

## Carbon exchange of an old-growth eastern hemlock (*Tsuga canadensis*) forest in central New England<sup>†</sup>

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**Summary** Carbon (C) exchange of a ~200-year-old eastern hemlock (*Tsuga canadensis* L.) forest in central Massachusetts, USA, was estimated from mid-October 2000 through October 2001 based on eddy covariance measurements and statistical modeling from microclimatic data. Measurements were made in 68% of the hours during the year of study, with > 50% coverage in all months except December and August. Data were filtered by wind direction and atmospheric turbulence to remove invalid measurements. Analysis of filtered data showed that photosynthetically active radiation (PAR) was significant in predicting C exchange, except during the winter. Daily minimum air temperature affected C exchange in autumn and winter, whereas time of day, water vapor pressure deficit and air temperature had significant effects on C storage in spring, summer and fall. Most C storage in the stand occurred in April through July and in October 2001, with maximum rates in April and May. Persistent cold weather prevented C storage in December through March. In early spring 2001, C uptake was sensitive to nocturnal frost: daily minimum air temperatures below 0 °C reduced C fixation, and minima below –5 °C caused its virtual cessation. Soil temperature was a poor predictor of C balance during this period. In August, high soil and air temperatures (averaging 16.7 and 21.1 °C, respectively) drove high ecosystem respiration, which approximately balanced C uptake. These patterns show potential for stimulated C storage in hemlock forests in a warmer climate with fewer spring and autumn frosts, but reduced C storage during warmer summers. Estimated annual C storage was 3.0 Mg ha<sup>-1</sup>, which is higher than for younger coniferous and deciduous forests during earlier years in the northeastern USA. Long-term data are needed to determine if the estimated high C storage in this hemlock forest is a result of interannual climate variation or an effect of forest composition.

**Keywords:** carbon balance, eddy covariance, frost, respiration, soil temperature.

### Introduction

Forest carbon (C) balance became a subject of great interest in the late 20th century because of increasing awareness of rising

atmospheric carbon dioxide concentration ([CO<sub>2</sub>]) and the major influence of this greenhouse gas on terrestrial vegetation. Inversion models using [CO<sub>2</sub>] and carbon isotope ratios from a global atmospheric CO<sub>2</sub> sampling network have shown that a large amount of C is being stored in the northern temperate zone (Tans et al. 1990, Fan et al. 1998). Eddy covariance measurements indicate that some of this storage is occurring in secondary forests of the eastern United States, established on land converted to agriculture in the 18th and 19th centuries and subsequently abandoned. Measurements of some of these forests indicate that they store 2–6 Mg C ha<sup>-1</sup> year<sup>-1</sup>, with the lower end of this range in the northeastern USA and the higher values in the southeast (Baldocchi and Vogel 1996, Hollinger et al. 1999, Barford et al. 2001).

To move beyond measurements at a few scattered locations to realistic estimates of C balance for large regions, carbon flux data or estimates are needed for diverse forest types. Forests in the northeastern USA vary substantially in age, edaphic and climatic conditions and species composition. Over several decades, the age of individual trees and forest ecosystems can strongly affect ecosystem respiration, gross primary productivity, or both (Waring and Schlesinger 1985, Yoder et al. 1994, Menuccini and Grace 1996, Ryan and Yoder 1997, Schulze et al. 1999).

We have initiated a series of measurements at different sites at the Harvard Forest to test effects of land use history, topography, climate, forest age and tree species composition on ecosystem carbon balance. Here we report a study of C exchange, determined by eddy covariance, in an area dominated by eastern hemlock (*Tsuga canadensis* L.) in central Massachusetts. This forest, which has been described in detail by Foster and Zebryk (1993), is located ~0.5 km from a red oak–red maple dominated forest where carbon exchange has been measured for more than a decade (Wofsy et al. 1993, Goulden et al. 1996a, Barford et al. 2001). The hemlock forest contrasts with the oak–maple forest in age (about 200 years old versus less than 100 years old), dominant tree species (extremely shade-tolerant conifer versus shade-intolerant deciduous species) and degree of past disturbance (land never cleared for agriculture versus cleared crop and pastureland). Eastern hem-

<sup>†</sup> In the caption to Figure 9, the stated value of  $u^*$  should have been >0.4, not >4 as published. The error has been corrected here. A notice of the correction will appear in a forthcoming issue of the print journal.

lock-dominated forests occur on almost 10% of the land in central and southern New England, and represents an end-point for long-term successional trends in the northeastern USA (Lutz 1928, Pacala et al. 1996). Eastern hemlock is currently threatened with decimation by an introduced insect, the hemlock woolly adelgid (HWA), *Adelges tsugae* Annand (Orwig and Foster 1998), and where it has been killed it is being replaced by a black birch-dominated (*Betula lenta* L.) deciduous forest. The eastern hemlock stand at Harvard Forest has thus far been unaffected by the woolly adelgid. We measured its C exchange to (1) estimate how much C eastern hemlock forests are currently storing in the northeastern USA; (2) determine potential effects of climatic variation on C storage in hemlock forests; and (3) gauge the potential effect of hemlock mortality caused by HWA on regional C exchange.

## Materials and methods

### Stand description

The study was conducted in a stand of trees ranging in age from 100 to around 230 years. This forest was never cleared for agriculture, although selected trees were removed from the stand during the 19th century for fuel and to harvest bark for the tanning industry (Foster and Zebryk 1993). In the early 20th century, some chestnut trees (*Castanea dentata* L.) were removed after being killed by the chestnut blight fungus, *Cyphonectria parasitica*. The hemlock-dominated forest occupies about 7 ha (Figure 1). It is bordered by forests dominated by red oak (*Quercus rubra* L.) and red maple (*Acer rubrum* L.), with scattered white pine (*Pinus strobus* L.) to the north and east, and a red pine (*Pinus resinosa* Ait.) plantation to the south. A bog with red spruce (*Picea rubens* Sarg.), black gum (*Nyssa sylvatica* L.) and red maple (*Acer rubrum* L.) is located west of the hemlock stand. Because of its proximity to the bog and water table, the hemlock forest is unlikely to suffer persistent water stress.

### Leaf area index and biomass estimates

Four large hemlock trees were sampled in midsummer 1997 to determine relationships between branch basal diameter and total branch leaf area. A repeat sampling was conducted in late fall of 1997 to determine the same relationships after senescence and abscission of older foliage. Foliage abscission occurred almost exclusively in September. On each tree, branches were selected on the north and south sides of the tree in the lower, middle and upper canopy. Five randomly selected branch tips from each selected branch were removed and dissected to determine the age distribution of the foliage. For each foliage class, 30 needles were collected and their total area and dry mass determined. From these measurements, the total leaf area in each age class and total leaf area per branch were estimated. Total leaf area was then regressed against branch basal diameter, yielding power relationships with  $r^2$  values ranging from 0.95 to 0.99. The basal diameters of all branches on the four trees around the canopy access

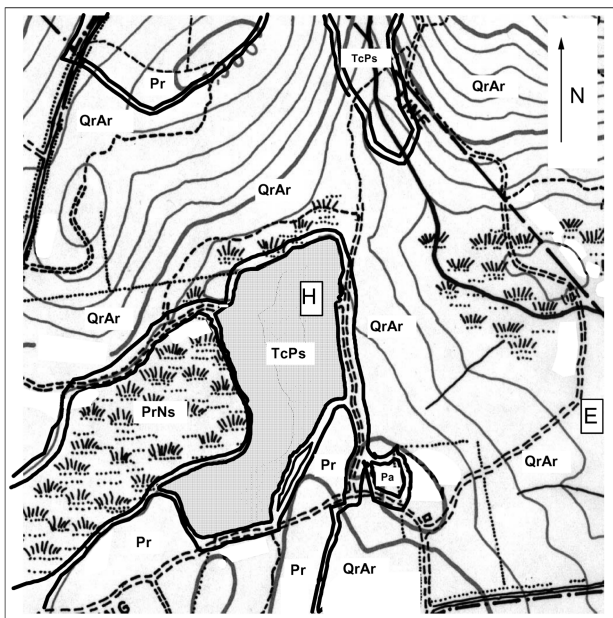


Figure 1. Map showing forest types near the eddy flux tower (H) and the old-growth eastern hemlock stand (shaded area). The entire area shown is 1 km<sup>2</sup>. Forest types are classified by dominant species as: Pr = *Pinus resinosa*; PrNs = *Picea rubens* + *Nyssa sylvatica*; Pa = *Picea abies*; QrAr = *Quercus rubra* + *Acer rubrum*; and TcPs = *Tsuga canadensis* + *Pinus strobus*. PrNs occurs in a swamp, and a second swamp with a stream flowing through it is indicated to the east of the hemlock stand. Single and double dashed lines indicate trails and unimproved roads. Dotted lines represent stone walls. Contour lines (~6 m) are also indicated. The letter E near the right-hand edge of the map is the location of long-term carbon flux measurements (Wofsy et al. 1993, Goulden et al. 1996, Barford et al. 2001).

tower were measured to give an estimate of total leaf area per tree. In fall 2001, leaf area index (LAI) for a larger area was estimated with an LAI-2000 sensor (Li-Cor, Lincoln, NE). Measurements were made at 25-m intervals from the canopy access tower along 50- to 200-m transects, at compass bearings of 195, 225 and 255° that passed through the central part of the old-growth hemlock stand.

About 150 trees were cored in summer 2000 to estimate aboveground C storage in recent years (see Smith 2001) and current standing aboveground biomass. Circular plots of 6-m radius were laid out along transects 15° apart in compass orientations, from 180 to 270°, starting from the location of the flux system. The center of each plot was determined by using randomly selected north, south, east and west coordinates in a grid centered at 50, 100, 150 or 200 m along each transect. Tree species and diameter at breast height were determined and cores were taken at a height of 1.25 m on the north and south sides of each tree. The mean of the north and south radial growth increments in each year were used to estimate C storage. Dry biomass of each tree in each year was estimated by published regressions (Tritton and Hornbeck 1982) and C content was assumed to be 50% of dry biomass (Barford et al. 2001).

### Environmental measurements

Air temperature and photosynthetically active radiation (PAR) were measured at a height of 24 m every 10 s and means were calculated every 30 min by instruments mounted on the same tower as the eddy covariance system. We measured PAR with a Li-Cor LI-190S quantum sensor and air temperature with a shielded 24-gauge copper constantan-thermocouple. Soil temperature was measured every 60 s with 20-gauge thermocouples at a depth of 10 cm at five randomly located points, 9 to 48 m from the canopy access tower. We used CR-10 data loggers (Campbell Scientific, Logan, UT) to store all data.

### Soil respiration

Soil respiration was measured at intervals of about 2 weeks during the spring through fall period and on a few dates during the winter. Soil surface collars were placed at randomly chosen *X,Y* coordinates within 5 m of plot centers at 25, 50, 100 and 150 m from the hemlock tower on 195, 225 and 255° transects. Soil respiration rate was determined from the rate of increase in [CO<sub>2</sub>] in a chamber 25 cm in diameter by 11.5 cm high, measured with a Li-Cor LI-6200 photosynthesis system over 12 successive 15-s intervals. If there was a decline in the rate of increase in [CO<sub>2</sub>] over the 12 measurements, a regression of rate of increase versus [CO<sub>2</sub>] was used to determine the rate at 400 ppm CO<sub>2</sub>, a typical [CO<sub>2</sub>] near the soil surface. Simultaneously with each soil respiration measurement, soil temperature at a depth of 10 cm was measured with a portable thermistor probe.

### Above-canopy carbon flux and carbon storage measurements

Data were collected by the eddy covariance or eddy flux procedure during 68% of hours in the year, with major data gaps

in December–January and August–September (Table 1). The eddy flux system was mounted on a 22 m scaffolding tower with a mast extending to a height of 27 m on the SW corner of the tower. A Campbell Scientific CSAT-3 sonic anemometer and air intake funnel were mounted on a boom extending 1 m to the west from the top of the mast. The scaffolding tower was 1.5 m by 2.1 m in cross section and may have influenced up-drafts from the SE and NE as recorded by the sonic anemometer. However, the tower probably had little effect when wind was from the SW, because of the position of the mast on the SW corner of the tower and the 5 m vertical distance between the top of the tower and the sonic anemometer.

The air intake funnel was connected by 27 m of polyethylene tubing to a closed-path Li-Cor LI-6262 CO<sub>2</sub>/H<sub>2</sub>O analyzer. The analyzer, a Campbell Scientific CR-23X data logger, and a computer were housed in an enclosure 15 m above ground on the scaffolding tower. The analyzer was calibrated weekly or after large changes (> 10 °C) in analyzer temperature. During cold weather, the analyzer was insulated and kept above 5 °C by a small electrical resistance heater. Raw millivolt (mV) signals were sent to the data logger and the manufacturer's mV versus [CO<sub>2</sub>] and H<sub>2</sub>O concentration equations were entered into the flux analysis program.

Air was drawn through the CO<sub>2</sub> analyzer at 5.7 l min<sup>-1</sup>. Data from the sonic anemometer and the analyzer were collected by a CR-23X data logger at 5 Hz and then transmitted to a computer that calculated covariances every 30 min. Lag times for CO<sub>2</sub> and water vapor transfer through the tubing to the analyzer were recalculated at monthly intervals, or when there were large changes in ambient humidity, which affected CO<sub>2</sub> lag times slightly and water vapor lag times substantially. Because of the long lag times for water vapor and unreliable measurement of short-term variation in water vapor concentration, only CO<sub>2</sub> flux measurements are presented here.

Table 1. Periods of data collection, periods of southwest wind (SWW), and periods when friction velocity ( $u^*$ ) was above the threshold (0.4 m s<sup>-1</sup>) for acceptable flux measurements.

Month	Daytime				Nighttime			
	% Hours with data	% Hours with data and SWW	% Hours with $u^* > 0.4$ and SWW	No. of usable 30-min sample periods	% Hours with data	% Hours with data and SWW	% Hours with $u^* > 0.4$ and SWW	No. of usable 30-min sample periods
November	57	13.1	8.3	49	32	4.2	1.9	16
December	40	9.7	7.8	44	38	10.5	3.6	33
January	56	19.6	11.4	67	61	23.9	7.0	63
February	78	29.2	21.8	129	79	31.0	14.0	105
March	65	15.1	13.0	96	64	18.2	8.2	61
April	93	17.7	15.5	125	83	18.4	7.9	50
May	80	25.1	16.3	148	83	34.7	9.1	53
June	81	36.8	25.5	233	79	41.6	18.1	95
July	94	45.6	30.0	278	94	51.6	17.8	100
August	29	18.1	12.2	105	30	15.8	6.2	39
September	55	16.7	10.8	81	61	13.0	2.5	17
October	97	52.8	44.6	306	96	50.7	28.5	229
Total	69	24.9	18.1	1661	67	26.1	10.4	861



Eddy covariance data were classified by wind direction and only data from the SW were retained as representative of hemlock forest because of inadequate fetch of the hemlock-dominated forest in other directions. We then examined the relationship between friction velocity ( $u^*$ ) and measured flux over 30-min intervals to determine a  $u^*$  threshold above which there was no statistically significant relationship (at  $P < 0.05$ ) between  $u^*$  and measured flux. In the case of nighttime measurements, the threshold was determined by averaging C flux measurements by  $u^*$  class (see Figure 6). For daytime fluxes,  $u^*$  was included in a multiple regression model along with PAR, air and soil temperatures, daily minimum air temperature and hour of the day (see section on flux models below). Aside from the minimum  $u^*$  filter, data were rejected during initial analysis only if there was an instrument error. The major sources of instrument error were moisture on the sonic anemometer, power surges and excessive electrical noise in the CO<sub>2</sub> analyzer signal.

A correction was made for flux loss at high frequencies as a result of air mixing during transit to and within the CO<sub>2</sub> analyzer or high-frequency noise in the analyzer signal. The time scale of covariances between vertical wind and [CO<sub>2</sub>] was compared to the time scale of covariances between vertical wind and air temperature as measured by the sonic anemometer. The air temperature data were then smoothed so that the covariance of air temperature and vertical wind had a similar time scale to the [CO<sub>2</sub>]-vertical wind covariance. A degraded sensible heat flux was calculated from the smoothed sonic temperature data for each time period, and CO<sub>2</sub> flux was increased by the ratio of actual to degraded heat flux (Goulden 1996b). Generally, this ratio was close to 1, averaging  $1.03 \pm 0.005$  during both day and night over the year. As a final processing step, constant or out-of-reasonable-range values for wind vectors and gas concentrations were removed from the data set before estimating C fluxes and developing C flux models.

Storage of CO<sub>2</sub> between the hemlock canopy and the ground was measured from early June through October at two locations. Two columns of 6.3 mm inside-diameter plastic tubing, 19 and 24 m long, with about fifty 20-gauge hypodermic needles inserted per column, were stretched from the ground to the upper canopy of two large hemlock trees. The trees were 75 and 100 m from the flux system along 225 and 255° transects. Air was pulled into the columns through the hypodermic needles and through a Li-Cor Gashound CO<sub>2</sub> analyzer on the ground at  $\sim 3 \text{ l min}^{-1}$ . Air was pulled through a tube connected to the middle of each column to equalize flow from the upper and lower halves. Flow measurements showed that there was a 10% drop in intake rate between the middle and ends of the column. To compensate, the space between intake needles located near the ends of the columns was decreased. The [CO<sub>2</sub>] in the analyzer was recorded every 10 s and the average recorded once every 2–5 min, depending on the data logger available at each site. Subcanopy CO<sub>2</sub> storage was calculated as the net change in [CO<sub>2</sub>] over 30-min intervals. These measurements were synchronized with the CO<sub>2</sub> flux measurements.

#### *Position and footprint of eddy flux measurement system*

The flux system was 50 m from the NE corner of the hemlock stand, which extended 200 m to the W and SW and 400 m to the SSW of the flux system. The sonic anemometer and intake funnel, at a height of 27 m, were above most of the hemlock canopy, which varied in height from  $\sim 15$  to 28 m. Scattered individuals of eastern white pine (*Pinus strobus* L.) reached 30 m in height. The nearest eastern white pine was  $> 27$  m tall and was located  $\sim 75$  m SW of the eddy flux system.

The Flux Source Area Model (FSAM, Schmid 1994) generated estimates of the footprint of the eddy flux system. Although the footprint estimates for this site are approximate because of the extremely rough canopy and presence of emergent pines, they provided useful information on the effect of footprint size on measured C flux. To gather data needed in the FSAM model, we measured the wind profile near the eddy flux system during periods of SW wind in winter 2001–2002.

Wind speed was measured at heights of 24, 26.5 and 30 m above ground. This was 2, 4.5 and 8 m above the estimated mean canopy height near the tower. Extrapolating mean wind speed versus log of height to a windspeed of zero gave a zero-plane displacement height ( $d$ ) of 17.2 m (Campbell and Norman 1998). With the flux system at a height of 27 m, this gave a measurement height ( $Z_m$  in the FSAM model of Schmid (1994)) of 9.8 m.

We calculated the roughness length ( $Z_0$  in FSAM notation) according to the equation of Campbell and Norman (1998):

$$u(z) = (u^*/0.4)/\ln((z-d)/Z_m)$$

Note that  $u(z)$  is wind speed at height  $z$  and that Campbell and Norman (1998) use  $Z_m$  to indicate roughness length, not measurement height. Based on our wind profile data, this gave a roughness length ( $Z_0$ ) of about 1.6 m.

The ratio of measurement height to roughness length ( $Z_m/Z_0$ ) was 6.1. Because this value is below the range recommended for use with the FSAM model, we ran the model with a wide range of values for  $Z_m/Z_0$  and  $Z_m/L$ , which is a second input in the FSAM model (where  $L$  is Monin-Obukhov length). From these runs, we calculated polynomial regressions to estimate the footprint parameters for  $Z_m/Z_0 = 6.1$  and various values of  $Z_m/L$  (Figure 2a). In a second step, we used footprint length at  $Z_m/Z_0 = 6.1$  and various values of  $Z_m/L$  to calculate a regression predicting footprint length only as a function of  $Z_m/L$  (Figure 2b). We used this regression equation to estimate footprint length based on data from the sonic anemometer for each 30-min interval in which CO<sub>2</sub> flux was calculated.

Although our procedure will not give as accurate an estimate of footprint size as with higher values of  $Z_m/Z_0$ , it provides a useful approximation because footprint size must approach zero as  $Z_m/Z_0$  tends toward zero (H.P. Schmid, personal communication). Polynomial regressions using multiple FSAM runs for values of  $Z_m/Z_0$  from 12 to 36 extrapolated to footprint lengths well above zero at  $Z_m/Z_0 = 0$  (Figure 2a), suggesting that the extrapolation overestimates footprint size at

$Z_m/Z_0 < 12$ . Thus, eddy covariance footprints estimated by the procedure probably extend further beyond the hemlock stand than is actually the case.

Notwithstanding this overestimation, estimated footprint lengths usually exceeded the minimum dimension of the hemlock stand in the SW direction (about 200 m), except during periods of unusually high turbulence and strong positive surface-to-atmosphere heat flux ( $F_h$ ) when the footprint estimate was as short as 100 m. To determine the effect of larger footprint sizes on measured C flux, estimated footprint length was included in multiple regression models for measured C flux. Because footprint length is determined by  $u^*$  and  $F_h$ , this is equivalent to including these parameters in a model for measured C flux.

#### Environmental models for carbon exchange

Restriction of data collection to periods of SW wind with  $u^* > 0.4$  meant that considerably less than half of the eddy flux data were valid measurements of hemlock forest C exchange. In months when the flux system was operating nearly full-time (February through July, plus October), valid flux measurements were available for 13 to 45% of the daylight hours, and 8 to 29% of nighttime hours (Table 1).

Because of the limited data set, seasonal and annual C exchange were estimated with statistical models. A stepwise multiple regression procedure in SYSTAT (V. 5 for Macintosh, Wilkinson et al. 1992) was used to develop predictive models based on all available environmental data that might influence tree or soil metabolic activity. Input variables were PAR, air temperature ( $T_a$ ), soil temperature ( $T_s$ ), daily minimum temperature ( $T_m$ ), severity of nocturnal frost (FROST) and hour of the day (HR). The variable FROST was calculated by classifying  $T_m$  into three ranges: no freezing ( $T_m > 0^\circ\text{C}$ , FROST = 0), light frost ( $T_m = 0$  to  $-5^\circ\text{C}$ , FROST = 1) and severe frost ( $T_m < -5^\circ\text{C}$ , FROST = 2). The natural logarithm of PAR and the squared value of HR were also included. After this procedure had identified variables significantly related to measured flux at  $P < 0.05$ , all interactions of significant variables were tested and eliminated if the interaction was not statistically significant at  $P < 0.01$ .

Because the main environmental influences on gas exchange in coniferous trees are known to change seasonally, when possible we used only data collected within a single month in the daytime models to obtain the best predictive power from these statistical models. For instance,  $T_m$  is an important influence in fall and spring (Smith et al. 1984, Hadley 2000a), whereas vapor pressure deficit (VPD) is a more important influence in summer (Larcher 1995). Vapor pressure deficit has also been observed to affect daytime ecosystem C flux in recent eddy covariance studies of coniferous forests (e.g., Chen et al. 2002). Exceptions to the one-month limitation for data used in model development were made when insufficient measurements were available in a single month to develop a model. This occurred in November through January, August, and September. Multiple-month models were also necessary in winter when variation in daytime C flux relative

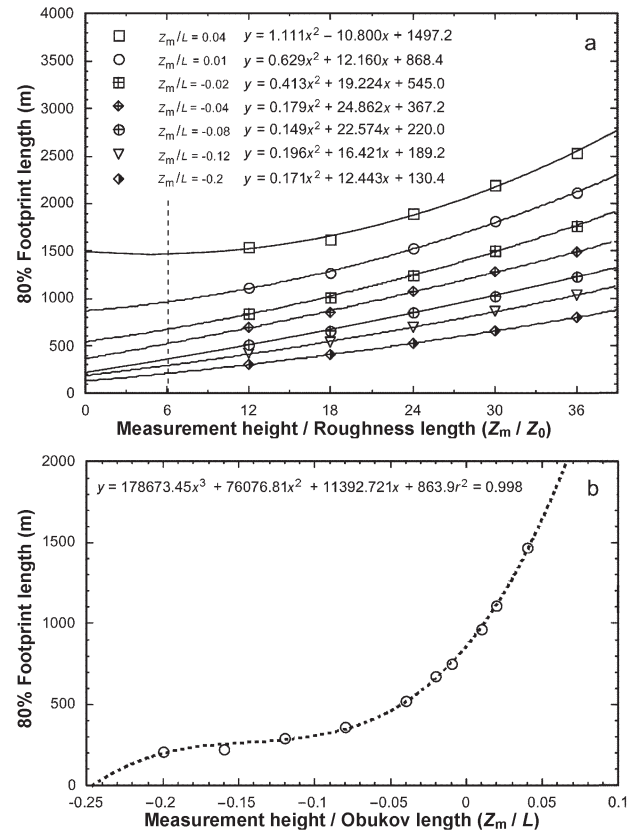


Figure 2. (a) Footprint lengths for 80% of carbon flux as estimated by the Flux Source Area Model (FSAM, Schmid 1994). Footprint length was calculated for various measurement heights,  $Z_m$ , above zero-plane displacement,  $d$ , divided by roughness length,  $Z_0$ . The  $Z_m/Z_0$  ratio for this study (6.1) is indicated by the vertical dashed line. The curves are regressions of FSAM model outputs generated at different values of  $Z_m/L$ , where  $L$  is Monin-Obukhov length and is calculated as:  $L = -(u^*)^3/k(9.8/T_{\text{air}})F_h$ , where  $u^*$  is friction velocity,  $k$  is the von Karmann constant (0.4),  $T_{\text{air}}$  is air temperature in degrees Kelvin and  $F_h$  is kinematic surface heat flux, equal to the covariance of vertical wind and air temperature  $wT_{\text{air}}$  (Stull 2000). (b) Relationship between 80% footprint length, determined as shown in Figure 2a, and  $Z_m/L$ .

to the mean was so high that the C flux data from any one month showed no significant relationship to the environmental data.

Models for nighttime C flux were based on longer periods of data than models for daytime C flux, because during any single month there was usually insufficient variation in  $T_a$  and  $T_s$ , which were the only environmental variables significantly related to nocturnal C flux.

## Results

### Leaf area index, biomass and recent aboveground carbon storage in the hemlock stand

A 1997 census of branch diameters on the four trees around

the canopy access tower gave an estimated leaf area index (LAI) of 3.5 in fall, winter and spring, and 4.4 during late June, July and August (after the development of new foliage, but before the abscission of older foliage). Optically based estimates of LAI in January 2002 at 21 sites in the hemlock stand gave values ranging from 3.0–4.2, with a mean of 3.6. For conifers, this optical LAI is actually a shoot silhouette area index rather than a true LAI. Because there is up to 20% needle overlap within shoots in the upper canopy, but almost none in the lower canopy (J. Hadley, unpublished data), the optical LAI value may underestimate true LAI by ~10%. On the other hand, the optical estimate also includes the silhouette area of unfoliated twigs and branches, which leads to a compensating overestimate of LAI. In fact, the destructive branch sampling and optical estimates of LAI agreed closely.

Aboveground live biomass of the hemlock stand averaged  $80 \pm 5.5 \text{ Mg ha}^{-1}$ . The biomass was 83% hemlock, 13% white pine, 2% oak (red oak and white oak, *Q. alba* L.), 1% maple (*Acer* spp.) and ~0.5% black birch. Annual C storage from 1990 through 1999 averaged  $1.2 \text{ Mg ha}^{-1} \text{ year}^{-1}$  (range =  $1.06\text{--}1.38 \text{ Mg ha}^{-1} \text{ year}^{-1}$ ). Over 80% of the annual C storage was in hemlock and most of the rest in white pine.

### Soil respiration

Soil respiration was low ( $< 0.5 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) in winter, and was strongly dependent on soil temperature from spring to fall (Figure 3). Soil water content had a relatively minor effect on soil respiration, although for the spring–fall period presented in Figure 3,  $r^2$  increased from 0.87 to 0.91 when gravimetric soil water content in the top 5 cm was included in the regression model.

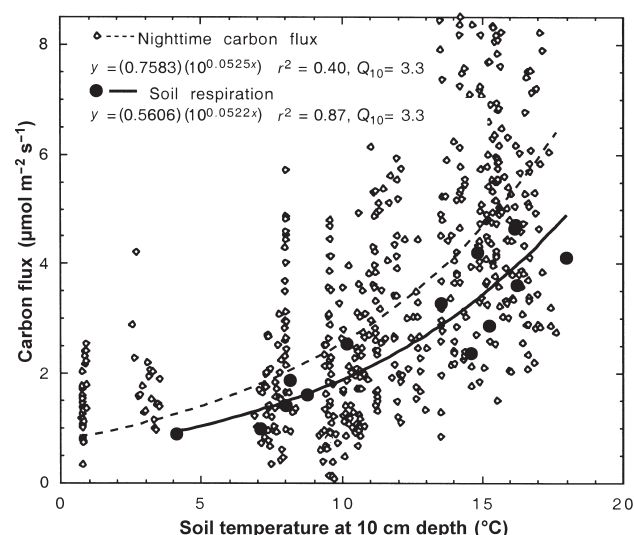


Figure 3. Nighttime carbon fluxes measured during SW winds with  $u^* > 0.4$  from April through October, plotted against soil temperature at 10-cm depth. Soil respiration rates measured on 14 dates between April 27 and September 25, 2001 are also shown.

### Effects of atmospheric conditions on carbon exchange measurements

Atmospheric turbulence was strongly related to measured above-canopy C flux, especially at night. During some months, measured nocturnal C release from the hemlock forest increased with friction velocity ( $u^*$ ) up to  $0.4 \text{ m s}^{-1}$  (Figure 4). All data with  $u^* < 0.4$  were therefore removed from analysis to avoid possible bias of C exchange estimates.

### Storage of $\text{CO}_2$ in the sub-canopy air space

Generally,  $\text{CO}_2$  storage averaged over 30-min intervals was only a few  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  and storage and loss of  $\text{CO}_2$  from the subcanopy air space balanced over periods of a few hours, resulting in no net change. Occasionally, large amounts of  $\text{CO}_2$  storage occurred. Between five and ten 30-min intervals with  $> 10 \mu\text{mol m}^{-2} \text{ s}^{-1}$  of subcanopy  $\text{CO}_2$  storage occurred monthly during June, July and August. However, within a few hours, these large storage events were followed by losses from subcanopy storage, producing noise in the eddy flux measurements but having no effect on daily, monthly or annual totals.

### Models of carbon exchange

During periods of low turbulence, ecosystem C exchange was estimated from multiple regression models developed from measurements of above-canopy C flux with  $u^* > 0.4$ . Variables in these models (Table 2) included those known to have strong effects on photosynthesis or respiration: PAR, air temperature ( $T_a$ ), soil temperature ( $T_s$ ), daily minimum temperature ( $T_m$ ), severity of nocturnal frost (FROST) and hour of the day (HR). For daytime C flux, the significant variables depended on season: PAR was significant in all periods except middle and late winter (which were unusually cold);  $T_a$  was

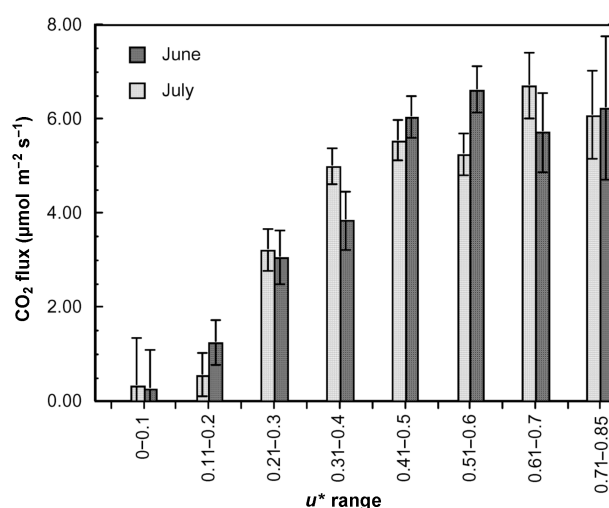


Figure 4. Mean measured nighttime  $\text{CO}_2$  flux in June and July for SW wind at different ranges of friction velocity,  $u^*$ . Bars are standard errors of means. Sample sizes ranged from 9 to 61, except when  $u^* = 0.71\text{--}0.85$  in June ( $n = 4$ ). Sample sizes were greater than 25 for all  $u^*$  values between 0.11 and 0.6.

Table 2. Models used to estimate carbon flux when the wind was not from the SW or friction velocity ( $u^*$ ) was  $< 0.4 \text{ m s}^{-1}$ . Abbreviations: FROST = daily minimum temperature class (see Materials and methods), HR = time of day, PAR = photosynthetically active radiation,  $T_a$  = air temperature,  $T_m$  = daily minimum air temperature,  $T_s$  = soil temperature at 10 cm depth, VPD = water vapor pressure deficit of the air, (lin) = linear function and (exp) = exponential function. The natural log of PAR and the square of HR are also presented for some models, but only the raw variables from which  $\ln(\text{PAR})$  and  $\text{HR}^2$  were derived are shown.

Period of model application	Period of model derivation	Physical variables	Interactions	<i>n</i>	<i>r</i> <sup>2</sup>	<i>P</i>
<i>Daytime models</i>						
Nov 1–Dec 15	Oct–Dec	PAR, $T_a$ , $T_m$ , $T_s$ , FROST	PAR $\times$ $T_a$ , PAR $\times$ $T_s$ , $T_a \times T_s$ , $T_m \times T_s$ , $T_s \times$ FROST	260	0.54	$< 0.001$
Dec 16–Jan 11	Nov–Jan	PAR, $T_a$ , $T_s$	PAR $\times$ $T_s$	160	0.56	$< 0.001$
Jan 12–March 31		$T_m$ , $T_s$	$T_m \times T_s$	284	0.07	$< 0.001$
April	April	HR, PAR, FROST, VPD	HR $\times$ PAR, HR $\times$ VPD, PAR $\times$ FROST, PAR $\times$ VPD	110	0.83	$< 0.001$
May	May	HR, PAR, $T_a$ , VPD	HR $\times$ VPD, PAR $\times$ VPD	139	0.65	$< 0.001$
June	June	HR, PAR, $T_a$	HR $\times$ PAR, $T_a \times$ PAR	223	0.58	$< 0.001$
July 1–Aug 3	July 1–Aug 3	HR, PAR, VPD	HR $\times$ VPD, PAR $\times$ VPD	281	0.58	$< 0.001$
Aug 4–Aug 21	July 1–Aug 21	HR, PAR, $T_a$	HR $\times$ PAR, HR $\times$ $T_a$	360	0.45	$< 0.001$
Aug 21–Sept 10	July 1–Sept 30	HR, PAR, $T_a$ , $T_s$	HR $\times$ $T_a$ , HR $\times$ PAR	440	0.43	$< 0.001$
Sept 10–Oct 31	Sept 10–Oct 31	HR, PAR, $T_m$ , $T_s$ , VPD	HR $\times$ PAR	373	0.60	$< 0.001$
<i>Nighttime models</i>						
Nov 1–Dec 15	Oct–Dec	$T_a$ (lin)		192	0.23	$< 0.001$
Dec 16–Jan 11	Nov–Jan	$T_a$ (lin), $T_s$ (exp)	None	111	0.26	$< 0.001$
Jan 12–March 31	Jan–March	$T_a$ (lin)		162	0.07	$< 0.001$
April–June	April–June	$T_s$ (exp)		194	0.50	$< 0.001$
July–Oct	July–Oct	$T_a$ (exp), $T_s$ (exp)	$T_a \times T_s$	377	0.32	$< 0.001$

significant in most periods;  $T_m$  and FROST were significant only in late fall, winter, and early spring; and HR was significant from early spring through early fall. For nighttime C flux,  $T_a$  and  $T_s$  were the only significant variables (Table 2).

The proportion of variation in C flux at  $u^* > 0.4$  explained by the models varied widely from 0.07 to 0.83 for daytime models and from 0.07 to 0.50 for nighttime models; however, all models explained a highly statistically significant portion of the variation. Models for daytime C flux tended to explain a greater proportion of the variation than models for nighttime flux, and models developed from data in spring and fall had greater predictive power than winter or summer models (Table 2). This is probably because of the small magnitude of C fluxes in winter and the high variability of C fluxes in summer (Figure 5).

Summed C exchange model estimates (SW wind only) were compared with summed eddy covariance data for April through October 2001 (Figure 6). Compared with measured values, models predicted substantially greater C loss from the forest at night, particularly during calm periods, leading to an average 20–30% greater estimate of C loss. During the day, model predictions approximated measured values for the entire April–July 2001 period, although measured fluxes and model estimates differed substantially in some months (Figure 6).

#### Annual pattern of carbon exchange

The hemlock forest reached maximum 30-min measured C

uptake rates of  $\sim 12 \mu\text{mol m}^{-2} \text{s}^{-1}$  and maximum measured ecosystem respiration rates of  $< 5 \mu\text{mol m}^{-2} \text{s}^{-1}$  (with a few exceptions) during fall 2000 (Figure 5a). Measured C uptake and release were low, generally less than  $3 \mu\text{mol m}^{-2} \text{s}^{-1}$ , during the winter. On April 10, 2001, there was a sudden increase in maximum C uptake rate to  $\sim 10 \mu\text{mol m}^{-2} \text{s}^{-1}$ , followed by a gradual increase to a maximum of  $24 \mu\text{mol m}^{-2} \text{s}^{-1}$  by early July. Maximum C uptake declined again to  $\sim 10 \mu\text{mol m}^{-2} \text{s}^{-1}$  by late October. Nocturnal C flux to the atmosphere (Figure 5b) began to increase in late April. Mostly, it did not exceed  $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ , but reached over  $20 \mu\text{mol m}^{-2} \text{s}^{-1}$  on a few occasions in July. Carbon flux to the atmosphere fell to low values again by late October 2001.

#### Environmental controls on carbon flux

From April through September, light was the primary variable controlling measured above-canopy C flux. Although half-hourly flux values were variable, the effect of light is seen in the highly significant ( $P < 0.0001$ ) curvilinear relationships between PAR and C uptake by the forest between April and September (Figures 7a and 7b). Maximum C uptake rates increased from April through July 2001, but variability in flux also increased greatly (note the low  $r^2$  value for July in Figure 7b). As a result, the mean response of C uptake to increasing PAR increased only slightly from April through July. The mean response function was similar in July and October (Figure 7b) although by October maximum PAR was markedly lower,  $\sim 1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ .



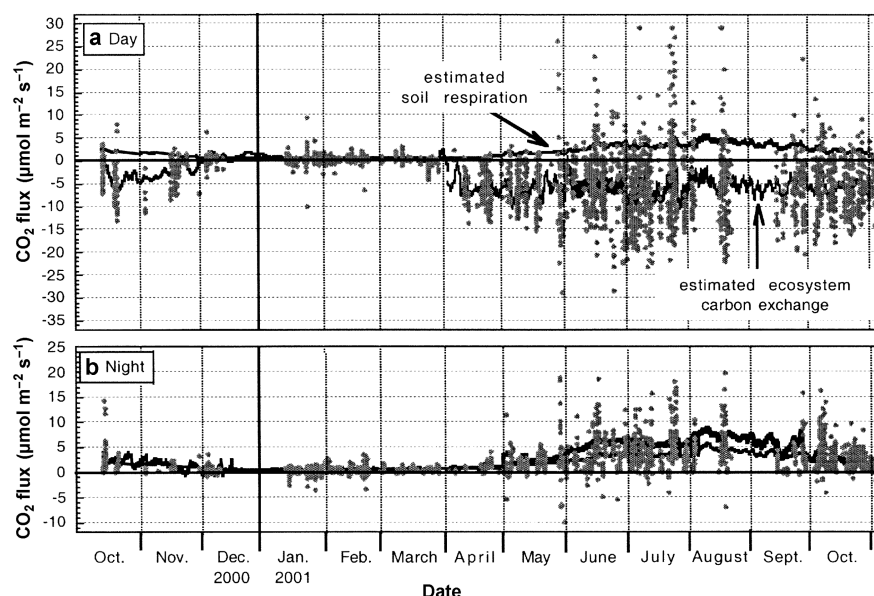


Figure 5. Thirty-min carbon exchange rates measured during the day (a) and at night (b) from mid-October 2000 through October 2001. Negative values in this and subsequent figures indicate carbon uptake by the forest. Only data obtained while there was a SW wind (from the direction of the hemlock forest) are shown. Gaps in the data resulted from rain, equipment failures, and calibration of the flux system against the system at the long-term Harvard Forest site in August and September 2001. Solid lines ranging from  $\sim -10$  to  $0$  in the upper panel and from  $0$  to  $\sim 8$  in the lower panel denote 24-h moving averages of C flux estimated from multiple regression models based on temperature, light and humid-

ity measurements in the hemlock forest canopy and soil (see Table 2). Solid lines ranging from  $0$  to  $\sim 5$  in both figures denote soil respiration estimated from soil temperature data and data from chamber measurements (see Figure 3).

In contrast to the generally frost-free months,  $T_a$  was a controlling variable for C uptake in the early spring and to a lesser extent in mid- to late fall. Low minimum night temperature

strongly limited light-saturated C uptake in spring 2001 (Figure 8), and the degree of nighttime frost generally explained more of the variation in C uptake than did  $T_s$ .

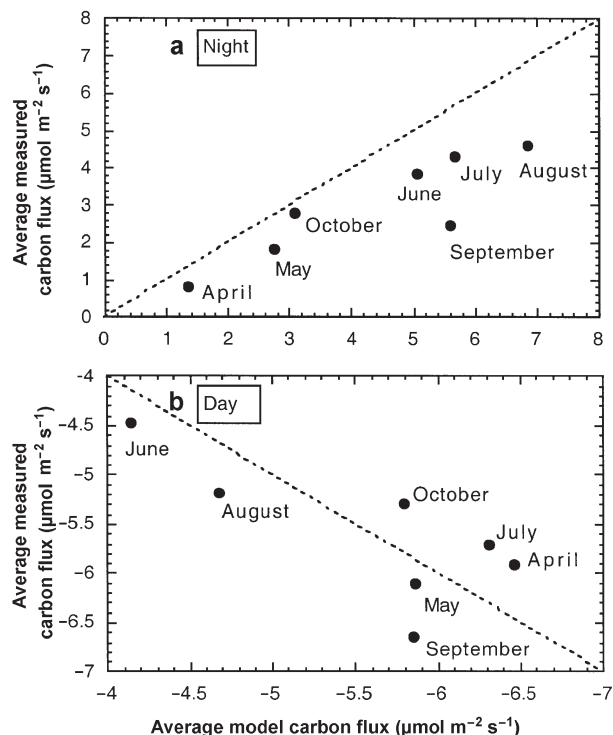


Figure 6. Mean measured monthly hemlock forest carbon exchange during (a) night or (b) day periods with a SW wind, plotted against the mean of multiple-regression model estimates (see Table 2) for the same time periods. All measured carbon fluxes, regardless of  $u^*$ , were included in the monthly totals for this figure only. Dotted lines show a 1:1 relationship between measured fluxes and model estimates.

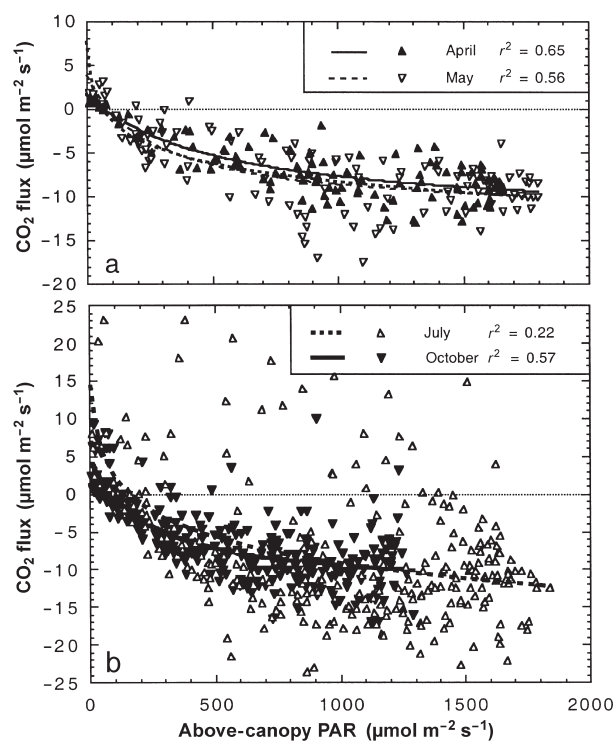


Figure 7. Response of carbon flux measured while there was a SW wind to photosynthetically active radiation (PAR) above the hemlock canopy, during (a) April and May, (b) July and October, 2001. Fitted curves are calculated from the formula  $C \text{ flux} = c + (aPAR/(b + PAR))$ , which approaches a constant value of C flux at sufficiently high values of PAR.



### Monthly carbon storage

The hemlock forest stored a small amount of C in November 2000 and lost small amounts of C in December through March. Net C storage then increased dramatically in April, remained similar in May, fell by ~50% in June and then increased in July before falling to near or below zero in August (Figure 9c). Some recovery in C storage occurred in September and October. Most of the variation in C storage between April and October was driven by changes in nighttime C loss (Figure 9b), whereas total daytime C storage was much less variable from month to month (Figure 9a).

### Footprint size estimates and effects on measured and estimated carbon exchange

Estimated footprint length for the flux system based on extrapolations of the FSAM model varied from < 100 m to > 2 km (Figures 10a and 10b). The smaller footprint lengths occurred almost always during daytime. At night, the footprint area almost always exceeded the size of the hemlock stand, and footprint length was frequently > 2 km (Figure 10b). As a result, it was impossible to gauge the influence of the hemlock stand on measured nocturnal fluxes from footprint estimates. However, footprint length had a significant effect during the day throughout most of the spring, summer and early fall. In April, July and August, C flux tended to become more positive (i.e., C uptake decreased) as footprint size increased, but the reverse occurred in September and October (Table 3).

## Discussion

### Possible errors in eddy flux measurements

Errors in forest-to-atmosphere gas flux measurements can be

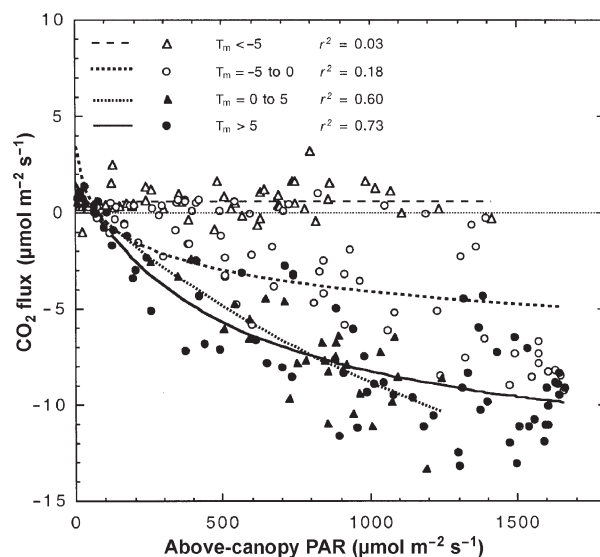


Figure 8. Response of carbon flux measured with SW wind to photosynthetically active radiation (PAR) following nights with different minimum air temperatures ( $T_m$ ) during March and April 2001. Fitted curves are of the same type as in Figure 7.

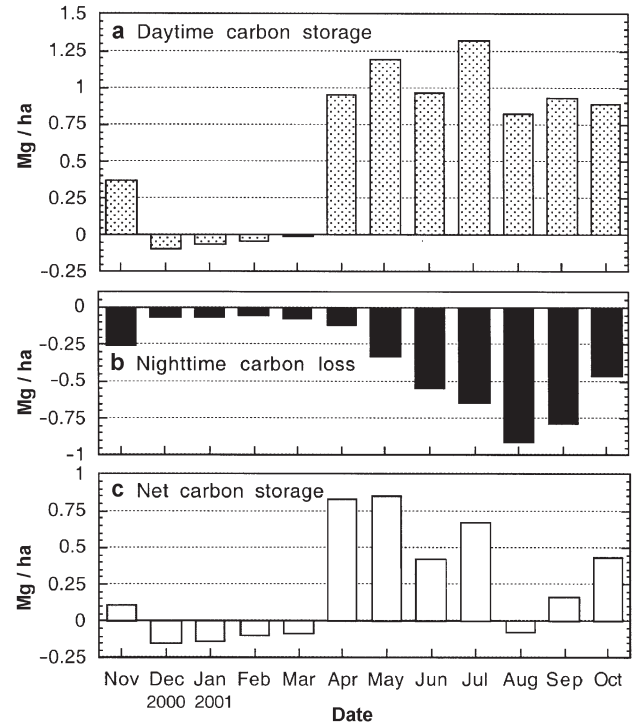


Figure 9. Monthly estimates of total carbon exchange during the day (a), at night (b) and for both day and night (c). Values were calculated by summing eddy flux data during periods when there was a south-west wind with  $u^* > 0.4$ , and summing the output of C exchange models (Table 2) the rest of the time.

caused by incorrect, slow or variable instrument responses. In this study, the  $\text{CO}_2$  analyzer was stable, changing less than 2% between calibrations. For calibration, we used a commercially available  $\text{CO}_2$  standard with  $[\text{CO}_2]$  accurate to within 2%. When using a closed-path analyzer, mixing of air during transport to the analyzer, mixing within the analyzer, and gas absorption and desorption from filters and air-supply tubing can prevent detection of gas fluxes in small, high frequency eddies. Absorption and desorption present more difficulties for detection of water vapor flux than for detection of  $\text{CO}_2$  flux (Goulden et al. 1996b). Because of the large loss of  $\text{H}_2\text{O}$  flux caused by absorption and desorption in our system, we did not attempt to estimate water vapor fluxes. Loss of  $\text{CO}_2$  flux caused by mixing of the air sample during transfer to the analyzer was determined by spectral analysis as described by Goulden et al. (1996b), and the corrections made resulted in about a 3% increase in flux during both daytime and nighttime. These corrections were imprecise but small, so that even a 50% error would have affected estimated flux by only about 4%.

The largest potential sources of error in the measurements, when they are scaled to represent whole-forest C flux (as opposed to above-canopy flux), are advective  $\text{CO}_2$  fluxes and under-sampling of vertical flux, especially at night. The latter could occur as a result of the presence of canopy gaps where there is a much higher than average turbulent transfer from the

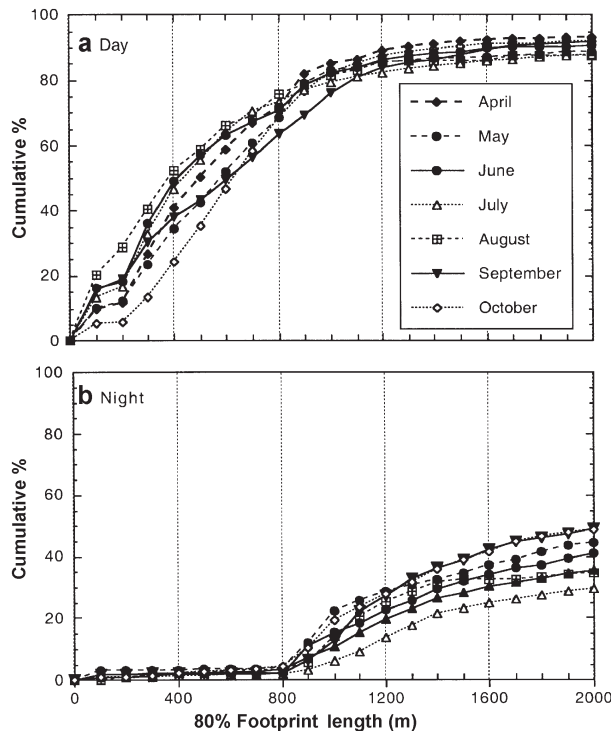


Figure 10. (a) Day and (b) night frequency distributions of footprint lengths and the source area for 80% of measured fluxes, derived from the FSAM model of Schmid (1994). For derivation of footprint lengths, see Materials and methods and Figure 2. Footprint estimates are presented only up to 2 km because of topographic relief and unpredictable turbulence patterns at long distances from the flux tower. Each curve includes between 300 and 1420 individual footprint estimates, each calculated from sonic anemometer measurements during a 30-min interval.

forest understory to the atmosphere. Both advection and under-sampling of vertical flux at night tend to result in underestimation of understory flux, which is usually dominated by soil respiration, and therefore lead to overestimates of ecosystem C storage (Fitzjarrald et al. 2001).

Advective CO<sub>2</sub> flux is most likely during low turbulence, in terrain of nonuniform slope (Lee 1998). The terrain to the SW of our flux tower (Figure 1) is level, with less than 6 m of vertical relief within 400 m of the tower to the SW. However, there is a strong topographic gradient from Little Prospect Hill, in the upper left portion of Figure 1, to a bog in the stream drainage at the right. The steepest portion of this gradient is to the north of the hemlock stand, and it seems likely that most nocturnal cold air drainage, which commonly causes advective fluxes at Harvard Forest (Fitzjarrald et al. 2001), would bypass the hemlock stand. However, neither advective fluxes nor under-measurement of CO<sub>2</sub> flux through canopy gaps can be ruled out.

Without H<sub>2</sub>O flux estimates, we cannot estimate energy balance closure, which eliminates one way of testing for under-measurement of C, water and sensible heat fluxes caused by advection and flux through canopy gaps. However, there was good agreement between the temperature response of nocturnal ecosystem respiration measured with the flux system and soil respiration measured with chambers (Figure 3). The difference between the best-fit exponential regression curves for measured ecosystem respiration and estimated soil respiration at all temperatures is roughly consistent with the relative values of below- and aboveground respiration estimated for deciduous stands at Harvard Forest (Wofsy et al. 1993). Therefore we conclude that, although there may have been some periods when advective C flux and C flux through canopy gaps were significant, it is unlikely that either was a serious problem over the 1-year duration of this study.

*Annual pattern of carbon exchange and the probable influences of hemlock and other tree species*

Carbon uptake showed a rapid increase in mid-April, which is seen both in the flux data (Figure 5) and in monthly C storage estimated from both measured C flux and models (Figure 9). Because no leaves were present on deciduous trees until early May, high C uptake in April indicated that conifers had a major impact on measured C flux, even if deciduous trees also had some influence. The effect of conifers is also shown by C

Table 3. Effect of estimated footprint length (FPL) on estimated monthly carbon flux (Mg C ha<sup>-1</sup>) for April–October 2001. Footprints are for 80% of flux and estimates are derived from the FSAM model (Schmid 1994).

Month	No-FPL model	With FPL estimates	FPL = 200 m	FPL = 600 m	FPL = 1000 m
April	– 0.95	– 0.92	– 1.07	– 0.92	– 0.80
May	– 1.16	0 <sup>1</sup>			
June	– 0.99	0 <sup>1</sup>			
July	– 1.35	– 1.47	– 1.74	– 1.51	– 1.27
August <sup>2</sup>	– 0.82	– 0.85	– 1.29	– 0.93	– 0.56
September <sup>3</sup>	– 0.92	– 0.92	– 0.85	– 0.90	– 0.95
October	– 0.92	– 0.92	– 0.81	– 0.89	– 0.97
5-Month sum	– 4.97	– 5.07	– 5.76	– 5.14	– 4.56

<sup>1</sup> There was no significant effect of footprint length on measured daytime fluxes in May or June.  
<sup>2</sup> The FPL model was used only until August 21; no model with a significant FPL effect was found for the last 10 days.  
<sup>3</sup> The FPL model was used only for September 12–30; no model with a significant FPL effect was found for early September.

uptake rates of at least  $10 \mu\text{mol m}^{-2} \text{s}^{-1}$  in late October (Figure 5a). Over 50% of all deciduous tree leaves, except for those of oak, had fallen by mid-October (J. O'Keefe, Harvard University, unpublished data) and the remaining leaves were clearly senescent.

The second most abundant species in the hemlock stand is white pine, with about 9% of basal area, 13% of biomass and 16% of aboveground C storage during the 1990s (Smith 2001). Because white pine has stored nearly twice as much C per unit basal area compared with hemlock in recent years, white pine has presumably raised daytime C uptake as well as C storage substantially above that predicted for a pure hemlock stand. This is supported by the finding that white pine saplings have a photosynthetic rate of about  $15 \mu\text{mol m}^{-2} \text{s}^{-1}$  at current ambient  $[\text{CO}_2]$  and saturating light (Bauer et al. 2001), which is more than twice the measured maximum photosynthetic rate of hemlock saplings (Hadley 2000b). The position of mature white pine canopies above most of the hemlock canopy in the mixed stand also means more frequent exposure of white pine foliage to high solar irradiances. If we assume that white pine has the same ratio of leaf area to basal area as hemlock, and replace the 9% of basal area currently occupied by white pine with a similar amount of hemlock with half the rate of C storage per unit basal area, total C storage in the stand would decrease about 9%.

Carbon exchange by the forest beyond the hemlock stand affected the measured fluxes because of the significant effect of footprint length on measured flux during the daytime in most months between April and October (Table 3). In general, the effect was positive, showing that trees beyond the hemlock stand were taking up less C per unit land area (negative fluxes indicate C uptake), or that there was higher soil respiration beyond the hemlock stand. Both of these effects are likely because immediately beyond the hemlock stand to the SW is a forested swamp dominated by red spruce and black gum (Figure 1). Black gum is slow growing, with the largest trees ~60 cm in diameter and up to 350 years old (D. Orwig, Harvard Forest, unpublished data), so it is likely to have low C uptake rates. Another bog near this site at Harvard Forest had a low soil respiration rate near its margins compared with forested upland sites on most sampling dates, but showed elevated respiration during a drought (Savage and Davidson 2001). Summer 2001 was quite dry, and it is therefore likely that some of the high positive C fluxes ( $> 20 \mu\text{mol m}^{-2} \text{s}^{-1}$ , Figures 5a and 5b) were a result of high respiration rates in the forested swamp.

The effects of estimated footprint length on C exchange rates indicate that, on average, daytime models that did not incorporate footprint size may have underestimated C storage by  $0.8 \text{ Mg ha}^{-1}$  from April through October (Table 3). At night, the estimated footprint of the flux system was so large that C fluxes cannot be attributed primarily to the hemlock forest, and it is impossible to estimate the effects of other specific forest types. However, there is evidence that the measured nocturnal C fluxes are what one would expect from the hemlock forest, because of the nearly identical temperature coefficients in exponential temperature regressions for soil respiration

measured with chambers, and ecosystem respiration measured by the eddy flux system (Figure 3). Furthermore, the constant in the exponential regression for ecosystem respiration as measured by the flux system (0.758) is ~35% larger than the constant in the regression for soil respiration measured in chambers (0.561). This difference is what one would expect if soil respiration constituted 75% of total ecosystem respiration, which is close to the estimate from other eddy covariance measurements in deciduous forest (Wofsy et al. 1993).

#### *Light response of carbon uptake and variability around the response curve*

Carbon uptake by the hemlock forest increased rapidly with increasing PAR at low irradiances, and then more slowly, but showed no clear light saturation (Figure 7). This response is consistent with the high shade tolerance of hemlock, which creates a canopy with heavily shaded lower foliage. Lower foliage is therefore on the steep portion of the photosynthetic light response curve when the upper leaves are light saturated.

The data showed considerable scatter around the mean response curve partly because of the short (30 min) averaging time for the eddy flux data. Another likely reason is the presence of gaps in the dense hemlock canopy caused by tree mortality or, from mid-October through April, the presence of scattered leafless deciduous trees. These gaps may create "chimneys" through which  $\text{CO}_2$ -enriched air from the forest understory can be vented to the atmosphere. The flux system was close to the top of the uneven hemlock canopy, creating a small footprint that might or might not include particular canopy gaps. If a plume of  $\text{CO}_2$ -enriched air from one of these gaps passed the flux system, it could create a large C flux to the atmosphere, even during daytime, as is seen in Figures 5 and 7, especially in July. We measured occasional large releases of  $\text{CO}_2$  from storage in the subcanopy air space. Such releases may account for the high C flux to the atmosphere sometimes seen in summer (Figure 5), although the measured losses of  $\text{CO}_2$  from the subcanopy did not correspond temporally with large positive C fluxes measured above the canopy. In contrast to venting of  $\text{CO}_2$  through canopy gaps, advective removal of  $\text{CO}_2$  from the forest understory during daylight hours could have resulted in unusually strong negative above-canopy fluxes, representing high C uptake, as seen in Figures 5 and 7.

The lack of a seasonal trend in the light response curves (Figure 7) is difficult to explain given the large differences in temperature between July and April or October. However, hemlock foliage showed very little change in light-saturated photosynthesis between 10 and  $30^\circ\text{C}$  in chamber measurements (Hadley 2000b). Furthermore, canopy carbon uptake rates were maximal in July (Figure 7), and most occurrences of daytime net C efflux also occurred in the warmer months, possibly reflecting sporadic  $\text{CO}_2$  effluxes generated by high soil respiration in the understory.

#### *Maximum instantaneous C storage and annual total*

Highest rates of carbon uptake were near  $22 \mu\text{mol m}^{-2} \text{s}^{-1}$ , with only 15 values exceeding this throughout the year (Figure 5).

This is close to the maximum C flux in a coniferous forest dominated by red spruce in northern New England (Hollinger et al. 1999), but less than the maximum rate ( $\sim 30 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) in a nearby deciduous area of Harvard Forest (Wofsy et al. 1993, Goulden et al. 1996a). The difference in maximum rates may be partly a result of differences in the systems used; a side-by-side comparison of the system used in this study with that at the deciduous site showed that there was a 7% lower measured uptake with the hemlock system as a result of lower measured vertical wind variance. Even with a 7% upward adjustment of measured hemlock forest C fluxes, however, the deciduous forest would have a higher maximum uptake. This can be explained on the basis that hemlock foliage has a much lower light-saturated photosynthetic rate ( $A_{\text{max}} = 10 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; Hadley 2000a) compared with red oak, the dominant deciduous tree in the area measured ( $A_{\text{max}} \sim 20 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; Bassow and Bazzaz 1997). Much higher photosynthetic capacity in red oaks versus hemlocks appears to more than compensate for the lower summer LAI in the hardwood forest. Mean maximum LAI for 20 hardwood-dominated stands in the deciduous forest was only 2.8 and 3.3 in 1998 and 1999, respectively, compared with 4.4 for the hemlock stand in summer.

Despite the low maximum rate of C uptake and lack of C storage during August, annually summed eddy covariance data and model outputs from November 2000 through October 2001 gave  $295 \text{ g m}^{-2} \text{ year}^{-1}$  ( $2.95 \text{ Mg ha}^{-1} \text{ year}^{-1}$ ) of C storage for the hemlock forest. This is substantially more than for the nearby deciduous forest in any year between 1992 and 2000 (Barford et al. 2001), or for a spruce forest 250 km to the northeast (Hollinger et al. 1999). It is also well above the estimate of  $\sim 1 \text{ Mg ha}^{-1} \text{ year}^{-1}$  of C storage by a 250-year-old ponderosa pine stand (Law et al. 2001).

It is possible that a longer photosynthetic season for the hemlock stand at Harvard Forest compared with the nearby deciduous forest (because hemlocks are evergreen) or compared to the spruce forest in Maine (because it is colder in Maine) could account for the high C uptake by the hemlock forest. However, the greater age of the hemlock forest makes it seem unlikely that it is storing this much C, and aboveground C storage over the decade from 1990–1999 was only  $1.06\text{--}1.38 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  (Smith 2001). Furthermore, the flux system could not measure at least some of the photosynthesis of the rapidly growing pines in the hemlock forest because it was too low relative to the pine canopies.

Further investigation will be needed to determine if  $\sim 3 \text{ Mg ha}^{-1} \text{ year}^{-1}$  is a realistic estimate of C storage for the hemlock forest for November 2000–October 2001. The summer of 2001 was drier than average at Harvard Forest, and soil respiration was somewhat limited by low soil water content (see Figure 3 legend). In 1998, which was a wet year, soil respiration reached  $6.1 \mu\text{mol m}^{-2} \text{s}^{-1}$  (J. Hadley, unpublished data), more than  $1 \mu\text{mol m}^{-2} \text{s}^{-1}$  above the highest rate measured in 2001 (Figure 3). This difference in soil respiration could account for most of the difference between the  $\sim 1.2 \text{ Mg ha}^{-1} \text{ year}^{-1}$  of C stored above ground in the hemlock stand in 1998

(Smith 2001) and the  $2.95 \text{ Mg ha}^{-1} \text{ year}^{-1}$  of C storage we estimated for November 2000–October 2001. Goulden et al. (1996a) and Barford et al. (2001) concluded that interannual variation in soil respiration, rather than variation in photosynthesis or aboveground C storage, accounts for most of the interannual variation in measured C uptake in hardwood-dominated parts of Harvard Forest.

#### *Seasonal carbon storage, temperature effects and potential effects of climate change*

The hemlock forest stored a small amount of C in late October (Figure 5) and November 2000 despite unusually low temperatures. There was no C storage during winter 2000–2001, which was cold with a deep snowpack that accumulated after the soil had cooled to near  $0^\circ\text{C}$ . Because spring activation of photosynthesis in early April (Figure 5) occurred while the ground was still snow-covered, and 3 weeks before any significant increase in soil respiration, it contributed strongly to a dramatic increase in C storage from March to April. Low soil respiration resulted in nearly the highest C storage of the year occurring in April (Figure 9), while deciduous trees were still leafless.

Carbon storage in spring and fall, but especially in spring 2001, was regulated more by  $T_m$  (Figure 8) than by  $T_s$ . This is consistent with physiological measurements of eastern hemlock (Hadley 2000a) as well as other species (Fahey 1979, Smith et al. 1984, DeLucia and Smith 1987). At another conifer forest in New England, Hollinger et al. (1999) found that, although C uptake in autumn decreased dramatically after the first frost below  $-1^\circ\text{C}$ , increasing C uptake in spring was more closely related to soil thawing than to  $T_a$ . In our study, the soil did not freeze, although  $T_s$  was below  $1^\circ\text{C}$  for 4 months (mid-December to mid-April). It is possible that, without the large insulating snowpack that accumulated in the hemlock forest in winter 2000–2001, the soil would have frozen and the increase in C gain seen in the hemlock stand in April 2001 would not have occurred.

During October 2001, which was unusually mild with only two subfreezing nights, C storage was high (Figure 9) despite the relatively short days, indicating the significance of relatively low C flux to the atmosphere at night in fall compared with summer (Figures 5 and 9). Ecosystem respiration was presumably low during the day and night in autumn, allowing for high C storage despite the short photoperiod. These results indicate that climate change leading to fewer frosts in spring and fall could significantly stimulate C storage in eastern hemlock stands.

The C exchange models combined with C exchange data for 10 days in August 2001 indicated a small C loss during this month (Figure 9). The main reasons for C loss were probably  $T_a$  and  $T_s$ , which averaged  $2.4$  and  $2^\circ\text{C}$  higher, respectively, in August than in July (Table 4). The model of nocturnal C exchange for mid-July through late September estimated an increase in C flux to the atmosphere of  $0.7 \mu\text{mol m}^{-2} \text{s}^{-1}$  per  $^\circ\text{C}$  increase in soil temperature. Therefore, the increase in mean soil temperature of  $2^\circ\text{C}$  from July to August led to an increase



Table 4. Mean air and soil temperatures (°C) in the hemlock forest during the study period.

Month	Mean air temperature	Mean daily minimum air temperature	Mean daily maximum air temperature	Mean soil temperature
November	2.5	− 0.6	6.0	5.7
December	− 5.7	− 10.1	− 1.8	0.5
January	− 4.7	− 8.6	− 0.8	− 0.2
February	− 4.2	− 9.1	0.3	0.2
March	− 1.3	− 4.8	2.3	0.7
April	7.4	1.7	12.7	1.9
May	13.5	8.1	19.6	8.8
June	19.2	14.0	24.7	13.5
July	18.7	11.8	25.1	14.7
August	21.1	16.4	26.4	16.7
September	15.4	10.8	20.3	14.4
October	10.2	5.4	15.5	10.6

in mean nocturnal C efflux of  $\sim 1.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  or  $\sim 0.19 \text{ Mg ha}^{-1}$  for all of the nighttime periods in August, representing 65% of the increase in nighttime C loss from the forest between July and August (Figure 9). Assuming that the response of ecosystem respiration to soil temperature is similar during the day and at night, and given the greater number of daylight versus nighttime hours ( $\sim 14$  versus  $\sim 10$ ), increasing soil temperature by  $2^\circ\text{C}$  would lead to an increase of  $\sim 0.26 \text{ Mg ha}^{-1}$  in daytime ecosystem respiration from July to August. This would result in a 55% ( $0.48 \text{ Mg ha}^{-1}$ ) decrease in estimated daytime C storage between July and August (Figure 9). The marked effect of hot summer weather in reducing net C uptake suggests that, unlike higher spring and fall temperatures, a climatic trend toward hotter summers could greatly reduce C storage in eastern hemlock forests. Simulations of C exchange throughout the year will be necessary to determine the net effect of warming in summer as well as in spring and fall.

#### *Possible effects of large-scale hemlock mortality on regional carbon balance*

Mortality of old hemlock stands could result in a large C flux to the atmosphere. We have not yet estimated ecosystem respiration during daytime, which is necessary to estimate gross primary productivity (GPP), or the C fixation that would be lost by complete mortality of the hemlock forest. However, because of higher daytime  $T_a$  and  $T_s$  ( $\sim 2^\circ\text{C}$ ), daytime respiration can be assumed to be at least equal to nocturnal respiration, which we estimate at  $4.5 \text{ Mg ha}^{-1}$  (based on summing the monthly nocturnal C exchange estimates in Figure 5). A conservative estimate of daytime respiration of  $4.7 \text{ Mg ha}^{-1}$  implies that total photosynthesis or GPP must be  $\sim 12 \text{ Mg ha}^{-1}$  (net daytime C uptake of  $7.6 \text{ Mg ha}^{-1}$  plus daytime respiration of  $4.7 \text{ Mg ha}^{-1}$ ). This large withdrawal of C from the atmosphere will be lost, probably resulting in net C loss from the ecosystem for an extended period after mortality of the hemlocks. A replacement deciduous forest (likely dominated by black birch; Orwig and Foster 1998) will take many years to reach a GPP approaching that of the current hemlock forest.

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