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Factors Controlling Long- and Short-Term Sequestration of Atmospheric CO₂ in a Mid-latitude Forest

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Net uptake of carbon dioxide (CO₂) measured by eddy covariance in a 60- to 80-year-old forest averaged 2.0 ± 0.4 megagrams of carbon per hectare per year during 1993 to 2000, with interannual variations exceeding 50%. Biometry indicated storage of 1.6 ± 0.4 megagrams of carbon per hectare per year over 8 years, 60% in live biomass and the balance in coarse woody debris and soils, confirming eddy-covariance results. Weather and seasonal climate (e.g., variations in growing-season length or cloudiness) regulated seasonal and interannual fluctuations of carbon uptake. Legacies of prior disturbance and management, especially stand age and composition, controlled carbon uptake on the decadal time scale, implying that eastern forests could be managed for sequestration of carbon.

The terrestrial biosphere has sequestered significant amounts of atmospheric CO₂ since 1980, with major contributions from northern mid-latitude forests (1–3). The sink has varied interannually by a factor of 2 or more, correlating with global-scale climate variations (4–6), and may have increased in the 1990s (3). The magnitude of uptake attributed to mid-latitude forests is controversial, however, partly due to sharp disagreement between atmospheric inverse models and forest inventories (7). The cause of net C uptake is also uncertain, with recent studies variously citing land-use change (8, 9), fire suppression (10), longer growing seasons (11), and fertilization by elevated CO₂ (12) or N deposition (13). These factors must be understood in order to predict growth rates of atmospheric CO₂ and to develop strategies for restraining future increases.

We report here rates of net ecosystem exchange (NEE) of CO₂ for 9 years in a northern hardwood forest (Harvard Forest, 42.5N, 72.2W) measured by using eddy-covariance techniques (14–16). These data are

compared with 8 years of biometric measurements of species-specific changes in C storage in live and dead wood, showing where and how the forest is storing C. We determine the C budget and responses to environmental forcing, including diel variations, weather patterns (14), phenology, and interannual climate variability (15). Eddy fluxes may underreport respiration at night in calm winds (17), and methods for removing this bias (18) remain controversial. Here we address possible errors in eddy-covariance data using the biometric data, and combine the observations to define the causes of C sequestration and its variation on time scales from hourly to decadal.

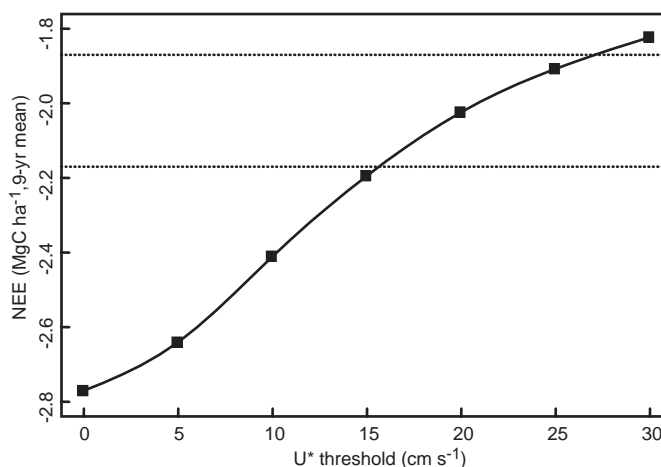
Eddy-covariance data extend from 28 Oc-

tober 1991 to 27 October 2000, with valid data for 46,500 of 79,000 hours. Gaps occurred for calibration, data transfer, intense precipitation, maintenance, equipment failure, and weak vertical exchange ($u^* < 20$ cm s⁻¹) (Fig. 1). Ecosystem respiration (R) was observed directly at night and extrapolated for daytime on the basis of day-night changes in soil temperature (18). Gross ecosystem exchange (GEE) was computed from (NEE – R). The 9-year mean annual NEE, -2.0 Mg C ha⁻¹ year⁻¹, is similar to observations at other forested sites in the northeastern United States (19, 20). Annual sums of NEE at this site are insensitive to u^* within the limits established for valid data (Fig. 1).

Biometric observations of tree growth and accumulation of coarse woody debris (CWD) were initiated in 1993 (21–24) to measure overall CO₂ sequestration and to provide more detailed information about C cycling at the site. Table 1 shows the mean C budget from biometric data. The average total rate of C sequestration, 1.6 ± 0.4 Mg C ha⁻¹ year⁻¹, agrees well with the cumulative sum of eddy fluxes, providing independent confirmation of the C budget from eddy covariance at this site (Table 2 and Fig. 1).

Carbon sequestration on the decadal time scale was driven by historical land-use and disturbance, which determine critical characteristics of the ecosystem. Agriculture at the site was abandoned in the 19th century, and by the 1930s a stand of “old field” white pine was established. A hurricane in 1938 and subsequent salvage removed 70% of the crown area (25) and disturbed the soil, allowing establishment of a hardwood stand dominated by northern red oak (*Quercus rubra* L.). The present stand has 100 Mg C ha⁻¹ above ground, which is ~80% of mean wood C in mature hardwood stands (9, 26). Aboveground woody increment (AGWI) dominated C uptake during 1993 to 2000, accounting for 70% of 8-year mean ecosys-

Fig. 1. Mean annual C uptake from eddy-covariance data versus the hourly-mean value, U^* , adopted for the minimum friction velocity u^* [$\equiv (-\text{momentum flux})^{1/2}$] threshold for valid data. Flux values for periods with $u^* < U^*$ are filled by interpolation (18). Dashed lines show the range of acceptable values for annual NEE (2.02 ± 0.15 Mg C ha⁻¹ year⁻¹) on the basis of the criteria established in (18). Inclusion of flux data with $u^* < 17$ cm s⁻¹ results in underestimation of R. Thresholds of $u^* > 30$ cm s⁻¹ leave insufficient flux data for meaningful annual sums.



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tem net uptake (biometric), a typical proportion for northern hardwoods (27). The rate of AGWI (mean rate of 1.4 Mg C ha⁻¹ year⁻¹) (Table 1) varied little from year to year (Fig. 2) (28). Significant C also accumulated in CWD (Table 1), although less than in live trees, as expected for a maturing forest (9). NEE will likely decline as the stand matures, and the rate of net C storage in CWD should also diminish (9).

Tree growth rates are relatively slow at Harvard Forest (29), possibly due to N limitation in soils (30) resulting from pre-20th century N export in crops and fuel wood.

Nitrogen limitation may also constrain the potential for CO₂ fertilization (31) at Harvard Forest. Deposition of anthropogenic N over past decades may have helped restore fertility, and thus contributed to C storage, but annual N deposition is modest, only ~12% of annual N mineralization (32).

Completely different processes govern NEE on shorter time scales, as shown by eddy-covariance data. Hourly and daily variations in NEE result from prompt ecosystem responses to ambient sunlight and temperature (14, 15). Monthly and seasonal anomalies reflect primarily weather and climate

variations (15). For example, low net uptake in 1998 (Table 2 and Fig. 2) was caused in part by reduced photosynthesis due to low temperatures and excess cloudiness in early summer (33). Net uptake was high in 1995 (15) because ecosystem respiration was depressed by dry surface soil in summer (34).

Seasonal climatic anomalies modify decomposition rates of fine organic matter, such as leaf litter, fine roots, and twigs. The resulting effects on NEE can emerge as variations on annual time scales, aliasing climatic variations. For example, winter anomalies in R (relative to 9-year monthly mean R) were positively correlated with R anomalies in the next growing season (Fig. 3, left panel), indicating that winter weather (e.g., snow cover) significantly influenced rates of decomposition over many months (35). Anomalies in winter NEE showed positive lagged correlations with early spring, when NEE ~ R, but a negative association with NEE in late summer (Fig. 3, right panel). High rates of decomposition in winter appear to stimulate anomalously strong gross uptake in the following summer, possibly by increasing the availability of inorganic nutrients. Turnover times of leaf litter and other fine organic matter are a year or more, allowing seasonal climate anomalies to induce annual and inter-annual variations in C fluxes (36).

Growth rates, like respiration, depend partly on C fixed in previous years (37). Radial tree growth in deciduous trees begins by production of springwood in early May, up to 2 weeks before the daily average NEE becomes negative and before new leaves start to export carbohydrate (Fig. 2) (37, 38). This springwood necessarily derives from stored carbohydrate and is affected by prior growing conditions.

Biometric C budgets should not be expected to reconcile with NEE in a single year due to annual shifts in C fluxes. For example, AGWI composed 100% of NEE in 1998 (Fig. 2), as compared with ~70% for the long-term mean, indicating a transient budget imbalance given expected mortality, belowground growth, and so forth. Episodic tree mortality (0.4, 1.0, and 0.3 Mg C ha⁻¹ year⁻¹ aboveground in 1998 to 2000, respectively) (39, 40) also contributed to annual budget imbalances. More observations are needed to reduce uncertainty in trends of mortality and CWD stocks. Reconciliation of a biometric budget with NEE in a single year is evidently subject to large errors, and several years are required to determine mean rates of C sequestration using either biometry or eddy covariance.

Short-term variations of NEE at Harvard Forest reflect prompt responses of the forest to environmental influences. Interannual variations reflect effects of weather and climate on ecosystem characteristics such as

Table 1. Carbon budget for Harvard Forest from biometry, and NEE (mean of 1993 to 2000, Mg C ha⁻¹ year⁻¹). Numbers in parentheses give the 95% confidence intervals. Belowground fluxes were inferred as 20% of aboveground values (27). CWD respiration was based on 6% mass loss per year (40) from the estimated stock of CWD (39). Mortality uncertainty was not included in error propagation because net C storage due to mortality is zero (tree death transfers C from live to dead pools, giving equal and opposite contributions to AGWI and CWD). Change in soil C is based on the residence time of ¹⁴C in Harvard Forest soils, measured by Gaudinski *et al.* (44).

Component	Totals
Δ Live biomass	
A. Aboveground	
1. Growth (AGWI)	1.4 (± 0.2)
2. Mortality	-0.6 (± 0.6)
B. Belowground (estimated)	
1. Growth	0.3
2. Mortality	-0.1
Subtotal	1.0 (± 0.2)
Δ Dead wood (CWD)	
A. Mortality	
1. Aboveground	0.6 (± 0.6)
2. Belowground	0.1
B. Respiration	-0.3 (± 0.3)*
Subtotal	0.4 (± 0.3)*
Δ Soil (net)	0.2 (± 0.1)
Comparison of budgets	
Σ Carbon budget (NEP)	1.6 (± 0.4)
Σ NEE [× (-1)]	2.0 (± 0.4)

*See (39).

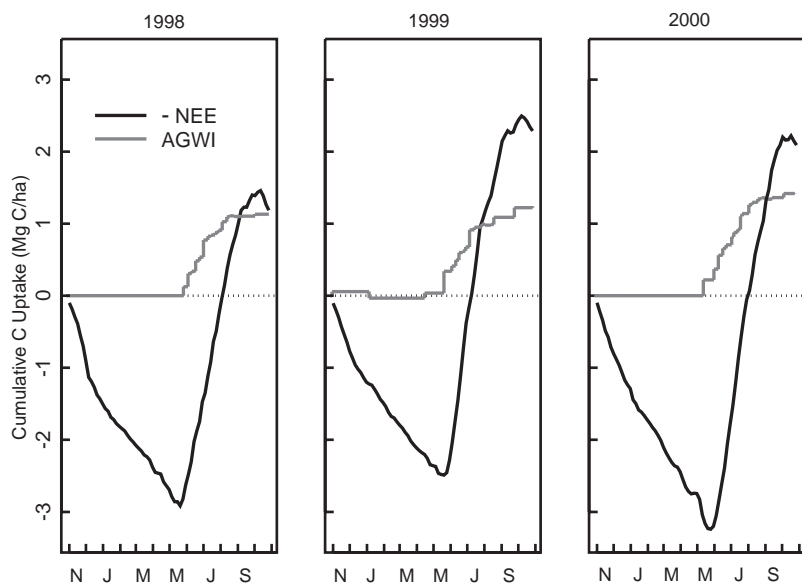


Fig. 2. Cumulative ecosystem net uptake ($-1 \times$ NEE) and AGWI for years with detailed dendrometry.

tree mortality, autotrophic and heterotrophic respiration, pool sizes of labile detritus, length of the growing season, and available light. Because seasonal and annual climatic anomalies are often coherent over large spatial scales (5, 6), the processes described here are important in mediating observed interannual variations of the rate of increase of global atmospheric CO₂.

Rates of long-term C sequestration at Harvard Forest change much more slowly, be-

cause they are driven by ecosystem properties that evolve slowly, i.e., stand composition, biomass and mortality, soil fertility, and CWD pool size. The large areas occupied by mid-succession forests (30 to 100 years old) have been cited as the major factor in present terrestrial uptake of C (41, 42). This work provides support for the view that historical legacies are a dominant factor in C sequestration for these lands. Unlike the environmental factors mediating interannual changes, the age structure, species composition, and health of forest ecosystems are subject to direct human intervention, indicating that long-term rates of C sequestration can be deliberately manipulated (43) through forest management.

Table 2. Annual CO₂ exchange (summed from 28 October of the previous year to 27 October of the nominal year). Negative values indicate CO₂ flux from the atmosphere to the ecosystem (i.e., storage).

Year	NEE	Annual exchange (Mg C ha ⁻¹ year ⁻¹)	
		GEE	R
1992	-2.0	-11.4	9.5
1993	-1.9	-13.3	11.4
1994	-2.0	-12.3	10.3
1995	-2.5	-12.3	9.9
1996	-2.0	-13.2	11.3
1997	-2.1	-13.9	11.8
1998	-1.2	-12.1	10.9
1999	-2.3	-13.9	11.6
2000	-2.1	-14.3	12.2
Mean	-2.0	-13.0	-11.0

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21. The biometric study measured net ecosystem production (NEP) by making sequential inventories of pools of C with relatively long turnover times (i.e., wood, dead wood, and soil; fine roots and litter stocks were not inventoried, but leaf litter fall was measured). NEP is equivalent to $-1 \times NEE$, and to net primary production (NPP) minus heterotrophic respiration. In July 1993 we measured diameter at breast height (DBH) of all trees > 10 cm DBH in 40 300-m² plots, randomly located within 100-m segments of eight 500-m transects extending northwest and southwest (the dominant wind directions, four transects along each direction) from the eddy-covariance tower. Live trees from the original sample plus trees grown into the 10-cm DBH size class (824 trees) were remeasured and fitted with steel dendrometer bands in April 1998. In 1998, 1999, and 2000, tree circumference was measured weekly in the growing season and at three other times per year. Woody biomass was calculated by using DBH and allometric equations (22). Aboveground wood increment (AGWI) was the annual increase in woody biomass of live trees; tree mortality (M) was determined separately at the end of each year [i.e., change in live, aboveground woody biomass ($\Delta AGWB$) = AGWI - M]. One hundred and fifty trees were fitted with a second band in the spring of 2000 to determine corrections for settling, applied to 1998 AGWI. DBH was also rechecked with tapes in October 2000. Coarse woody debris (CWD, dead wood > 7.5-cm diameter) was surveyed in 27 of 40 plots. CWD biomass was calculated by using measured volumes (23) and densities from a study of northern hardwood CWD at similar latitude and elevation (24). Leaf litter was collected weekly during September to November from three 0.13-m² traps per plot, sorted by genus, dried, and weighed. Dry biomass was assumed to be 50% C in live wood, CWD, and leaf litter.
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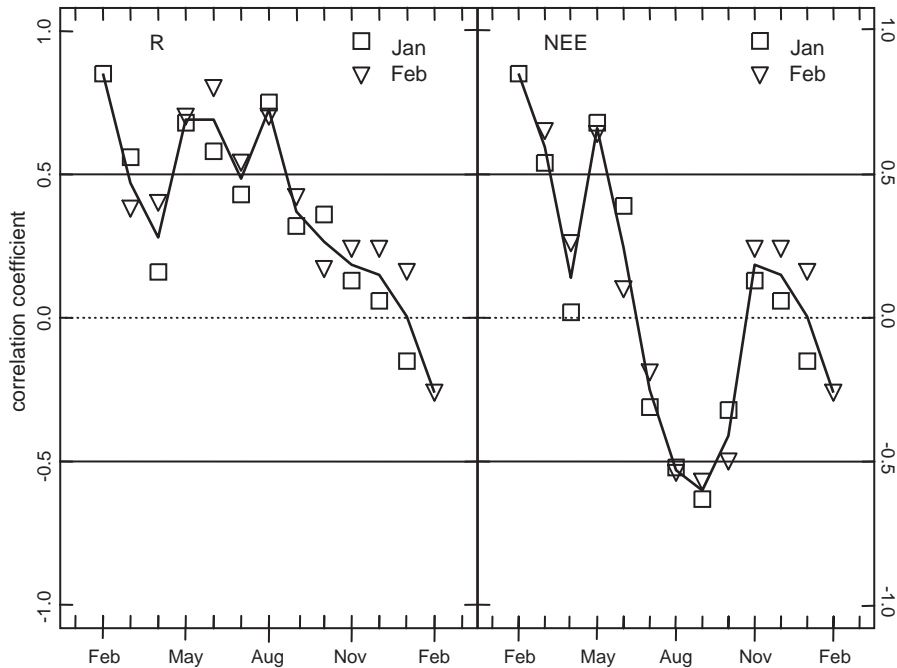


Fig. 3. Correlations of anomalies in NEE and R. Eddy-covariance data were block-averaged into monthly intervals, and anomalies were computed relative to the 9-year monthly averages. Coefficients (r) of correlations between the anomalies of R in winter (January and February) and anomalies of R in subsequent months (x axis) are shown in the left panel. Correlations between winter and subsequent anomalies in NEE are shown in the right panel. Note that during November through February, NEE ≈ R. The set of correlation coefficients observed here is significant at the 95% confidence level (assuming a null hypothesis in which anomalies at lags < 3 months are autocorrelated, the probability of observing this pattern of correlations at lags ≥ 3 months with |r| > 0.5 is < 0.05 for both R and NEE) (33).

ration, because annual litter fall in our study was quite consistent (e.g., 1.30 and 1.37 Mg C ha⁻¹ in 1998 and 1999, respectively).

36. See www.lternet.edu/hfr/symposium/symp01/symp01abs.html#davidson
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38. The daily average NEE at Harvard Forest normally becomes negative in late May (16). This roughly coincides with the date that new leaves begin to export C to the trees (>50% leaf expansion) (37). See Harvard Forest phenology data at www.lternet.edu/hfr/data/hf003/hf003.html.
39. Annual variation in tree mortality did not contribute directly to uncertainty in the biometric C budget (see Table 1), but did add uncertainty to the estimate of the mean CWD respiration rate. To find this rate, we began with the current (year 2000) measured stock of aboveground CWD (7.5 Mg C ha⁻¹; composed of 5.5 Mg C ha⁻¹ standing snags and 2.0 Mg C ha⁻¹ logs). We then calculated the aboveground CWD present midway through the study, assuming constant tree mortality (mean mortality for 1993 to 2000 = 0.64 Mg C ha⁻¹ year⁻¹ aboveground). We assumed dead woody roots = 20% of aboveground CWD (27). We then calculated 6% annual loss of C (40) from the total time-averaged CWD pool. The confidence interval for CWD respiration (and thus for ΔCWD) reflects only the statistical uncertainty in the CWD pool size. There was no statistical basis for estimating the uncertainty associated with our choice of 6% annual respiration of CWD, and therefore we omitted it from the overall budget. Thus, it is possible that the confidence interval about the estimate of NEP should be slightly larger. However, we believe that the central estimate is conservative because the majority of standing snags in the CWD pool argues against rapid CWD decomposition.
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