

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Table 19.2. Carbon Sequestration in Forests: Expectations versus Results, Harvard Forest

<table>
<thead>
<tr>
<th>Expectations</th>
<th>Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>Uptake of CO₂ (photosynthesis): limited by light, water, nutrients; insensitive to T, short season (near optimum)</td>
<td>Uptake of CO₂ (photosynthesis): very sensitive to short season, light and water; large increase in CO₂ uptake in warm years</td>
</tr>
<tr>
<td>Land cover change → small CO₂ uptake: reforestation after agriculture completed</td>
<td>Land cover change → big CO₂ uptake: reforestation after agriculture creates a long-lasting legacy, amplified by warming</td>
</tr>
<tr>
<td>Decomposition and respiration very sensitive to temperature → strong release of CO₂ with warming</td>
<td>Decomposition and respiration temperature limited in winter, but water limited in summer → weak T ↔ respiration response</td>
</tr>
<tr>
<td>Carbon storage in temperate forests expected to cease after 50–100 years after reforestation and to decrease in response to climate warming.</td>
<td>Carbon storage in temperate forests persists for &gt;100 years after reforestation and increases in response to climate warming.</td>
</tr>
</tbody>
</table>

est, but the following years were low-uptake years. Some of the forest components were still affected by stress and mortality from the drought, and there was more-than-average readily decomposed organic matter on the forest floor. Thus, the effects of drought enhanced uptake in the near term and reduced uptake later.

Even in the Northeast, the immediate effects of drought may differ among sites, depending on soil depth and moisture-holding capacity. For example, in 1997 Xuhui Lee of Yale University observed net release of CO₂ at an oak-dominated site at the Great Mountain Forest in northwestern Connecticut, not far from the Harvard Forest. This site is on a ridge top and has much shallower soils, and leaf senescence occurred weeks early. Evidently, to assess regional or global effects of the climate anomalies of 1997, we would need to observe the responses of forests over major land areas, which could be obtained from remote sensing. We would also need observations of net CO₂ exchange from representative sites, which can be obtained from towers like the Harvard Forest EMS.

The results have provided a new way of viewing ecosystem processes. Formerly, the only way to study ecosystem carbon flows with fine resolution over long timescales and large spatial scales was to develop and exercise models that incorporate results of small-scale studies of ecosystem processes. Sometimes, it is not possible to compute carbon uptake from environmental, physiological, and meteorological data alone, and it is impossible to check these calculations against long-term flux data, when the structure of the ecosystem (for example, the number and composition of leaves), demography and turnover of organic matter and respiration, provide a more reliable check and to develop new concepts.

Table 19.2 summarizes the many slow, slowly varying environmental reactions before the start of the event. The forest community was rather different from what was expected.

- Over most of North America, the drought persisted for years. Summertime temperatures were high, but rates of respiration were therefore expected to decrease. This caused an increase in the intake of CO₂. The opposite effect was observed in winter, when temperatures have in fact not changed much. Summer values were observed in winter and vice versa. The strength of the ecosystem response was stronger than expected.

- The forest is relatively old, with some patches of forest in the Northeast, and these patches would not have been affected by the drought. Outgrowing red maples formed a new forest, and the old forest showed an increase in net primary productivity, such as the leaf area index.

- Most ecosystem models represented the situation in a very simplified manner. It was not recognized that episodic changes in the forest, such as the loss of a major species, had the opposite sign and magnitude.

A summary of what we have learned from our long-term study is presented in Figure 19.4. The time course of the rise in CO₂ uptake by trees, the amount of organic matter in the forest, and successional replacement of carbon by the forest, are significantly different in the growing season and in snow cover have also been observed, with the lengthening of the growing season being the most important factor. It is hard to define unambiguous results from these processes, but any negative effects of air pollution have not been observed.
of ecosystem processes. Some of these models are very complex and attempt to compute carbon uptake and release in terms of diverse environmental, physiological, and ecological parameters. It was difficult or impossible to check these computations by direct measurements. The long-term flux data, when combined with measurements of the structure of the ecosystem (for example, leaf area index and nitrogen content of leaves), demography and growth of trees, and data on soil organic matter and respiration, provide powerful new ways to check the models and to develop new conceptual paradigms.

Table 19.2 summarizes the response of the Harvard Forest to several slowly varying environmental factors and contrasts them with expectations before the start of the eddy flux measurements. What was expected was rather different from what was observed:

- Over most of North America, climate has warmed over the past thirty years. Summertime temperatures are close to the optimum for photosynthesis, but rates for respiration should increase with temperature. It was therefore expected that climatic trends would be linked to decreasing uptake of CO₂. The opposite was observed, for two reasons. Summer temperatures have in fact not changed recently in New England, but warming has been observed in winter and spring, leading to a longer growing season. The strength of the ecosystem response to a longer growing season was stronger than expected.
- The forest is relatively old, seventy to ninety years, compared with many forests in the Northeast, and it was not anticipated that recovery and succession would currently sustain significant annual sequestration of carbon. It is clear, however, that the red oaks are currently overtopping and outgrowing red maples from upland areas through exactly the process documented here by Chad Oliver in the 1970s. Their larger stature and higher wood density lead to net carbon accumulation even though other factors, such as the area index of the canopy, do not perceptibly change.
- Most ecosystem models represent soil hydrology and rooting depths in a very simplified manner. It was not anticipated that dry summer conditions would lead to seasonal transients with more uptake of carbon, nor was it recognized that episodic dry periods would play signal roles in driving the successional replacement of maples by oaks. Thus, the summer drought had the opposite sign and much larger delayed effects than expected.

A summary of what we have learned about the factors regulating monthly and annual net uptake of CO₂ at the Harvard Forest is presented in Figure 19.4. The legacies of the past control the size of the trees, the amount of organic matter in soils, the species composition of the forest, and successional trends. These are the primary drivers for net carbon uptake by the forest. The principal climatic effect has been the lengthening of the growing season over the past thirty years. Variations in snow cover have also been important, but the effects are complex and hard to define unambiguously. We looked for, but were unable to detect, any negative effects of air pollution or episodic droughts. We have been
Why does Harvard Forest take up carbon?

- CO₂ increase
- N-fertilization
- climate warming

Legacies of Land Use ± Hurricane
- maturation of trees
- succession of species
- development of soil organic matter

Organic matter
- ozone pollution
- N-saturation
- timber harvest
- land development
- pests (gypsy moth, adelgids)

Figure 19.4. Controls on the uptake and release of CO₂ at the Harvard Forest. The major factor driving carbon dynamics is recovery from prior agricultural land use, logging, and disturbance by the 1938 hurricane. The rate of uptake is modulated by numerous environmental factors. Factors promoting sequestration or inhibiting decay of organic matter are placed in the upper arrow; others inhibiting sequestration or promoting the oxidation of organic matter are placed in the lower arrow.

able to quantify the effects of these factors, at least to first approximation, with a combination of eddy flux measurements and careful adaptation of more traditional ecological biometric studies.

A number of critical questions remain to be answered, especially in relation to factors that have changed little over the course of the study and to issues on the future course of the forest. Rising levels of CO₂ and inputs of nutrients from fossil fuel combustion are both expected to enhance forest growth, but these factors do not exhibit sufficient variance for us to detect effects in our experiment. Manipulation experiments addressed elsewhere in this volume are needed to understand these factors. We cannot confidently predict the future course of succession of the vegetation assemblage. We note the current dominance of red oak but a puzzling lack of recruitment of oak seedlings. We don’t know what the future climate will be.

We would like to think that studies of the Harvard Forest, and the other sites in the AmeriFlux and Euroflux networks, can tell us what the forests of the United States and Europe are currently doing, and what
they will do in the future, with respect to carbon sequestration. Can we design management strategies to enhance carbon uptake and simultaneously optimize economic return and environmental services (flood and erosion control, aesthetics, pollution uptake, moderation of microclimate)? These are the challenges of the future, to which the work represented in this book is dedicated.