

Water use and carbon exchange of red oak- and eastern hemlock-dominated forests in the northeastern USA: implications for ecosystem-level effects of hemlock woolly adelgid

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Summary Water use and carbon exchange of a red oak-dominated (*Quercus rubra* L.) forest and an eastern hemlock-dominated (*Tsuga canadensis* L.) forest, each located within the Harvard Forest in north-central Massachusetts, were measured for 2 years by the eddy flux method. Water use by the red oak forest reached 4 mm day⁻¹, compared to a maximum of 2 mm day⁻¹ by the eastern hemlock forest. Maximal carbon (C) uptake rate was also higher in the red oak forest than in the eastern hemlock forest (about 25 versus 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Sap flux measurements indicated that transpiration of red oak, and also of black birch (*Betula lenta* L.), which frequently replaces eastern hemlock killed by hemlock woolly adelgid (*Adelges tsugae* Annand.), were almost twice that of eastern hemlock.

Despite the difference between species in maximum summertime C assimilation rate, annual C storage of the eastern hemlock forest almost equaled that of the red oak forest because of net C uptake by eastern hemlock during unusually warm fall and spring weather, and a near-zero C balance during the winter. Thus, the effect on C storage of replacing eastern hemlock forest with a forest dominated by deciduous species is unclear. Carbon storage by eastern hemlock forests during fall, winter and spring is likely to increase in the event of climate warming, although this may be offset by C loss during hotter summers. Our results indicate that, although forest water use will decrease immediately following eastern hemlock mortality due to the hemlock woolly adelgid, the replacement of eastern hemlock by deciduous species such as red oak will likely increase summertime water use over current rates in areas where hemlock is a major forest species.

Keywords: climate change, invasive insects, *Quercus rubra*, *Tsuga canadensis*.

Introduction

Dominant tree species that largely control nutrient cycling and

forest–atmosphere gas exchange, have been termed foundation species (Ellison et al. 2005). In the northeastern United States, an endpoint of forest succession is represented by eastern hemlock (*Tsuga canadensis* L.), a slow-growing, shade-tolerant foundation species that can live many hundreds of years and exclude most other tree species from the forest. Even though seeds of other species may be present, few seedlings and saplings survive in the deep shade beneath a hemlock forest canopy (Pacala et al. 1993).

Oaks (*Quercus* sp.) are the dominant trees in most forested areas of the eastern USA south of central New England and New York, and they differ strongly from eastern hemlock in the high irradiances they need to survive and in their capacity for rapid establishment after disturbances such as agricultural use and fire. Other deciduous forest trees, including species of maple (*Acer*) and birch (*Betula*), are generally more shade-tolerant than oaks, but less so than eastern hemlock.

In the 1980s, an exotic insect, the hemlock woolly adelgid (*Adelges tsugae* Annand, hereafter HWA), began killing eastern hemlock in the southern New England region of the USA. In some stands, all trees were killed within a few years, and were replaced mainly by black birch (*Betula lenta* L.) (Orwig and Foster 1998, Orwig et al. 2002) and other deciduous species, thus reversing the normal succession. The HWA has spread northward to southern Maine and New Hampshire. Low temperatures kill overwintering HWA (Parker et al. 1999, Skinner et al. 2003) and provide the only known barrier to its continued northward spread. Thus, if winters become milder in coming decades, replacement of eastern hemlock by deciduous species is likely to occur throughout New England.

Our objectives were to obtain information about carbon and water cycling in an eastern hemlock- and red oak-dominated (*Quercus rubra* L.) forests that will help predict the effects on water and carbon cycling of the replacement of eastern hemlock by deciduous species.

Materials and methods

Site description

The eastern hemlock-dominated forest (hereafter referred to as the eastern hemlock forest) studied was previously described by Foster and Zebryk (1993) and Hadley and Schedlbauer (2002). Trees range in age to 230 years, and the stand has not been subject to agricultural use, fire or other stand-clearing disturbance. The stand is located on nearly level ground adjacent to a swamp that lies about 200 m to the W and SW of the eddy-covariance tower (Hemlock; Figure 1). The red oak-dominated forest (hereafter referred to as the red oak forest) is on the W- to NW-facing slope of Little Prospect Hill about 660 m NNW of the eastern hemlock forest tower, with the eddy flux tower indicated by LPH in Figure 1. The hillside where the tower is located has a 6–10% slope, was cleared for agriculture in the 19th century then returned to forest in the late 19th and early 20th centuries. An intense fire in 1957, which killed most trees within 300 m of the flux tower, was followed by salvage logging. Red oak is the dominant tree species both in basal area (almost 60% within 300 m of the eddy flux tower) and leaf area (nearly 70% of the total biomass of leaf litter collected in 2002 to 2006). Canopy height of the red oak forest at LPH ranges between 16 and 20 m, which is lower than for the eastern hemlock forest (average height about

22 m) or the more wind-sheltered red oak forest (25 m) surrounding the eddy flux tower at the Harvard Forest Environmental Measurement Site (HFEMS; Figure 1). Wofsy et al. (1993), Barford et al. (2001) and Urbanski et al. (2007) have all described the forest measured by the HFEMS tower and reported carbon exchange rates measured at that site. Some physical properties and ecosystem-level characteristics of the forests near the LPH and Hemlock towers are summarized in Table 1.

Forest–atmosphere gas exchange and environmental measurements

At both sites, water vapor and CO₂ fluxes were measured by the eddy covariance or eddy flux technique (Baldocchi et al. 1988, Wofsy et al. 1993). Data were collected at 5 Hz with CSAT-3 sonic anemometers (Campbell Scientific, Logan, UT) and closed-path CO₂/H₂O analyzers (Li-Cor, Lincoln, NE) located at a height of 27 m (about 5 m above the mean local canopy height) on the Hemlock tower and 20.5 m (4.5 m above the mean local canopy height) on the LPH tower. Air samples were drawn at 5.7 l min⁻¹ through aluminum tubing with a polyethylene liner (Dekoron), about 4 mm inside diameter, to the analyzers. The intake tubing was about 35 m in length at the Hemlock tower and 25 m at the LPH tower and had Teflon filters with 2- μ m pores at the air intake point, and 1- μ m filters

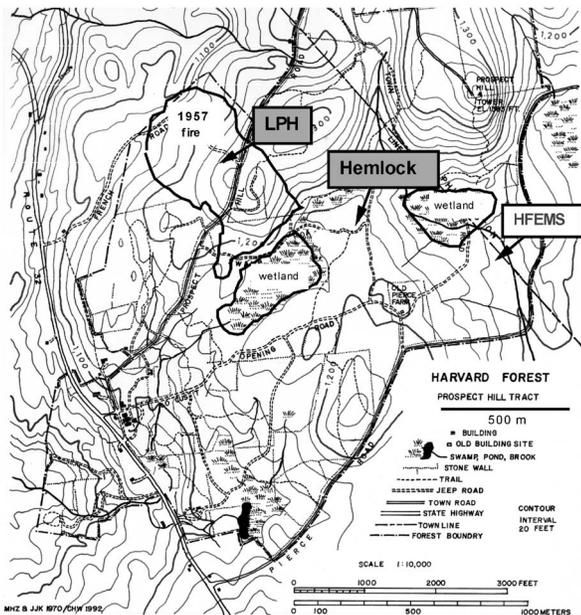


Figure 1. Locations of eddy flux towers at the Harvard Forest in central Massachusetts, USA. Towers labeled with a gray background were used to collect study data. The Little Prospect Hill (LPH) site was established in 2002 within the area burned by a stand-replacing forest fire in 1957. Hemlock denotes the location of an eddy covariance tower in an eastern hemlock forest (see Hadley and Schedlbauer 2002). The Harvard Forest Environmental Measurement Site (HFEMS) was not used in this study, but is the location of continuing forest–atmosphere carbon exchange measurements that began in 1991 (Wofsy et al. 1993, Barford et al. 2001, Urbanski et al. 2007).

Table 1. Physical and ecological characteristics of the red oak (*Quercus rubra*) and eastern hemlock (*Tsuga canadensis*) forests for 2004–2006.

Forest characteristic	Eastern hemlock	Red oak ¹
Elevation (m)	360	390
Forest age (years)	100–230	45–100
Mean canopy height (m)	22	16–20
Tree density (ha ⁻¹)	620	930–600
Total tree basal area (m ² ha ⁻¹)	65	20–33
Aboveground carbon in live biomass (Mg ha ⁻¹)	80	38–90
<i>Species present (% basal area)</i>		
<i>Tsuga canadensis</i>	82	7
<i>Quercus rubra</i>	–	58
<i>Pinus strobus</i>	11	–
<i>Pinus</i> spp.	–	20
Other deciduous spp.	7	15
Annual aboveground live biomass increment (Mg C ha ⁻¹ year ⁻¹)		
	1.3	1.4–1.8
Annual leaf litterfall (Mg C ha ⁻¹ year ⁻¹)		
	2.2	1.4–1.6
ANPP (Mg C ha ⁻¹ year ⁻¹)		
	3.5	2.8–3.4
Leaf area index		
	4.5	4.0–5.0

¹ Ranges are given for properties of the red oak forest, because tree height, biomass, basal area, aboveground carbon, annual biomass increment and annual litterfall increase with distance downhill from the LPH tower to the west or northwest, particularly when some older and larger trees that survived the 1957 fire are found at dis-

just before the gas analyzer.

Covariances between vertical wind and CO₂ and H₂O concentrations were calculated every 30 min based on deviations from 10-min running means. The appropriate time interval between measurements of wind vectors and gas concentrations, to allow for air sample transport from the intake point to the analyzer (the lag time), was recalculated every 2 months by determining the lag times resulting in maximum covariance of CO₂ or H₂O concentration with vertical wind. Lag times for H₂O were longer than for CO₂, probably because of slight adsorption and desorption of water vapor from the polyethylene tube walls. The coordinate plane of wind direction at both sites was rotated for each 30-min interval so that mean vertical wind was zero, to separate turbulent vertical transport from advection by mean flow along the streamlines.

Examination of the relationship between nighttime C flux and turbulence as measured by friction velocity (u^* = square root of momentum flux), showed that, for the eastern hemlock forest, measured C flux declined at u^* values below 0.4 m s⁻¹ (cf. Hadley and Schedlbauer 2002). A similar analysis for the red oak forest at LPH showed a u^* threshold of 0.35 m s⁻¹ for nighttime C fluxes not limited by low turbulence when the canopy was foliated during summer (Figure 2a), but a u^* threshold of 0.45 m s⁻¹ when the canopy was leafless (Figure 2b). All C flux data collected with u^* values below these threshold values were ignored in the data analysis and replaced with C flux estimates from models developed from data collected in periods with higher u^* . Because the true H₂O flux from forest to atmosphere can be turbulence-limited, a turbulence threshold was not used in H₂O flux calculations.

The extent of high-frequency loss of flux was checked by a spectral correction procedure (Goulden et al. 1996), in which power spectra of sonic air temperature, CO₂ and H₂O concentrations were compared to determine a mathematical filtering for the temperature signal that matches the smoothing of CO₂ and H₂O signals due to gas mixing and adsorption/desorption of water vapor in the gas inlet line, plus smoothing by the CO₂/H₂O analyzer. The ratio of original and smoothed temperature covariance with vertical wind estimated the CO₂ or H₂O covariance lost by attenuation of higher frequency variations. Corrections for loss of high-frequency flux typically increased short-term CO₂ flux estimates by 3–5%, with little change in cumulative CO₂ flux. However, the H₂O flux correction typically increased both short-term and cumulative H₂O flux by about 15%.

At both the Hemlock and LPH flux towers, we also measured photosynthetically active radiation (PAR) above the canopy with Li-Cor LI190-SA quantum sensors, and air temperature and relative humidity with a Campbell HMP-45C temperature/relative humidity probe (Campbell Scientific, Logan, UT). Data were collected every 60 s and averaged every 30 min. Soil temperature at 10-cm depth at five locations near the base of the Hemlock tower, and at two locations near the base of the LPH tower, as well as 200 m to the NW and SW of the tower, were measured every 60 s with copper-constantan thermocouples and averaged at the same time intervals. Mean midday PAR readings were compared with an LI-190 SA sen-

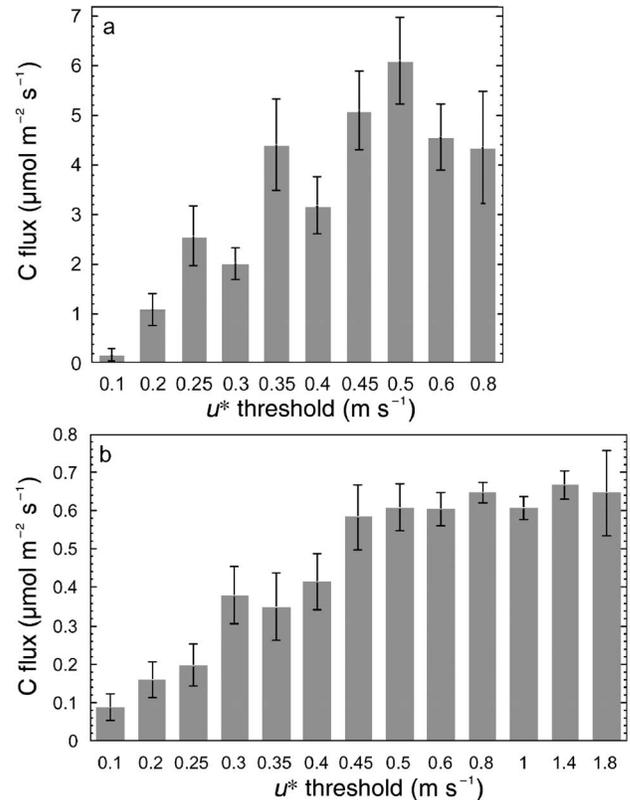


Figure 2. Mean nighttime carbon (C) flux measured at the Little Prospect Hill tower for various ranges of friction velocity (u^*) when the canopy was (a) foliated in July and August 2002 and 2003 and (b) leafless in January through March 2003 and 2004. Only data collected during 30-min periods when mean wind direction was between 215° and 360° are included. Error bars are standard errors of means for sample sizes ranging from (a) 51 to 170 and (b) 61 to 530 per bin.

sor at the Harvard Forest Meteorological station (HF met station), which is recalibrated and changed annually, and adjusted when necessary. Air temperatures measured with the HMP-45C probe were compared with measurements with a shaded thermocouple located 50 cm above it, which showed a small but predictable increase in temperature during periods of strong solar radiation, but otherwise was within 0.5 °C of the HMP-45C temperature probe; both sets of temperature measurements were checked for consistency with an air temperature sensor located 2 m above ground in an open field at the HF met station, which showed a small but predictable increase in temperature at times of high solar radiation. Water vapor pressure (WVP) calculated from the temperature and RH probe was checked against a probe of the same model at the HF met station, which was recalibrated annually. The HMP-45C probes at the LPH and Hemlock towers gave similar WVP to the met station during periods of low transpiration, but during periods of high transpiration, measured WVP was higher at the forested sites, especially at the LPH site. This was presumably because greater surface-to-atmosphere water vapor flux from the forests, especially the red oak forest, raised the humidity of

the atmosphere just above the tree canopy compared with the air at the met station in the open field.

Biometric measurements and leaf area index

For each species in the red oak forest, tree density, basal area, aboveground live biomass, aboveground carbon and annual aboveground biomass and carbon increments were estimated for 296 trees more than 10 cm in diameter at 1.25 m height, which were fitted with dendrometer bands. The trees were in circular plots 100, 200, 300 and 400 m from the flux tower, on transects following compass bearings of 225° to 345° from the tower, in 15° increments. Plots at 100 m were 6 m in diameter; other plots were 9 m in diameter. In the eastern hemlock forest, the same quantities for each species were estimated from 161 trees above 10 cm diameter, located in 6 m diameter plots 50, 100, 150 and 200 m from the tower, along transects following compass bearings of 80° to 270° from the tower, in 15° increments.

Annual leaf litter, which was classified by species, was collected in 36 litter baskets in the red oak forest, and 12 litter baskets in the eastern hemlock forest, all placed in the plots where aboveground biomass was measured.

Leaf area index (LAI) was measured in both the eastern hemlock and the red oak stands with a Li-Cor LAI-2000 plant canopy analyzer. Data were collected each year in early September for the red oak forest and once in November for the eastern hemlock forest from 36 sampling locations in the red oak forest, and from 12 sampling locations (at distances of 50, 100, 150 and 200 m from the tower along transects following compass bearings of 195°, 225° and 255°) in the eastern hemlock forest. In addition, projected LAI for the eastern hemlock forest in both summer (August) and winter (March) was estimated by destructive sampling of four randomly selected branches from the lower, mid and upper canopy, to estimate total projected leaf area per branch from projected leaf area-to-dry mass ratios, and regression of the resulting leaf area per branch estimates against branch basal diameter. These relationships were then applied to four canopy-dominant eastern hemlock trees near the flux tower on which all branch basal diameters were measured, and the total estimate of leaf area for these four trees was divided by the ground area beneath the grouped canopies of the four trees to derive LAI.

Wind direction, turbulence and data acceptability

Because the flux tower in the eastern hemlock forest in the NE corner of the stand (see detailed map in Hadley and Schedlbauer 2002), the forest has a dominant influence on CO₂ and H₂O flux measurements only if there is a SW wind. Therefore we accepted only these data and used statistical models derived from data with SW wind (described below) to estimate fluxes with other wind directions.

At LPH, the acceptable wind directions were also limited, because the eddy covariance technique depends on a canopy surface that is horizontal or of fairly uniform slope, to ensure that flux measurements are not unduly affected by large scale-eddies driven by pressure variations produced as wind flows over hills. We observed that, at the LPH site, unusually large C

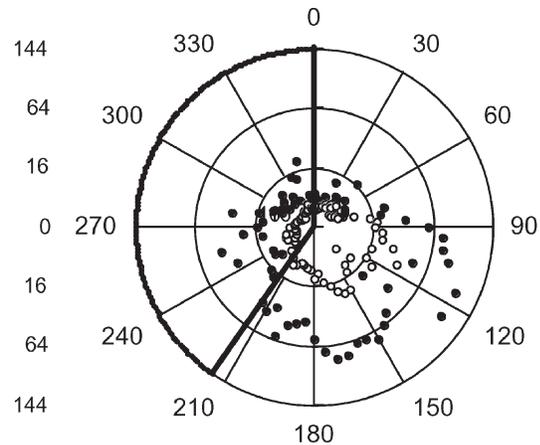


Figure 3. Apparent mean (○) and maximum (●) nighttime carbon fluxes calculated from eddy covariance data (on radial axis as shown at left) as a function of wind direction at the Little Prospect Hill site during July and August of 2002 and 2003. Data were binned by 5° increments of wind direction. The heavy black line indicates the range of wind directions where measured values were judged acceptable as valid carbon flux data.

fluxes were measured with E and S winds. The magnitude of these C fluxes far exceeded those observed at the eastern hemlock site, or with westerly winds (Figure 3). We believe that these high values were artifacts of lee-slope turbulence generated by east or south winds flowing over the summit ridge of LPH (see Figure 1). Accordingly, flux data were accepted only with wind directions between 215° and 360°, which produced no anomalous high C flux values.

The 6–10% slope of the LPH site creates conditions where CO₂ flux can be underestimated from eddy flux data because of a large advective flux due to cold air drainage during still conditions. To evaluate this, we plotted nighttime CO₂ flux as a function of turbulence expressed as u^* . The u^* required to prevent significant nighttime advective CO₂ flux may differ according to whether the canopy has foliage or is leafless. A leafless canopy allows greater cooling of the forest floor by radiant heat transfer, but creates less of a barrier to mixing of sub-canopy and above-canopy air. Our analysis (Figure 2) indicated that a minimum u^* of about 0.35 m s⁻¹ was necessary to remove effects of understory advection when the forest had foliage, and a value of 0.45 m s⁻¹ when it was leafless.

For the red oak site, acceptable C flux measurements covered about 36% of the daytime hours and 25% of the nighttime hours during the study, varying slightly from year to year (Table 2). The day-to-night difference was primarily due to lower atmospheric turbulence above the forest at night. For the eastern hemlock site, the corresponding mean figures are 23% and 14%, varying somewhat from year to year (Table 3). The amount of acceptable data varied seasonally: at the red oak site, acceptable C flux data ranged from highs of about 60% during the day and 35% at night from December through February, to lows of 21% during the day and only 6% at night during July and August. At the eastern hemlock site, the amount of acceptable data varied less over the year, because NW

Table 2. Number of daytime (D) and nighttime (N) measurements collected by month, and the percentage of hours for which acceptable data were obtained in the red oak (*Quercus rubra*) stand (Little Prospect Hill).

Month	2004			2005			2006		
	D	N	% (D/N)	D	N	% (D/N)	D	N	% (D/N)
Jan	–	–	–	502	291	85/33	216	294	39/34
Feb	–	–	–	368	235	62/31	346	351	58/47
Mar	–	–	–	426	273	57/37	235	212	31/29
Apr	–	–	–	182	129	23/20	161	105	20/17
May	–	–	–	251	99	28/17	290	104	32/18
Jun	–	–	–	119	41	13/8	271	81	30/15
Jul	215	51	23/9	175	29	19/5	–	–	–
Aug	242	55	28/9	116	17	14/3	–	–	–
Sep	217	72	29/11	258	90	34/13	–	–	–
Oct	230	210	33/26	287	222	43/27	–	–	–
Nov	228	312	39/37	306	231	52/27	–	–	–
Dec	192	257	34/28	479	385	83/42	–	–	–
Total	1324	957	30/22	3469	2042	39/24	1519	1147	34/28

winds, which are common in winter, prevented acquisition of acceptable data. Here, the mean proportion of acceptable monthly data varied between 17 and 32% during the day and between 8 and 21% at night, with minimum values in May and September and maximum values in November and December (Tables 2 and 3).

The proportion of acceptable H₂O flux data was larger, because no turbulence threshold was imposed. For the red oak forest, acceptable H₂O flux values were obtained during 40% of all hours, with monthly variation between 17 and 62%. For eastern hemlock forest H₂O flux, acceptable values were obtained for 25% of all hours, with monthly values of between 10 and 43%.

Transpiration measurements

Constant-heat sap flux sensors (Granier 1985) were installed in a set of trees in the eastern hemlock stand, within 20 m of the

eddy covariance tower (Table 2). Similarly, sap flux sensors were installed in eight black birch and eight red oak trees located on LPH 300–400 m from the eddy covariance tower. The sensors were 20 mm long and contained a copper-constantan thermocouple junction. At least two sets of sensors were installed on opposite sides of each tree to account for circumferential variability. All sensors were protected from precipitation and water by shielding with plastic containers, and from direct solar heating and air temperature variations by reflective insulation. To express transpiration rates on a projected crown area basis, crown area was calculated for each tree from a polygon created by measuring the distance from the stem to the edge of the crown along eight axes separated by 45° angles.

Modeling of ecosystem water and carbon fluxes

Regression models of CO₂ and H₂O flux based on acceptable

Table 3. Number of daytime (D) and nighttime (N) measurements collected by month, and the percentage of hours for which acceptable data were obtained in the eastern hemlock (*Tsuga canadensis*) stand.

Month	2004			2005			2006		
	D	N	% (D/N)	D	N	% (D/N)	D	N	% (D/N)
Jan	–	–	–	145	70	23/8	121	113	21/13
Feb	–	–	–	174	87	29/12	77	96	13/13
Mar	–	–	–	250	124	33/17	94	44	13/6
Apr	–	–	–	145	71	18/11	163	96	20/15
May	–	–	–	115	31	13/5	187	83	21/14
Jun	–	–	–	274	146	30/28	138	47	15/9
Jul	200	79	22/14	206	97	26/21	–	–	–
Aug	191	90	22/14	–	–	–	–	–	–
Sep	126	53	17/8	–	–	–	–	–	–
Oct	135	87	20/11	153	123	23/15	–	–	–
Nov	166	141	28/17	208	174	35/21	–	–	–
Dec	116	132	21/14	203	249	35/27	–	–	–
Total	934	582	21/13	1873	1172	26/16	780	479	17/12

data and driven by environmental variables recorded at the flux tower sites were based on 1–2 month data runs to reduce the chance that response functions changed seasonally. Variables available to the regression models included only those known to affect the following tree physiological or physical parameters and processes: stomatal conductance, photosynthesis, ecosystem respiration and evaporation. The variables included PAR, VPD, time of day, air temperature, soil temperatures and nighttime minimum air temperature if monthly minimum air temperatures fell below freezing. Data gaps were filled by models using only measured values of these variables as inputs.

In most H₂O flux models, PAR explained the most variation, but VPD, hour of day, and soil and air temperatures also explained a significant fraction of the H₂O flux variation in some models (Table 4). Typically, except during months with freezing night temperatures, PAR explained 60 to 70% of the variation in H₂O flux at each site, and VPD explained 10 to 20%. The coefficients for PAR and VPD changed over the course of the year, most dramatically during leaf development and leaf abscission in the red oak forest (during May and June and in October, respectively), and also more slowly during aging of red oak forest foliage in late summer to early fall. In spring and fall, H₂O flux in eastern hemlock trees was affected by the nighttime minimum temperature, which has been shown to affect leaf conductance in many conifers including hemlock (Smith et al. 1984, Hadley 2000a).

Most daytime CO₂ flux models had more input variables than transpiration or nighttime CO₂ flux models. For daytime periods when possible, we first derived a rectangular hyperbola of the form:

$$\text{C flux} = c + \frac{a \text{ PAR}}{b + \text{ PAR}} \quad (1)$$

where *a* is maximum C uptake rate, *b* is a coefficient and *c* is an approximation of C flux at zero PAR, to describe PAR–C flux relationships. At the eastern hemlock site, these models (Table 5a) explained 70% to more than 90% of the variation in C flux during March–October, and a similarly high proportion at the LPH site during June through September. Residuals from the PAR–C flux models were modeled by stepwise linear multiple

regression, with the input variables mentioned above. For months when daytime C uptake was too low to fit a simple PAR–C flux model, C flux was modeled directly by stepwise multiple regression with the same input variables (Table 5b). For nighttime periods, C flux was modeled as a linear function of soil temperature, air temperature or both (Table 5c).

Results

Energy balance closure

Analysis of site energy balance, expressed as total net radiant energy exchange (*R*) versus total turbulent heat exchange (sensible heat (*H*) + latent heat of water vapor transfer (*L_E*)) indicated that turbulent heat exchange was slightly less than net radiant exchange in both summer and winter. At the LPH site for the foliated-canopy months of July through September, (*H* + *L_E*) versus *R* showed a linear relationship with a slope of 0.86. For the leafless canopy in winter, the (*H* + *L_E*) versus *R* relationship became nonlinear at high positive values of *R* (400–700 W m⁻²), where there was no relationship between measured values of *R* and (*H* + *L_E*). However, it was approximately linear at *R* < 400 W m⁻², with the slope of (*H* + *L_E*) versus *R* increasing from 0.72 for *R* ranging from –80 to 400 W m⁻², to 0.90 for *R* ranging only from –80 to 100 W m⁻². The slope of the (*H* + *L_E*) versus *R* relationship is typically 0.8 to 0.9 at other flux measurement sites (Wilson et al. 2002), so these numbers do not indicate excessive heat loss from the forest due to advection. At the eastern hemlock site in summer, the slope of the *H* + *L_E* versus *R* relationship was only about 0.74; however, measured net radiation may not be representative of the forest for which turbulent fluxes were measured, because (unlike the case at the LPH site), the top platform of the Hemlock tower forms a significant portion of the area measured by the net radiometer.

Water use by forests and individual trees

In July 2004, maximum daily H₂O flux to the atmosphere (evapotranspiration; ET) from the red oak forest reached about 4 mm day⁻¹, about twice that from the eastern hemlock forest. Water use by both forests declined and mean daily ET converged by late September, just before deciduous leaf-fall, and before the short period when ET of the eastern hemlock

Table 4. Water flux models for the red oak (*Quercus rubra*) and eastern hemlock (*Tsuga canadensis*) forests. The *P*-values are from *F*-tests; the largest *P*-value for any of the models in a group of months is given. In all cases *n* > 100. Parameters are: PAR = photosynthetically active radiation; VPD = vapor pressure deficit; *h* = hour of day; *D* = day of month (used in May and October only); *T_a* = above-canopy air temperature; *T_s* = soil temperature at 10-cm depth; and *T_m* = previous night minimum air temperature. Frost is a measure of severity of night freezing as follows: 0 if *T_m* was above –2 °C, 1 if *T_m* was between –2 and –5 °C, 2 if *T_m* was between –5 and –10 °C, and 3 if *T_m* was below –10 °C.

Years	Months	Red oak forest			Eastern hemlock forest		
		Parameters	<i>R</i> ²	<i>P</i>	Parameters	<i>R</i> ²	<i>P</i>
2004	Jul–Sep	PAR, VPD, <i>h</i> , <i>h</i> ²	0.67–0.71	< 10 ⁻¹⁶	PAR, VPD	0.71–0.81	< 10 ⁻¹⁶
2004–05	Oct–May	PAR, VPD, <i>h</i> , <i>h</i> ² , <i>D</i> , <i>T_m</i> , <i>T_s</i>	0.30–0.47	10 ⁻¹²	PAR, VPD, <i>h</i> , <i>h</i> ² , <i>T_a</i> , <i>T_m</i> , Frost	0.30–0.69	10 ⁻¹⁴
2005	Jun–Oct	PAR, VPD, <i>h</i> , <i>h</i> ²	0.68–0.75	< 10 ⁻¹⁶	PAR, VPD, <i>h</i> , <i>h</i> ²	0.75–0.86	< 10 ⁻¹⁶
2005–06	Oct–May	PAR, VPD, <i>h</i> , <i>h</i> ² , <i>D</i> , <i>T_m</i> , <i>T_s</i>	0.20–0.47	10 ⁻¹²	PAR, VPD, <i>h</i> , <i>h</i> ² , <i>T_s</i> , Frost	0.24–0.76	< 10 ⁻¹⁶
2006	Jun	PAR, VPD	0.62	< 10 ⁻¹⁶	PAR, VPD	0.63	< 10 ⁻¹⁶

Table 5. Carbon flux models for the red oak (*Quercus rubra*) and eastern hemlock (*Tsuga canadensis*) forests. Parameters are: PAR = photosynthetically active radiation; VPD = vapor pressure deficit; *h* = hour of day; *D* = day of month (used in May and October only); *T_a* = above-canopy air temperature; *T_s* = soil temperature at 10-cm depth; and *T_m* = previous night minimum air temperature. Frost is a measure of severity of night freezing as follows: 0 if *T_m* was above -2 °C, 1 if *T_m* was between -2 and -5 °C, 2 if *T_m* was between -5 and -10 °C, and 3 if *T_m* was below -10 °C. In 5b, *h*·VPD and PAR·*T_s* indicate the products of hour of day and vapor pressure deficit, and PAR and soil temperature, respectively. In 5c, where no model explained a significant fraction of the variation (in April 2005 for the eastern hemlock forest and June 2006 for the red oak forest), the mean nighttime C flux for all hours in the month was used in filling in all data gaps for calculating a monthly sum. The *P*-values in 5b and 5c are from *F*-tests. Abbreviations: na = data not available; and ns = not significant (*P* < 0.05).

Table 5a. Models for daytime CO₂ flux (C flux = *c* + *a*PAR/(*b* + PAR)).

Months	Red oak forest					Eastern hemlock forest				
	<i>a</i>	<i>b</i>	<i>c</i>	<i>n</i>	<i>R</i> ²	<i>a</i>	<i>b</i>	<i>c</i>	<i>n</i>	<i>R</i> ²
<i>2004</i>										
Jul–Aug	-36.2	495	6.3	458	0.93	-21.8	363	6.3	391	0.70
Sep	-30.8	999	1.3	221	0.94	-20.1	489	1.9	126	0.76
Oct	-14.6	1025	1.4	189	0.62	-16.9	615	0.9	135	0.85
Nov	na	na	na	na	na	-13.1	818	0.8	167	0.70
<i>2005</i>										
Apr	na	na	na	na	na	-14.8	339	2.2	108	0.93
May	na	na	na	na	na	-17.6	309	2.7	115	0.96
Jun	-32.6	456	5.6	201	0.88	-23.1	439	6.9	274	0.76
Jul	-37.6	554	6.5	338	0.94	-27.0	273	8.2	204	0.80
Aug						na	na	na	na	na
Sep	-28.1	489	3.2	299	0.95	na	na	na	na	na
Oct	-4.9	244	1.8	242	0.21	-17.6	325	1.7	152	0.93
Nov	na	na	na	na	na	-13.3	569	0.9	208	0.72
<i>2006</i>										
Jan	na	na	na	na	na	-4.0	99	1.4	121	0.62
Feb	na	na	na	na	na	-0.9	115	0.2	77	0.49
Mar	na	na	na	na	na	-13.0	928	1.2	113	0.78
Apr	-0.8	534	1.0	161	0.43	-18.6	661	1.3	144	0.95
May	-3.8	259	2.6	290	0.11	-18.2	307	3.2	186	0.91
Jun	-23.8	268	4.5	325	0.86	-24.1	327	5.6	215	0.77

Table 5b. Models with dependent variable (DV) daytime C flux (D) or residual from PAR model (R).

Months	Red oak forest					Eastern hemlock forest				
	DV	Ind. variables	<i>n</i>	<i>R</i> ²	<i>P</i>	DV	Ind. variables	<i>n</i>	<i>R</i> ²	<i>P</i>
<i>2004</i>										
Jul–Aug	R	<i>h</i> , <i>h</i> ² , <i>T_a</i> ²	457	0.02	0.01	R	<i>h</i> , <i>h</i> ² , VPD, <i>T_s</i>	523	0.14	< 10 ⁻¹⁵
Sep	R	<i>D</i> ² , <i>h</i> , <i>h</i> ² , <i>T_a</i>	220	0.31	< 10 ⁻¹⁵	R	<i>h</i> , <i>h</i> ² , VPD, <i>T_a</i>	125	0.32	< 10 ⁻⁹
Oct	R	<i>D</i> , <i>D</i> ² , <i>h</i> , <i>h</i> ²	227	0.64	< 10 ⁻¹⁶	R	<i>h</i> , <i>h</i> ² , <i>T_a</i> , <i>T_s</i> , <i>T_s</i> ²	134	0.40	< 10 ⁻¹²
Nov–Dec	D	<i>T_s</i>	456	0.15	< 10 ⁻¹⁵	R	Frost, <i>T_s</i> , <i>T_s</i> ²	283	0.48	< 10 ⁻¹⁶
<i>2005</i>										
Jan–Feb	D	Frost, <i>h</i> , <i>h</i> ² , <i>T_a</i> , <i>T_s</i>	501	0.11	< 10 ⁻¹⁰	D	Frost, <i>h</i> , <i>h</i> ² , <i>T_s</i>	156	0.38	< 10 ⁻¹³
Mar	D	<i>T_a</i> , <i>T_m</i> , VPD	442	0.12	< 10 ⁻¹¹	D	Frost, PAR, <i>T_s</i> , PAR· <i>T_s</i>	148	0.85	< 10 ⁻¹⁶
Apr	D	<i>D</i> , <i>h</i> , PAR, <i>T_a</i>	223	0.30	< 10 ⁻¹⁴	R	<i>h</i> , <i>T_a</i> , <i>T_m</i> , <i>T_s</i> , VPD	106	0.56	< 10 ⁻¹⁴
May	D	<i>D</i> , <i>h</i> , <i>h</i> ² , PAR, <i>T_a</i>	277	0.47	< 10 ⁻¹⁶	R	<i>h</i> , VPD, <i>h</i> ·VPD	114	0.18	< 10 ⁻⁴
Jun	R	<i>D</i> , <i>h</i> , <i>h</i> ² , VPD	200	0.42	< 10 ⁻¹⁶	R	<i>h</i> , <i>h</i> ² , <i>T_a</i> , VPD	267	0.44	< 10 ⁻¹⁶
Jul–Aug*	R	<i>h</i> , <i>h</i> ² , <i>T_s</i> , VPD	337	0.07	< 10 ⁻⁴	R	<i>h</i> , <i>h</i> ² , VPD	200	0.21	< 10 ⁻⁹
Sep	R	<i>D</i> , <i>h</i> , <i>h</i> ² , <i>T_a</i> , VPD	294	0.23	< 10 ⁻¹³	R	na	na	na	na
Oct	R	<i>D</i> , <i>h</i> , <i>h</i> ²	241	0.33	< 10 ⁻¹⁶	R	<i>h</i> , <i>h</i> ² , <i>T_a</i> , <i>T_s</i>	151	0.19	< 10 ⁻⁵
Nov						R	Frost, <i>T_a</i>	207	0.58	< 10 ⁻¹⁶
Dec	D	<i>h</i> , <i>h</i> ² , <i>T_a</i>	511	0.19	< 10 ⁻¹⁶	D	Frost, <i>h</i> , <i>h</i> ² , <i>T_a</i> ²	202	0.34	< 10 ⁻¹⁶

Continued overleaf

Table 5 (Con't.). Carbon flux models for the red oak (*Quercus rubra*) forest and eastern hemlock (*Tsuga canadensis*) forest. Parameters are: PAR = photosynthetically active radiation; VPD = vapor pressure deficit; h = hour of day; D = day of month (used in May and October only); T_a = above-canopy air temperature; T_s = soil temperature at 10-cm depth; and T_m = previous night minimum air temperature. Frost is a measure of severity of night freezing as follows: 0 if T_m was above -2 °C, 1 if T_m was between -2 and -5 °C, 2 if T_m was between -5 and -10 °C, and 3 if T_m was below -10 °C. In 5b, $H \cdot VPD$ and $PAR \cdot T_s$ indicate the products of hour of day and vapor pressure deficit, and PAR and soil temperature, respectively. In 5c, where no model explained a significant fraction of the variation (in April 2005 for the eastern hemlock forest and June 2006 for the red oak forest), the mean nighttime C flux for all hours in the month was used in filling in all data gaps for calculating a monthly sum. The P -values in 5b and 5c are from F -tests. Abbreviations: na = data not available; and ns = not significant ($P < 0.05$).

Table 5b (Con't). Models with dependent variable (DV) daytime C flux (D) or residual from PAR model (R).

Months	Red oak forest					Eastern hemlock forest				
	DV	Ind. variables	n	R^2	P	DV	Ind. variables	n	R^2	P
2006										
Jan	D	T_a	215	0.02	0.05	R	Frost, h , h^2	106	0.44	$< 10^{-12}$
Feb	D	h , h^2 , PAR ^a	345	0.03	0.01	R	Frost, T_a	75	0.48	$< 10^{-10}$
Mar	D	h , PAR, T_s	234	0.09	$< 10^{-4}$	R	Frost, h , h^2 , T_s	112	0.50	$< 10^{-14}$
Apr	R	h , T_a	159	0.10	$< 10^{-3}$	R	h , h^2 , VPD, T_s	143	0.07	0.05
May	R	h , h^2 , D , D^2 , T_a	289	0.54	$< 10^{-16}$	R	h , VPD, T_a , T_s	185	0.45	$< 10^{-16}$
Jun	R	h , h^2 , D	324	0.20	$< 10^{-15}$	R	h , h^2 , T_a	214	0.07	$< 10^{-3}$

Table 5c. Models with dependent variable (DV) nighttime C flux (N).

Months	Red oak forest					Eastern hemlock forest				
	DV	Ind. variables	n	R^2	P	DV	Ind. variables	n	R^2	P
2004										
Jul–Aug	N	T_a	105	0.06	0.01	N	T_s	200	0.13	$< 10^{-7}$
Sep	N	T_s	71	0.34	$< 10^{-7}$	N	T_s	52	0.14	0.01
Oct	N	T_a	210	0.10	$< 10^{-6}$	N	T_s	86	0.10	0.01
Nov–Dec	N	T_a , T_s	569	0.29	$< 10^{-16}$	N	T_a , T_s	276	0.06	$< 10^{-3}$
2005										
Jan–Feb	N	T_a , T_s	522	0.09	$< 10^{-10}$	N	T_s	159	0.07	$< 10^{-3}$
Mar	N	T_a , T_s	296	0.06	0.05	N	T_s	137	0.16	$< 10^{-5}$
Apr	N	T_s	109	0.16	$< 10^{-5}$	N	ns	45	< 0.01	ns
May	N	T_s	273	0.02	0.07	N	T_s	30	0.38	$< 10^{-3}$
Jun	N	T_a , T_s	40	0.35	$< 10^{-7}$	N	T_a	143	0.06	0.01
Jul–Sep ¹	N	T_a	125	0.11	$< 10^{-7}$	N	T_a	96	0.02	0.05
Oct						N	T_a	122	0.69	$< 10^{-16}$
Nov	N	T_a , T_s	831	0.29	$< 10^{-16}$	N	T_a	173	0.32	$< 10^{-15}$
Dec						N	T_s	248	0.03	0.01
2006										
Jan	N	T_a	293	0.05	$< 10^{-4}$					
Feb	N	T_s	352	0.12	$< 10^{-10}$	N	T_a	112	0.07	0.01
Mar	N	T_a	210	0.02	0.05	N	T_s	59	0.58	$< 10^{-11}$
Apr	N	T_s	104	0.37	$< 10^{-11}$	N	T_s	83	0.30	$< 10^{-7}$
May	N	T_s	102	0.20	$< 10^{-5}$	N	T_s	81	0.32	$< 10^{-7}$
Jun	N	ns	91	< 0.01	ns	N	T_s	77	0.34	$< 10^{-7}$

¹ In 2005, a model was derived for July through September for the red oak forest, but only for July at the eastern hemlock forest.

forest exceeded that of the red oak forest (Figure 4a). In 2005 and 2006, the difference in ET between forests was less marked, but the red oak forest had about 50% higher maximum daily H₂O flux in June and July than the eastern hemlock forest (Figure 4b).

Evaporation from the two forests was similar during late autumn and winter when trees of the red oak forest were leafless, presumably stopping transpiration, although we have few tran-

spiration data for November through May in either forest. Evapotranspiration for the leafless red oak forest may have remained equal to ET for the eastern hemlock forest because of significantly greater evaporation and sublimation from soil and snow (cf. Hadley 2000b). The eastern hemlock forest lost more water to the atmosphere than the red oak forest only briefly during spring and fall (Figures 4a and 4b). Estimated annual ET of the red oak forest was 90 mm or 28% greater than

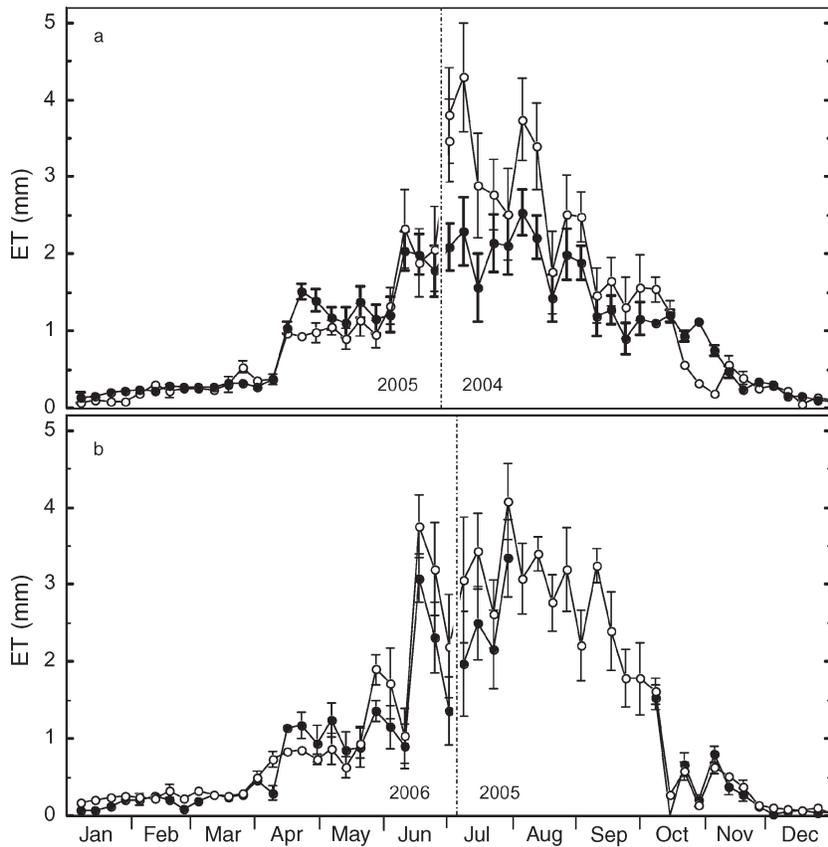


Figure 4. Weekly means of estimated daily evapotranspiration (ET) from (a) July 2004 through June 2005 and (b) July 2005 through June 2006 for red oak (*Quercus rubra*; ○) and eastern hemlock (*Tsuga canadensis*; ●) forests. The section of each panel to the right of the vertical dotted line indicates earlier data. Error bars indicate the standard error of the seven daily values in each week for each site indicating temporal variation. Estimated annual ET in 2004–2005 was 417 mm in the red oak forest and 327 mm in the eastern hemlock forest. In 2005–2006 it was 451 mm for the red oak forest. Data from the eastern hemlock forest from late July to late September 2005 are missing because of instrument damage.

that of the eastern hemlock forest from July 2004 through June 2005 (Figure 4a), and ET from the red oak forest was nearly equal to cumulative precipitation from mid-June to early September 2004, whereas ET from the eastern hemlock forest was about 100 mm less than cumulative precipitation (Figure 5). Photosynthetically active radiation had a greater influence on ET than any other measured environmental variable, and the difference in summertime ET between the red oak and eastern hemlock forests was reflected in a higher slope of the ET–PAR

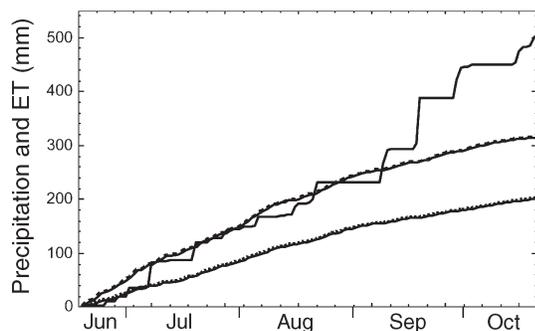


Figure 5. Cumulative precipitation measured at the Harvard Forest Meteorological station (solid line) and estimated evapotranspiration (ET) for the red oak (*Quercus rubra*; dashed line) and eastern hemlock (*Tsuga canadensis*; dotted lines) forests from mid-June through late October 2004.

relationship for the red oak forest during summer in both 2004 and 2005 (Figure 6). Over most of the study, there were differences between the red oak and eastern hemlock forests in the slope of the ET–PAR and ET–VPD relationships (Figure 7). The red oak forest lost more water to the atmosphere per unit PAR than the eastern hemlock forest in the summers of 2004

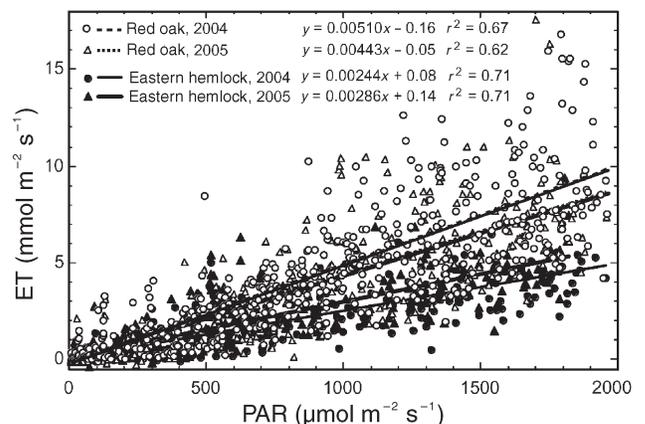


Figure 6. Photosynthetically active radiation (PAR) versus measured evapotranspiration (ET) for the red oak (*Quercus rubra*) and eastern hemlock (*Tsuga canadensis*) forests during early summers (June 18–July 14) 2004 and 2005. Each value is one observation over a 30-min period.

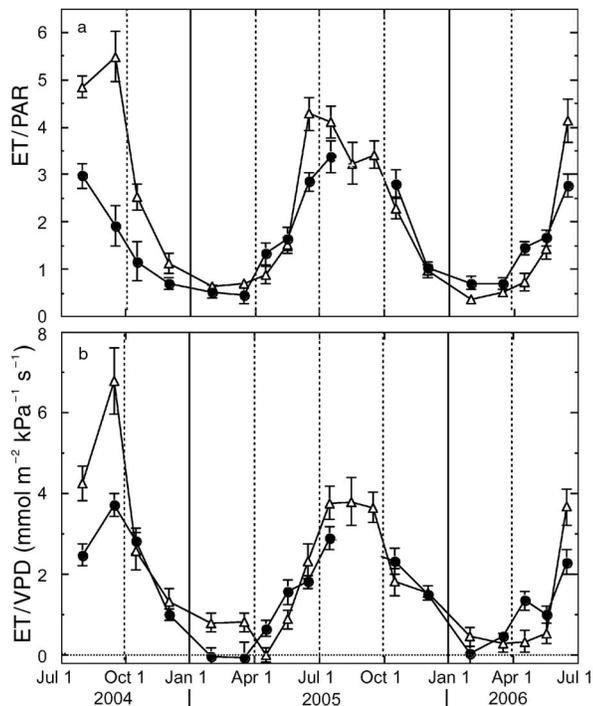


Figure 7. Slopes of linear regressions between measured evapotranspiration (ET) and (a) photosynthetically active radiation (PAR) and (b) vapor pressure deficit (VPD) in the eastern hemlock (*Tsuga canadensis*; ●) and red oak (*Quercus rubra*; △) forests. Each value was calculated from data covering a 1- or 2-month period, with November and December and January and February combined in each year, as well as July and August in 2004. Data for the eastern hemlock forest for August and September 2005 are missing due to instrument failure. Each value is plotted at the midpoint of the time period covered. Sample sizes ranged from 130 to 733, with a mean of 304. Error bars are 95% confidence intervals of means. All slopes for PAR are significant at $P < 10^{-6}$; all slopes for VPD are significant at $P < 10^{-9}$ except those below the dotted line ($P = 0.02$ to 0.0001 , except for the three lowest values in early 2005 and the low value in early 2006, which were not statistically significant).

and 2005, but the difference was much larger in 2004, whereas the eastern hemlock forest showed the greatest response to PAR in the winter and early spring of 2006.

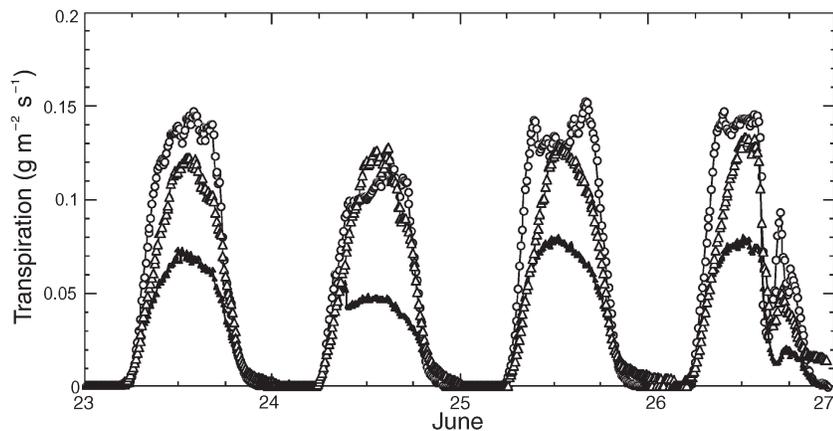


Figure 8. Transpiration of eastern hemlock (*Tsuga canadensis*; ▲), black birch (*Bentula lenta*; ○) and red oak (*Quercus rubra*; △) trees on four representative days in late June 2005, expressed per unit ground area beneath the live canopy of each tree.

Individual tree transpiration in late June showed interspecific differences consistent with the relative ET of the eastern hemlock and red oak forests in summer. Transpiration in eastern hemlock reached a maximum near midday that was 40 to 60% of maximum rates of red oak and black birch (Figure 8).

Forest carbon exchange

Forest-atmosphere C exchange rates were greater for the red oak forest than for the eastern hemlock forest in summer. Light-saturated C uptake typically reached 20 to 25 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for the red oak forest versus 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$ or less for the eastern hemlock forest (Figure 9a). Nocturnal C loss did not differ greatly between forests (Figure 9b), but large nighttime C releases were more frequent from the eastern hemlock forest. For instance, in summer 2004, there were more than fifty 30-min C flux values above 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the eastern hemlock forest compared with 10 values of this magnitude in the red oak forest. The eastern hemlock forest also showed many more instances of net C efflux during daylight (Figure 9a).

Net carbon exchange of the two forests can be compared by examining the response of daytime C flux to PAR, as well as by examining mean daytime and nighttime C fluxes. Coefficient a in the rectangular curve fits of net C flux to PAR (Equation 1) was higher in the red oak forest than in the eastern hemlock forest from June through September (Figure 10a). Mean daytime net C fluxes showed the same pattern (Figure 10b). Mean nighttime C fluxes were higher for the eastern hemlock forest than for the red oak forest during summer and early autumn, at least in 2004, but the reverse was true in winter (Figure 10c).

Although we estimated that the eastern hemlock forest stored relatively little C compared with the red oak forest in summer (June through September), it stored considerable amounts of C in April and May, and to a lesser extent in October. During much of this time, the red oak forest either had no leaves (April) or had foliage during only part of the month (May and October). We observed that, in the eastern hemlock forest, C storage was limited by subfreezing nights in spring and fall, as noted earlier (Hadley and Schedlbauer 2002).

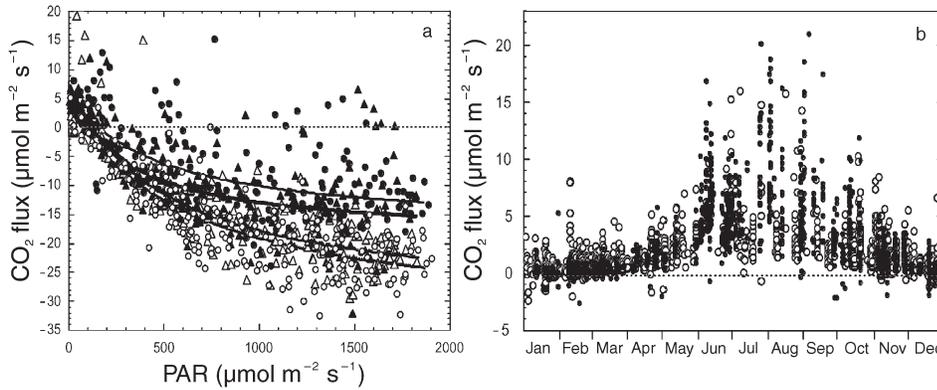


Figure 9. (a) Daytime photosynthetically active radiation (PAR) versus CO₂ flux for the red oak (*Quercus rubra*; open symbols) and eastern hemlock (*Tsuga canadensis*; closed symbols) forests during July 2004 (○, ●) and 2005 (△, ▲). Negative numbers indicate carbon uptake by the forest. The fitted curves are of the form: C flux = $c + aPAR / (b + PAR)$. (b) Measured nighttime CO₂ flux for the red oak (○) and eastern hemlock (●) forests for the June 2004 to July 2005 sampling period, when wind direction and turbulence met the requirements for valid flux measurements.

However the spring months of 2005 and 2006 were warm relative to long-term means, and air temperatures during April and May were below freezing on only a few nights. This boosted

spring C storage in 2005 and 2006 relative to 2001 (Figure 11). The winter months of 2004–2005 and 2005–2006 were also warm, allowing short periods of C uptake by the eastern hem-

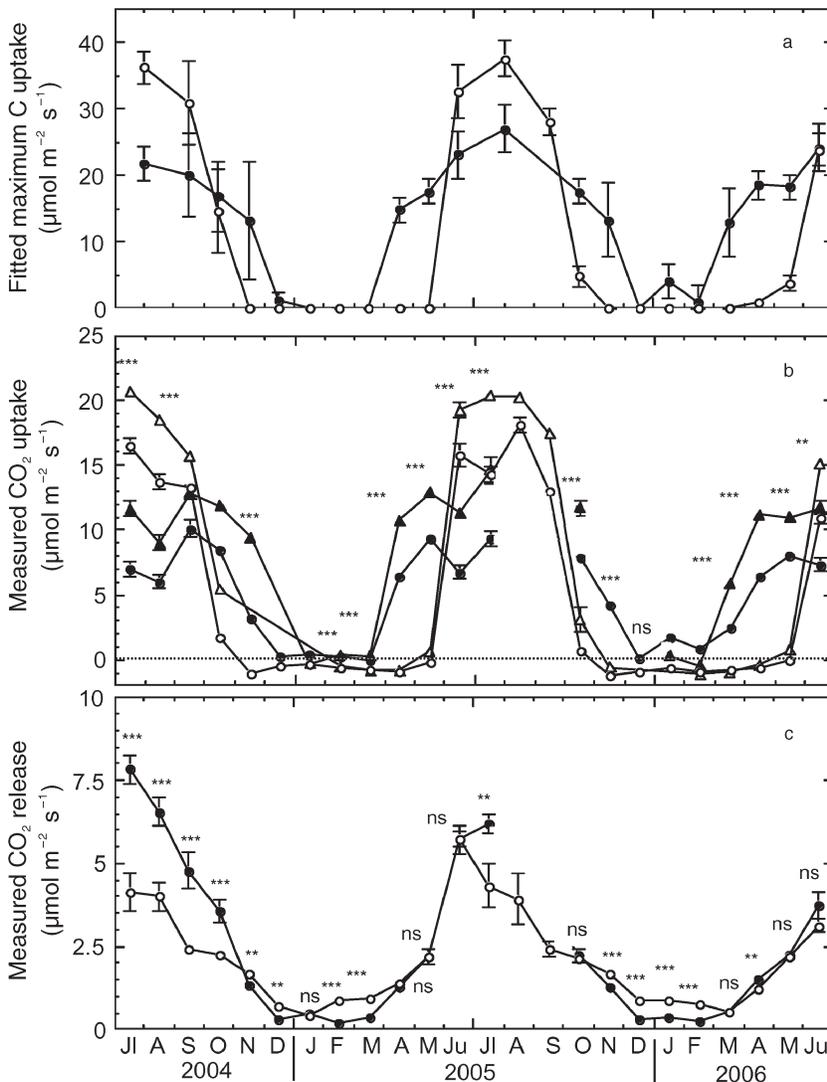


Figure 10. Carbon (C) exchange data for the red oak (*Quercus rubra*) and eastern hemlock (*Tsuga canadensis*) forests. (a) Maximum C uptake rate (coefficient *a*) calculated by non-linear curve fits of the form: C uptake = $c + aPAR / (b + PAR)$ for each month where this could be calculated. Zero values in fall, winter and early spring for red oak (○) and sometimes for eastern hemlock (●) forests, indicate that a response of C flux to PAR could not be fitted. July and August were grouped in 2004, but not in 2005 when there was no August data for the eastern hemlock forest. Bars show 95% confidence intervals for means. (b) Mean measured daytime C uptake by month, both for all daylight hours (red oak (○) and eastern hemlock (●) forests), and for PAR values approaching light saturation (PAR > 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for red oak (△) and eastern hemlock (▲) forests). During some November, December or January periods, this PAR value was not reached. Data for the eastern hemlock forest for August and September 2005 are missing due to instrument failure and data for PAR > 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the hemlock forest are missing for November and December 2005 because valid data were unavailable during the short periods when PAR reached this value. (c) Mean nighttime C flux in red oak (○) and eastern hemlock (●) forests. Bars in b and c indicate standard errors of means. Sample sizes were 77 to 458 (mean 218) for fitted maximum C flux and mean daytime C flux, 21 to 142 (mean 59) for C flux at PAR > 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and 17 to 355 (mean 135) for nighttime C flux. Significant differences between means of the two forest types, based on *t*-tests after normalizing the data, are indicated as: **, $P < 0.01$; and ***, $P < 0.001$.

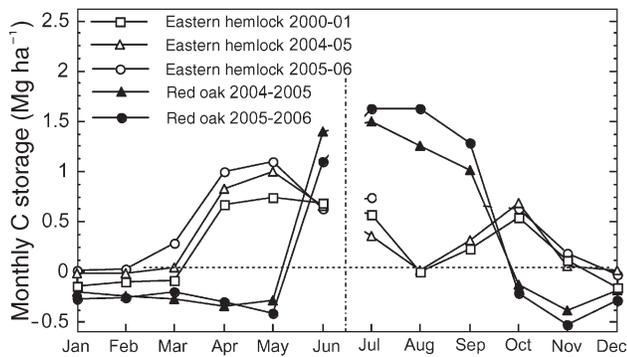


Figure 11. Estimated monthly net carbon (C) storage by the red oak (*Quercus rubra*) and eastern hemlock (*Tsuga canadensis*) forests. Because the first comparative data for this study are from July 2004, each curve starts on the right-hand side of the figure and continues on the left. Previously published data for the eastern hemlock forest from 2000 and 2001 (Hadley and Schedlbauer 2002) are included for comparison. Data from the eastern hemlock forest for August and September 2005 are missing because of instrument failure. Error estimates for measured values and for model parameters for individual 1 to 3-month periods are given in Figure 10. Estimated annual C storage was 3.1 Mg C ha^{-1} (2000–2001) and 3.8 Mg C ha^{-1} (2004–2005) for the eastern hemlock forest, and 3.2 Mg C ha^{-1} (both 2004–2005 and 2005–2006) for the red oak forest.

lock forest, resulting in a near zero net C flux in December through February.

Discussion

Forest water use

We found a large difference in estimated summertime ET between the red oak and the eastern hemlock forests (Figures 4 and 5), which was due to a greater response of ET to both PAR and VPD by the foliated red oak forest than by the eastern hemlock forest (Figures 6 and 7). The difference between forests was greatest in July and August 2004, when we estimated that about 3 cm more water was used each month by the red oak forest than by the eastern hemlock forest. This is equal to about 30% of mean monthly precipitation. In 2004, all of the precipitation from late June to early September was returned to the atmosphere by the red oak forest, whereas about 40% of the precipitation was added to soil and to aquatic systems in the eastern hemlock forest (Figure 5). Thus, conversion of eastern hemlock forest to red oak forest in the aftermath of the eastern hemlock woolly adelgid could result in significant reductions in summertime aquatic habitat, stream flow and rates of water input to lakes and reservoirs. Most deciduous forests that replace eastern hemlock forests will not be dominated by red oak, at least initially. However, the species that has most commonly replaced eastern hemlock thus far, black birch, (see Orwig and Foster 1998) also had higher sap flow than eastern hemlock, both per unit tree basal area and per unit ground area beneath the canopy (Figure 8), suggesting that a mature black-birch-dominated forest will also use more water than a eastern hemlock forest in summertime.

In contrast to our results, Stoy et al. (2006) found that ET of a loblolly pine (*Pinus taeda*) forest in North Carolina was greater than or equal to ET of a neighboring red oak forest, except during a severe drought, when the pine forest used less water.

Carbon exchange

Higher rates of net C uptake in summer for the red oak forest compared with the eastern hemlock forest (Figures 9a, 10a and 10b) were consistent with the highest photosynthetic rates observed at Harvard Forest for these species. Maximum rates were around $20 \mu\text{mol m}^{-2} \text{ s}^{-1}$ for red oak (Bassow and Bazzaz 1997) and about $9 \mu\text{mol m}^{-2} \text{ s}^{-1}$ for eastern hemlock (cf. Hadley 2000a). Thus, maximum ecosystem-level C uptake for forests dominated by red oak and eastern hemlock correlates with their maximum physiological capacity for C storage on a leaf area basis.

Estimated maximum monthly C storage rates for the red oak forest during the 2 years of study were much higher than for the eastern hemlock forest (Figure 11). The highest monthly C storage for the eastern hemlock forest occurred in April and May, and by July and August, when peak C storage occurred in the red oak forest, net C storage in the eastern hemlock forest was declining. By August 2004, C uptake by the eastern hemlock forest during daylight hours equaled nighttime C loss from the ecosystem, resulting in no net C uptake for the month, as also occurred in 2001 (Figure 11).

In contrast to the red oak forest, which lost an estimated 0.2 to 0.4 Mg C ha^{-1} each month from November through May in both study years, we estimated that the eastern hemlock forest lost no C in these months (Figure 11). This differs from the result of Hadley and Schedlbauer (2002), who estimated slight C losses from the eastern hemlock stand for December through February. The approximately neutral C balance of eastern hemlock forest in the winter months of 2004–2005 and 2005–2006 was associated with warmer-than-average winter weather, which was followed by warmer spring weather in March through May of 2005 and 2006, compared with the year of the earlier study (2001). As a result of warmer weather, photosynthesis in late winter and spring was enhanced in 2005 and 2006 (Figure 11; see also Figures 10a and 10b), leading to our estimate that the eastern hemlock forest stored more C than the red oak forest (3.8 versus 3.2 Mg C ha^{-1}) from July 2004 through June 2005, despite its lower rate of summer C storage. This indicates that a warming trend in fall, winter and spring could favor carbon storage in coniferous forests relative to red oak forests, unless the foliated season for deciduous trees lengthens. There is evidence that the mean date of deciduous leaf abscission at Harvard Forest has been increasingly delayed during the last 15 years, and modeling analyses indicate that spring onset in the Northeast has advanced by 1–2 days per decade over the last 50 years (Wolfe et al. 2005, Richardson et al. 2006b). In contrast to the effect of warmer fall, winter and spring weather, dramatic increases in summer temperatures could result in net C loss from the eastern hemlock forest in August, so the effect of a year-round temperature increase on eastern hemlock forest C balance remains unclear.

The question of how C storage may change in a warmer climate is likely to become moot for most eastern hemlock forests in the northeastern USA in coming decades. If winter climate becomes warmer, more northerly eastern hemlock forests may die from HWA infestation, which will no longer be limited in its distribution by lethal winter temperatures ($-25\text{ }^{\circ}\text{C}$) (Parker et al. 1999, Skinner et al. 2003). Death of eastern hemlock forests will result in transfer of C to the atmosphere, as the organic matter in dead trees decomposes, along with continued decomposition of forest floor material and soil organic matter. The period in which annual decomposition exceeds photosynthesis will depend on how quickly the dead trees decompose, and on the rate of development of a new tree canopy. Chamber measurements of photosynthesis show that black birch, the first dominant species after eastern hemlock mortality in southern New England, had a midsummer light-saturated photosynthetic rate of about $15\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$ compared with about $10\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$ for eastern hemlock (B.R. Hardiman and J. Hadley, unpublished data). Thus, once the LAI of the black birch forest approaches that of the current eastern hemlock forest, summertime C uptake could approach or exceed that of the current eastern hemlock forest.

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