Contributions of coniferous and broad-leaved species to temperate forest carbon uptake: a bottom-up approach[1]

S. Catovsky and F.A. Bazzaz

Abstract: Changes in forest species composition could influence ecosystem carbon uptake rates. To understand how species differed in their contributions to canopy photosynthesis, we investigated how the dominant coniferous (eastern hemlock, *Tsuga canadensis* (L.) Carr.) and broad-leaved (northern red oak, *Quercus rubra* L.; red maple, *Acer rubrum* L.) species in a central Massachusetts forest differed in canopy carbon uptake rates. We considered what factors influenced in situ leaf-level photosynthesis and then used a bottom-up summation approach to estimate species-specific total canopy carbon uptake rates. Variation in canopy light strongly influenced leaf-level photosynthetic rates: sunlit leaves had significantly higher rates than shaded leaves, and photosynthesis increased with canopy height. Species also differed in leaf-level photosynthetic rates, with the broad-leaved species having up to twofold higher rates than hemlock. Within hemlock, needles older than 2 years had lower photosynthesis than younger needles. Variation in leaf-level photosynthesis scaled up to influence canopy carbon uptake rates. Red oak consistently had the highest canopy photosynthetic rates, while through the season, hemlock's relative contribution to carbon flux increased and that of red maple decreased. Thus, in such mixed forests, future changes in species composition could have substantial impacts on forest carbon dynamics, particularly if red oak is the primary broad-leaved species to expand at the expense of hemlock.

Résumé : Des changements dans la composition des espèces forestières pourraient influencer le taux de prélèvement du carbone par les écosystèmes. Afin de comprendre comment diffère la contribution de chaque espèce à la photosynthèse de la canopée, les auteurs ont étudié les espèces résineuses (pruche du Canada, *Tsuga canadensis* (L.) Carr.) et feuillues (chêne rouge, *Quercus rubra* L.; érable rouge, *Acer rubrum* L.) dominantes quant à leur différents taux de prélèvement du carbone par la canopée dans une forêt du centre du Massachusetts. Ils ont d'abord déterminé les facteurs qui influencent in situ la photosynthèse foliaire et utilisé, ensuite, l'approche de la sommation progressive pour estimer le taux, par espèce, de prélèvement total du carbone par la canopée. Le taux de la photosynthèse au niveau de la feuille est fortement influencé par la variation de la lumière dans la canopée : les feuilles de lumière ont un taux significativement plus élevé que les feuilles d'ombre et la photosynthèse augmente avec la hauteur de la canopée. Les espèces diffèrent aussi quant à leur taux de photosynthèse foliaire, les espèces feuillues ayant des taux jusqu'à deux fois plus élevés que la pruche. Chez la pruche, la photosynthèse est plus faible chez les aiguilles de plus de 2 ans que chez les aiguilles plus jeunes. La variation dans la photosynthèse foliaire influence, en l'augmentant, le taux de prélèvement du carbone par la canopée. Le chêne rouge a constamment les taux de photosynthèse les plus élevés de la canopée, alors que durant la saison, la contribution relative de la pruche au flux du carbone augmente et celle de l'érable diminue. Par conséquent, dans des forêts mixtes semblables, les changements futurs dans la composition spécifique pourraient avoir un impact substantiel sur la dynamique forestière du carbone, surtout si le chêne rouge est la principale espèce feuillue à prendre de l'expansion au dépend de la pruche.

[Traduit par la Rédaction]

Introduction

Temperate forests are currently a significant terrestrial sink for atmospheric CO_2 and consequently play an important role in the contemporary global carbon cycle (Fan et al.

S. Catovsky[2] and F.A. Bazzaz. Department of Organismic and Evolutionary Biology, Harvard University, The Biological Laboratories, 16 Divinity Avenue, Cambridge, MA 02138, U.S.A.

[1]Contribution to Harvard Forest's Long-Term Ecological Research Program.
[2]Corresponding author. e-mail: catovsky@fas.harvard.edu

1998; Houghton et al. 1998). As forest systems have the potential to slow future increases in atmospheric CO_2 concentrations (Dixon et al. 1994; Woodwell et al. 1998), it is now critical to understand the factors that regulate forest ecosystem processes. Using eddy covariance, we can measure the total amount of carbon taken up by forests with a high degree of accuracy (Baldocchi et al. 1988), and we can relate carbon uptake to environmental conditions on different temporal scales (e.g., Grace et al. 1995; Goulden et al. 1996). These broad-scale measurements do not, however, allow us to predict future forest function should canopy composition change. As a result of natural and human-induced disturbance processes, and subsequent patterns of successional recovery (Bormann and Likens 1979; Bazzaz 1996), ecosystems are

in a constant state of flux, and their composition is likely to vary over time. Functional differences among species may give rise to a close coupling between population and ecosystem processes (Jones and Lawton 1995; Chapin et al. 1997; Tilman et al. 1997). Thus, changes in forest canopy composition could directly affect forest productivity and carbon storage (Bolker et al. 1995; Canham and Pacala 1995; Bazzaz et al. 1996).

To predict patterns of carbon uptake and storage by forest ecosystems under a range of scenarios in the future, more mechanistic studies of controls on forest function are required to complement 'big leaf' approaches (Meinzer and Goldstein 1996; Bassow and Bazzaz 1998). In this study, we address the consequences of changes in temperate forest community composition for canopy carbon uptake. We investigate how the major species of a mixed conifer–hardwood forest in northeastern United States differ in their capacity for carbon uptake. Addressing links between community and ecosystem dynamics may be particularly important in these mixed forests where two contrasting groups of canopy trees co-occur. As evergreen coniferous and broad-leaved deciduous species differ from one another in their basic biology (Waring and Franklin 1979; Bond 1989; Smith and Hinckley 1995), they are likely to show contrasting responses to both natural disturbance processes and to novel environmental perturbations currently threatening temperate forests, such as increasing atmospheric CO_2 concentrations and nitrogen deposition (Bazzaz et al. 1996; Magill et al. 1997; Saxe et al. 1998). Thus, we expect that forest community composition will change in the future. In addition, we expect that these changes in composition will significantly influence ecosystem-level processes, because these distinct groups of species have different functional roles within forest ecosystems (Baldocchi and Vogel 1996; Reich et al. 1997; Willis et al. 1997). As coniferous and broad-leaved species often have contrasting natural distributions, very few studies have directly compared these different groups in areas where they naturally co-occur.

In the present study, we address how canopy photosynthetic rates differ for mature trees of eastern hemlock (*Tsuga canadensis* (L.) Carr.), northern red oak (*Quercus rubra* L.), and red maple (*Acer rubrum* L.). These species represent the currently dominant coniferous (hemlock) and broad-leaved (oak, maple) species at the study site (Harvard Forest). To develop a mechanistic understanding of different components of total canopy carbon uptake, we first consider leaf-level gas exchange processes in temperate forest tree canopies. We ask what environmental, ontogenetic, and phylogenetic factors are responsible for heterogeneity in canopy leaf-level photosynthetic rates. We hypothesize that light availability is the major determinant of leaf-level photosynthesis, and that carbon uptake is further modified by species identity and leaf age. We predict that the broad-leaved species will have higher leaf-level photosynthetic rates than hemlock (a conifer) (Bond 1989) and that, for hemlock, photosynthesis will decline with increasing needle age (Oren et al. 1986). These leaf-level measurements are then used to estimate instantaneous total canopy carbon uptake rates with a bottom-up summation approach (Ehleringer and Field 1993). We predict that hemlock will have higher canopy carbon uptake rates than the broad-leaved species,

because of its evergreen habit and resulting deeper canopy (Schulze et al. 1977*b*; Bond 1989).

Because of the intensity of our canopy sampling scheme, we restrict our measurements to times when photosynthetic rates are likely to be maximal (clear, sunny days during the main growing season). In this way, we place considerable emphasis on understanding the photosynthetic capacity of each species, rather than on total carbon gain throughout the whole year. The majority of carbon gain in temperate forests in this region, however, is between June and August (Goulden et al. 1996). Previously, with this approach, we have been able to account for a large portion of the flux in the system (Wofsy et al. 1993; Bassow and Bazzaz 1998).

Materials and methods

Canopy photosynthetic measurements

All canopy measurements were made on trees in Harvard Forest (Petersham, Mass., 42°32′N, 72°11′W; elevation, 340 m). The forest is located in the transition hemlock – white pine (*Pinus strobus* L.) – northern hardwoods vegetation zone (Spurr 1956; Westveld 1956), and the study area comprised principally of red oak, red maple, yellow birch (*Betula alleghaniensis* Britt.), black birch (*Betula lenta* L.), hemlock, white pine, and paper birch (*Betula papyrifera* Marsh.) (in approximately decreasing order of importance).

In situ leaf-level photosynthetic measurements were made in the canopies of mature trees of red maple, red oak, and eastern hemlock. Measurements were taken on three sunny days in both mid-June and mid-August 1996, from 08:00 to 14:00 each day, before the late-day decline in photosynthesis often observed in temperate trees in this site (Bassow and Bazzaz 1998). Air temperatures did not differ significantly between months (average air temperature was 28°C for both months). Each day, leaves from one tree of each species were measured. All trees measured on a particular day were located next to one another in mixed forest stands, and the order in which trees were sampled was random each day. Trees chosen were 30–50 cm diameter at breast height and 15–20 m in height.

Canopy access was achieved using a mobile aerial lift with a 22-m boom (Shaughnessy, Worcester, Mass.). The rotation and extension of both boom and attached basket allowed access to parts of trees that were in closed forest. In situ photosynthesis was measured using a LI-COR 6200 gas exchange system (LI-COR, Lincoln, Neb.), with a 0.25-L chamber. For each measurement, chamber orientation was adjusted to match natural leaf orientation, and conditions within the chamber were set to match external conditions (CO_2 concentration, 340–360 $\mu L \cdot L^{-1}$; air temperature, 20–25°C; relative humidity, 30–60%). Flow through the chamber was regulated such that chamber relative humidity was kept constant throughout each measuring period (1–2 min). Leaf areas of broad-leaved species were estimated from a grid in the leaf chamber, while hemlock needle leaf areas were obtained by running needles through a LI-COR 3000A portable leaf area meter (LI-COR, Lincoln, Neb.) at the end of the day. Measurements of photon flux density (PFD) falling on leaves were taken at the same time as gas exchange, using a LI-COR PAR quantum sensor (LI-COR, Lincoln, Neb.) attached to the chamber to match the orientation of leaves measured.

Canopy sampling

Our sampling regime incorporated factors that we hypothesized would substantially contribute to heterogeneity in leaf-level photosynthesis within tree canopies. The first division separated tree canopies into different vertical strata. Red oak and red maple canopies were divided into three equivalent strata, while hemlock

canopies, because they are deeper (see later), were divided into four strata. Within each canopy layer, we measured leaves that were either sunlit (intercepting direct beam radiation) or shaded (receiving only diffuse beam radiation). Canopy models have previously found that dividing leaves into sunlit and shaded classes at different canopy heights provided a good estimate of total canopy photosynthesis (Norman 1980; Caldwell et al. 1986; Hollinger 1992). In addition, for hemlock (an evergreen species), needles of different ages were sampled: those produced that season (current-season needles), 1-year-old needles, and those 2 years old or more. As hemlock rarely retains needles older than 3 years, aggregating needles older than 2 years seemed very appropriate. For every layer × sun–shade (× leaf age) combination, three individual leaves were measured each day, giving a total of 18 measurements for each tree of red oak and red maple (3 layers × 2 sun–shade × 3 replicates) and 72 measurements for each hemlock tree (4 layers × 2 sun–shade × 3 ages × 3 replicates).

Components of canopy summation approach and sensitivity analysis

We scaled from leaf-level measurements of photosynthesis to total canopy carbon uptake by incorporating information on canopy structure into a bottom-up summation scheme (Norman 1980, 1993). We calculated leaf area index (LAI) of each canopy layer by dividing the total leaf area index of red oak – red maple and hemlock stands by the number of canopy layers, and assuming that foliage was distributed evenly through the canopy layers (Aber 1979; Ellsworth and Reich 1993). An LAI of 3 $m^2 \cdot m^{-2}$ was used for mixed red oak – red maple stands in the area of Prospect Hill, based on previous extensive leaf litter trap data (Wofsy et al. 1993). For pure hemlock stands, we used an LAI of 4.4 $m^2 \cdot m^{-2}$, obtained from destructive sampling of branches in the canopy of a hemlock stand in the vicinity (J. Hadley, personal communication). Nondestructive LAI measurements taken using an LAI 2000 (LI-COR, Lincoln, Neb.) in the same summer as the photosynthesis measurements fell within the range of the litter/destructive LAI estimates, assuming that 15–20% of canopy LAI is contributed by branches (Wofsy et al. 1993). The proportion of sunlit and shaded LAI within each canopy layer was derived from Norman's (1980, 1993) formulation, using a solar elevation angle of 70° for midday in the summer at 42°N. This relationship assumes that light attenuation follows Beer–Lambert's law. In addition, for hemlock, the proportion of different needle age-classes within each canopy layer was estimated from destructive branch samples. Three full branches were sampled in each canopy layer of each tree measured. For each canopy layer, the sunlit–shaded proportions and the different hemlock needle age-classes were used to weight each of our leaf-level measurements according to their contributions to LAI. These weighted photosynthetic rates were then first summed within each canopy layer and subsequently across all canopy layers (see Norman (1993) for full discussion of the method). As our total canopy carbon flux estimates are scaled to ground area, they should represent appropriate measures of species contributions to forest carbon flux, provided canopy structure does not change dramatically between stand types.

To investigate the assumptions of our canopy summation scheme, we carried out a sensitivity analysis, where the inputs of each of the model parameters were varied, and the resulting output (total canopy carbon uptake) investigated. The assumptions tested were (i) total LAI; (ii) proportion of sunlit and shaded leaves; (iii) vertical distribution of foliage; and (iv) proportion of hemlock needle age-classes in each canopy layer.

Statistical analysis

Leaf-level photosynthesis and PFD measurements were analyzed by pooling replicate measurements in each month × day ×

Fig. 1. Photon flux density (PFD) falling on sunlit (*a*) and shaded (*b*) leaves of different species (red maple (light gray), red oak (dark gray), and hemlock (black)) in different canopy layers (1 is the top layer). Columns represent mean PFD levels falling on leaves of three individuals of each species pooled across months ±1SE. Values for mean and standard error based on back-transformed log PFD data.
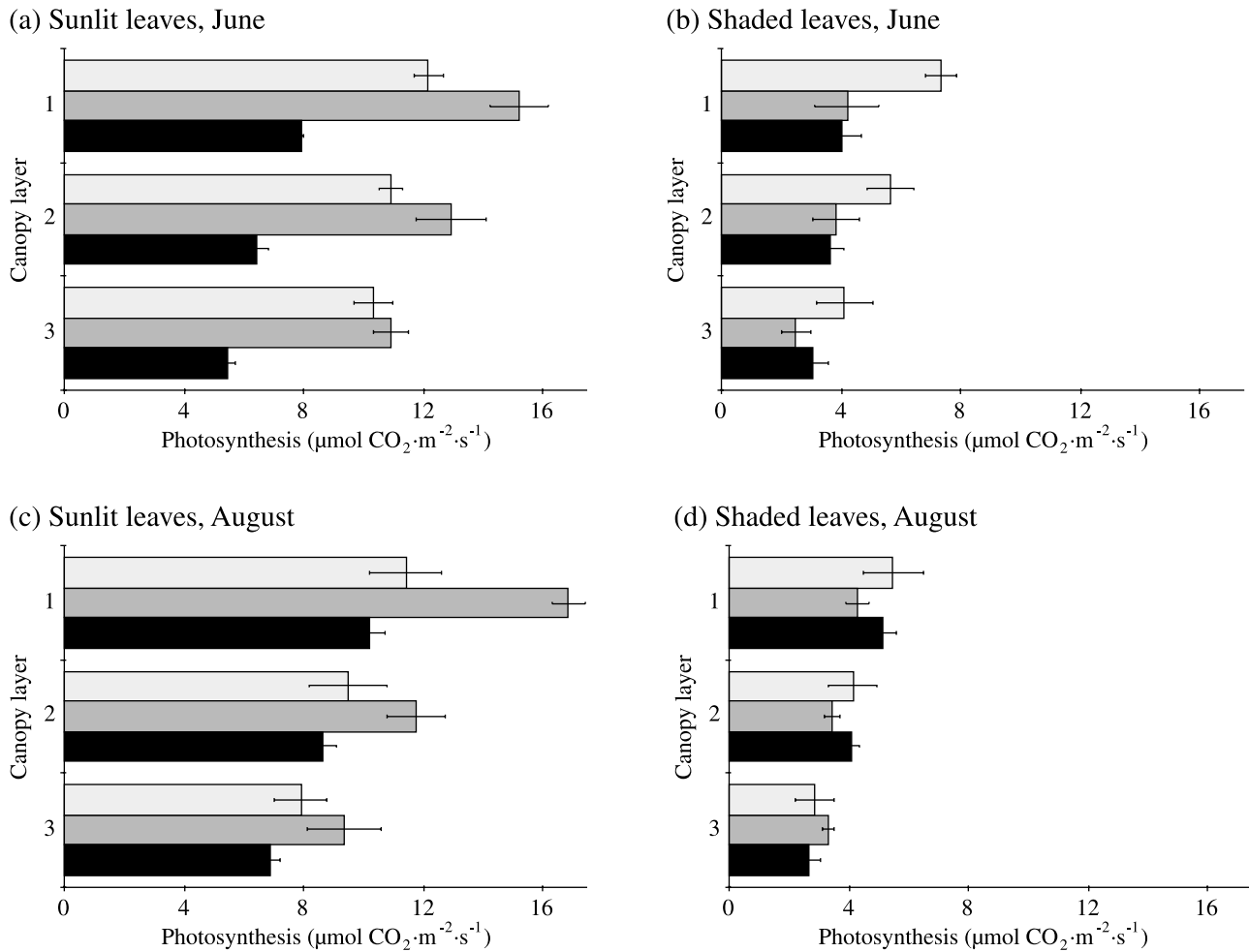

(a) Sunlit leaves
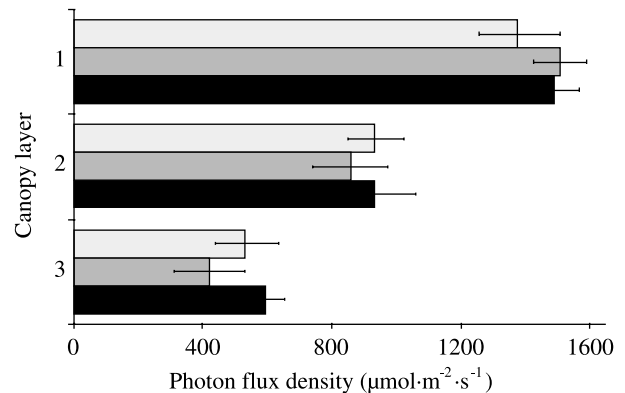
(b) Shaded leaves
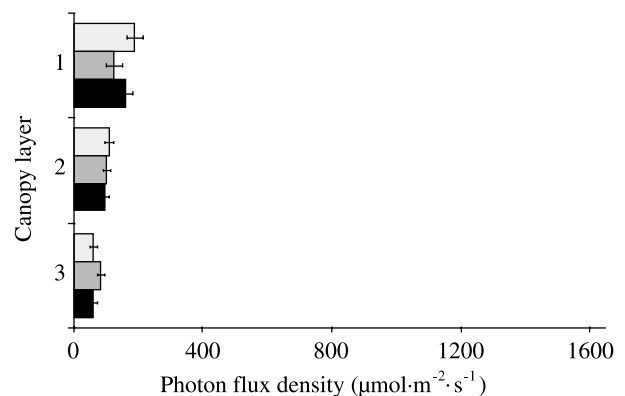
layer × sun–shade × species (or leaf age) class. To compare both photosynthesis and canopy light environment between species, we additionally pooled measurements for different hemlock needle age-classes and only considered the top three canopy layers. We performed multiway analyses of variance, with month, species, layer, and sun–shade as fixed factors, and day as a random factor nested within month. We carried out an additional analysis of variance comparing different hemlock needle age-classes in a similar way but replacing the species term with needle age. Light-saturated photosynthetic rates (A_{max}) were compared using two-way analysis of variance (species/age-class and month as main effects) on all gas exchange values measured at >1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PFD. Subsequent Bonferroni-corrected planned comparisons were made between species within each month for both leaf photosynthetic characteristics (Sokal and Rohlf 1995). Estimates of total canopy carbon uptake were compared in a three-way analysis of variance, with species and month as fixed factors, and day as a random factor nested within month. In all cases, we ensured that the data met the assumptions of ANOVA (normality of residuals, homoscedascity). Photon flux density data were log transformed, so that residuals would be normally distributed. Following each test, for each significant main effect with more than two levels and for each significant interaction, we examined the significance of individual

Fig. 2. Leaf-level photosynthetic rates in June (*a* and *b*) and August (*c* and *d*) for sunlit (*a* and *c*) and shaded (*b* and *d*) leaves in different canopy layers (1 is the top layer) of red maple (light gray), red oak (dark gray), and hemlock (black) trees. Columns represent mean photosynthetic rates of three individuals of each species ±1SE.

(a) Sunlit leaves, June

(b) Shaded leaves, June

(c) Sunlit leaves, August

(d) Shaded leaves, August

treatment mean comparisons using Scheffé post hoc tests (Day and Quinn 1989; Sokal and Rohlf 1995). All statistical analysis was carried out with DataDesk version 4.2 (Data Description Inc., Ithaca, N.Y.).

Results

Canopy light environment

The distribution of light through tree canopies varied with both sun–shade class and canopy position (Fig. 1). Photon flux density was significantly greater on sunlit leaves than shaded leaves (881 and 105 $\mu mol \cdot m^{-2} \cdot s^{-1}$ respectively; $F_{1,62} = 961.5$, $p < 0.0001$) and decreased significantly with decreasing canopy height ($F_{2,62} = 63.5$, $p < 0.0001$; all post hoc comparisons, $p < 0.001$). Canopy light environment, however, did not vary significantly between species or between months ($F_{2,62} = 0.43$ and $F_{1,4} = 0.59$, $p > 0.05$). There were no significant higher order interactions between any factors ($F_{1-4,62} < 2.0$, $p > 0.05$).

Leaf-level photosynthesis: species comparisons

Variation in canopy light environment strongly influenced leaf-level photosynthesis (Table 1). Sunlit leaves had sub-

stantially higher rates of photosynthesis than shaded leaves (Fig. 2; 10.3 and 4.1 $\mu mol \cdot m^{-2} \cdot s^{-1}$ respectively; $p < 0.0001$), and classifying leaves as sunlit or shaded explained most of the variation in photosynthesis through the canopy ($F_{1,68} = 1101.5$; Table 1). Photosynthesis also significantly declined with canopy height (Table 1, Fig. 2; $p < 0.0001$). The decline for sunlit leaves was significantly faster than for shaded leaves (layer × sun–shade interaction, $p < 0.001$).

Species differed in their leaf-level photosynthetic rates (Table 1, Fig. 2), with broad-leaved trees having higher rates of photosynthesis than hemlock trees (7.9 vs. 5.7 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively; post hoc, $p < 0.0001$). In addition, within broad-leaved species, red oak had consistently higher rates of photosynthesis in the sun than did red maple (significant species × sun–shade interaction; post hoc, $p < 0.0001$). Leaves of broad-leaved species were more sensitive to variation in canopy light environment than were hemlock needles (Table 1; significant species × sun–shade and species × layer × sun–shade interactions, $p < 0.0001$ and $p < 0.01$, respectively). Red oak showed particularly marked declines in photosynthesis from sunlit to shaded leaves (72% decrease vs. 53% for red maple and 51% for hemlock). In addition, red oak photosynthesis declined faster with canopy height in

Table 1. Results of (A) analysis of variance comparing leaf-level photosynthetic rates for different species and (B–D) Scheffé post hoc comparisons of single factors.

(A) ANOVA

Effect	df	F^a
Month	1	0.06ns
Day (month)	4	12.49***
Species	2	68.69***
Layer	2	82.26***
Sun–shade	1	1101.50***
Month × species	2	17.81***
Month × layer	2	2.48ns
Month × sun–shade	1	0.86ns
Species × layer	4	1.49ns
Species × sun–shade	2	74.14***
Layer × sun–shade	2	8.35***
Month × species × layer	4	0.60ns
Month × species × sun–shade	2	2.87ns
Month × layer × sun–shade	2	2.16ns
Species × layer × sun–shade^b	4	4.97**
Month × species × layer × sun–shade	4	1.13ns

(B) Between sunlit and shaded leaves

	Red maple			Red oak			Hemlock		
	Layer 1	Layer 2	Layer 3	Layer 1	Layer 2	Layer 3	Layer 1	Layer 2	Layer 3
Sun vs. shade	***	***	***	***	***	***	***	***	***

(C) Among species

	Sun		Shade	
Species	Oak	Hemlock	Oak	Hemlock
Layer 1				
Maple	***	***	**	*
Oak	—	***	—	ns
Layer 2				
Maple	**	***	ns	ns
Oak	—	***	—	ns
Layer 3				
Maple	ns	***	ns	ns
Oak	—	***	—	ns

(D) Among canopy layers

	Sun		Shade	
Layer	Layer 2	Layer 3	Layer 2	Layer 3
Red maple				
1	ns	***	ns	***
2	—	ns	—	ns
Red oak				
1	***	***	ns	ns
2	—	**	—	ns
Hemlock				
1	ns	***	ns	
2	—	ns	—	ns

Note: Month, species, layer, and sun–shade were fixed factors, and day was a random factor nested within month.

[a]The mean square of every effect was tested over the model error mean square (0.94, df = 68), except for month which was tested over day mean square (12.49). ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

[b]For the highest order significant interaction, Scheffé post hoc comparisons involving a change in one single factor are shown below. Significance of each comparison is shown as for the ANOVA table.

Table 2. Light-saturated photosynthetic rates (A_{max}) derived from photosynthesis–light curves.

Species	Leaf age (years)	Light-saturated photosynthetic rate ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	
		June	August
Red maple	—	11.27 (0.46)a	10.26 (0.54)ab
Red oak	—	15.45 (0.47)b	14.35 (0.73)c
Hemlock	0	6.51 (0.23)c	11.25 (0.31)a*
Hemlock	1	8.58 (0.26)d	9.16 (0.36)bd
Hemlock	2+	7.27 (0.29)cd	8.13 (0.51)d

Note: Values are means with SE given in parentheses. Values within columns with different letters are significantly different ($p < 0.05$), based on sequential Bonferroni-corrected planned comparisons.

*Significantly different from June mean, based on sequential planned comparisons.

the sun than in the shade, while red maple photosynthesis declined faster in the shade (Fig. 2, Table 1). As a result of these changes, differences in photosynthesis between hemlock and broad-leaved species, and between red oak and red maple, were most evident for sunlit leaves and for leaves higher in the canopy (Table 1, post hocs).

Photosynthesis varied daily but did not vary through the season (Table 1). Trees did, however, show species-specific seasonal changes in in situ photosynthesis (month × species interaction, $p < 0.0001$). Red oak photosynthesis did not change through the season (post hoc, $p > 0.05$), while that of hemlock increased from 5.1 to 6.3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (post hoc, $p < 0.01$) and that of red maple declined from 8.4 to 6.9 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (post hoc, $p < 0.0001$). As a result, red maple photosynthesis was only significantly greater than that of hemlock in June but not in August.

There were significant differences between species' light-saturated photosynthetic rates (A_{max}), and many of the differences varied through the season (significant month × species interaction, $F_{4,161} = 61.6$, $p < 0.0001$). Red oak leaves consistently had significantly higher A_{max} values than either red maple or hemlock leaves (Table 2; $F_{1,161} > 15.6$, $p < 0.05$, sequential Bonferroni). In June, red maple leaves had a significantly higher A_{max} than hemlock ($F_{1,161} > 31.9$, $p < 0.05$). Later in the season, however, there were no significant differences between red maple and hemlock needles younger than 2 years ($F_{1,161} < 5.4$, $p > 0.05$). Part of the change was driven by a marginal, but nonsignificant, decline in photosynthetic capacity of red maple leaves, and a marginal increase in photosynthetic capacity of 1-year-old hemlock needles. Current-season hemlock needles showed the most marked increase in photosynthetic capacity (73%) through the season ($F_{1,161} = 81.9$, $p < 0.05$).

Leaf-level photosynthesis: hemlock needle age comparisons

As in the previous multi-species analysis, hemlock leaf-level photosynthesis was influenced by canopy light environment (Table 3; significant sun–shade, layer, and sun–shade × layer effects, $p < 0.01$) and by daily conditions ($p < 0.001$). In addition, in this more detailed analysis for hemlock, we found photosynthesis varied both with needle age and seasonally (Fig. 3, Table 3). Hemlock needles that were at least 2 years old had significantly lower rates of photo-

Table 3. Summary results of (A) analysis of variance comparing leaf-level photosynthetic rates for different needle age-classes of hemlock and (B–D) Scheffé post hoc comparisons of single factors.

(A) ANOVA

Effect	df	F^a
Month	1	7.72*
Day (month)	4	5.85***
Layer	3	84.16***
Age	2	8.98***
Sun–shade	1	588.71***
Month × layer	3	3.70*
Month × age	2	14.72***
Month × sun–shade	1	22.46***
Layer × age	6	0.59ns
Layer × sun–shade	3	4.71**
Age × sun–shade	2	4.39*
Month × layer × age	6	0.42ns
Month × layer × sun–shade	3	0.48ns
Month × age × sun–shade^b	2	4.55*
Layer × age × sun–shade	6	0.51ns
Month × layer × age × sun–shade	6	0.23ns

(B) Between months for leaf ages 0, 1, and 2+ years

	Sun			Shade		
	0	1	2+	0	1	2+
June vs. August	***	ns	ns	ns	ns	ns

(C) Between sunlit and shaded leaves for leaf ages 0, 1, and 2+ years

	June			August		
	0	1	2+	0	1	2+
Sun vs. shade	***	***	***	***	***	***

(D) Among leaf ages (0, 1, and 2+ years)

	Sun		Shade	
	1	2+	1	2+
June				
0	***	ns	ns	ns
1	—	**	—	ns
August				
0	ns	***	ns	ns
1	—	***	—	ns

Note: Month, age, layer and sun-shade were fixed factors, and day was a random factor nested within month. ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.
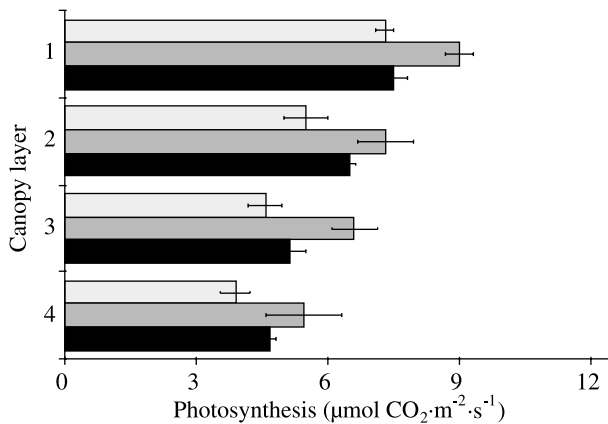
^{a}The mean square of every effect was tested over the model error mean square (0.80, 92 df), except for month which was tested over day mean square (5.85).

^{b}For the highest order significant interaction, Scheffé post hoc comparisons involving a change in one single factor are shown below. Significance of each comparison is as in the ANOVA table.
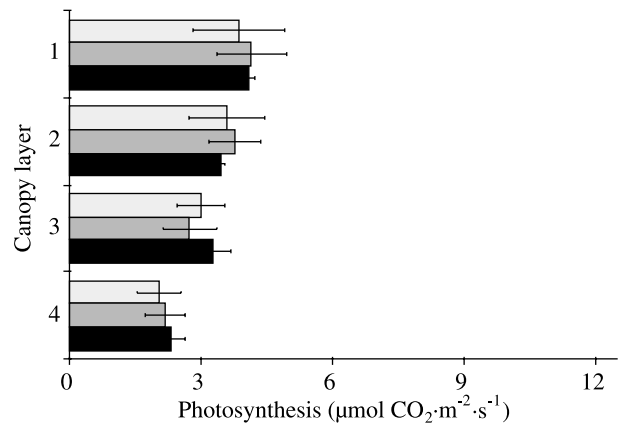
synthesis than younger needles (post hocs, $p < 0.05$). Hemlock photosynthesis increased significantly through the summer, and this change was driven by a seasonal increase in photosynthesis for current-season needles from 4.2 to 6.4 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Table 3; significant month × age interaction, $p < 0.0001$). This increase was particularly strong for

Fig. 3. Leaf-level photosynthetic rates in June (*a* and *b*) and August (*c* and *d*) for hemlock sunlit (*a* and *c*) and shaded (*b* and *d*) leaves of different ages (new-season (light gray), 1 year old (dark gray), and older than 1 year (black)) in different canopy layers (1 is the top layer). Columns represent mean photosynthetic rates of three individuals of each species ±1SE.
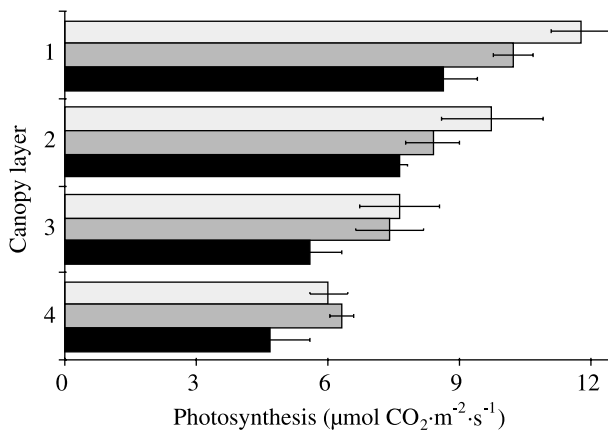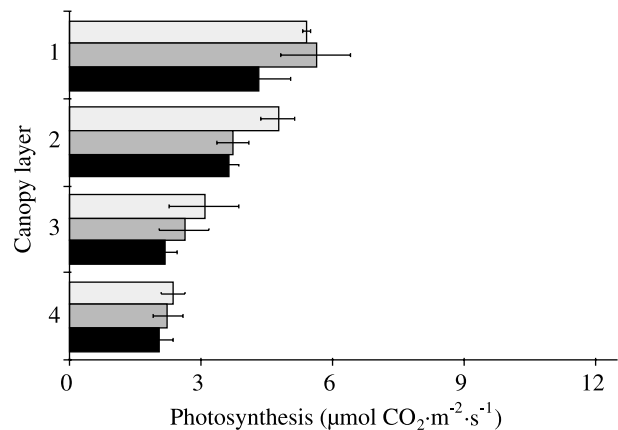

(a) Sunlit leaves, June

(b) Shaded leaves, June

(c) Sunlit leaves, August

(d) Shaded leaves, August

Total canopy carbon uptake

We scaled leaf photosynthesis to total canopy carbon uptake by weighting our leaf-level measurements according to their contribution to LAI of each canopy layer (Fig. 4) and then summing these weighted measurements together. Leaf area index was estimated from pure stands of oak–maple or hemlock and was used to assess species' contributions to total carbon flux on a ground area basis. We found that weightings varied with canopy height. The proportion of sunlit leaves and the proportion of current-season needles (for hemlock) increased with increasing canopy height (Fig. 4).

Modeled total canopy carbon uptake varied seasonally in species-specific ways (month × species interaction, $F_{2,8} = 8.86$, $p < 0.01$). In June, the broad-leaved species had significantly higher rates of total canopy carbon uptake than did hemlock (25.2 and 19.6 μmol·m^{-2}·s^{-1} respectively; Fig. 5; $F_{1,8} = 13.6$ and 16.4 for maple–hemlock and oak–hemlock

sunlit current-season needles higher up in the canopy (Fig. 3), as shown by a number of significant higher order interactions: month × sun–shade, month × layer, age × sun–shade, and month × age × sun–shade (Table 3).

comparisons, $p < 0.05$ for both). Later in the season, however, hemlock total canopy photosynthesis increased significantly to 24.1 μmol·m^{-2}·s^{-1} ($F_{1,8} = 9.6$, $p < 0.05$), and it no longer differed significantly from total canopy photosynthesis of broad-leaved species. Maple photosynthesis tended to decrease through the season. The decrease was only marginally significant ($F_{1,8} = 8.0$, $p < 0.1$) but did result in red maple having significantly lower canopy photosynthesis than red oak later in the season ($F_{1,8} = 13.9$, $p < 0.05$).

Sensitivity analysis

Our estimates of total canopy carbon uptake were most sensitive to variation in stand LAI (Table 4). As LAI was a direct scaling factor in the summation scheme, any perturbation in this parameter strongly influenced estimates of total canopy carbon uptake (all relative LAI impacts between 0.7 and 0.8). Overall, perturbations to other model parameters had much smaller influences on canopy photosynthesis estimates (Table 4). Model sensitivity to the proportion of sunlit and shaded leaves in tree canopies varied with species, with total canopy photosynthesis most sensitive to this parameter for red oak.

Fig. 4. For different hemlock canopy layers (1 is top layer), proportion of (*a*) sunlit (light gray) and shaded (dark gray) leaf area index at midday during midsummer, and proportion of (*b*) different needle age-classes (new-season (light gray), 1 year old (dark gray), 2 years and older (black)). Red oak and red maple canopies show similar, but not identical, patterns for sunlit–shaded leaf proportions, with only three canopy layers recognized in this study.
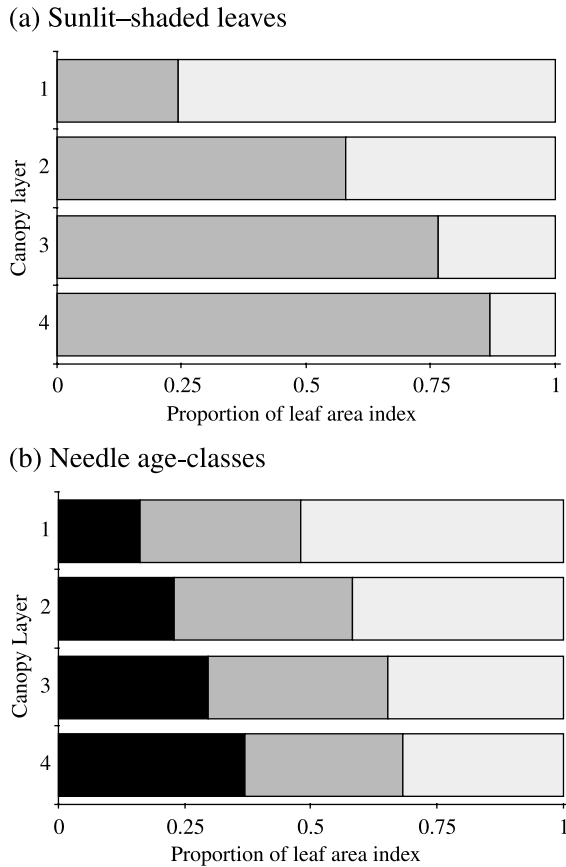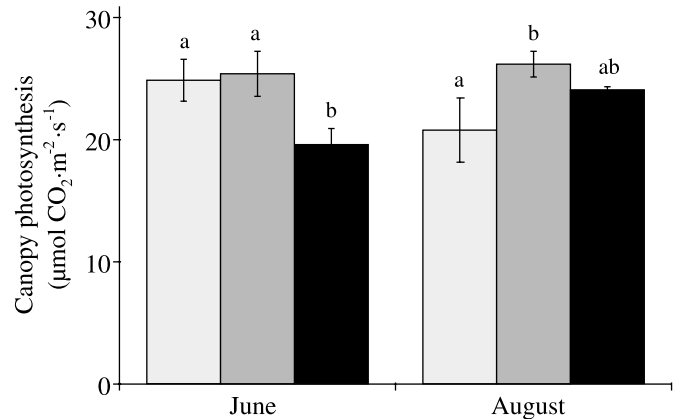
(a) Sunlit–shaded leaves

(b) Needle age-classes

Fig. 5. Modeled total canopy carbon uptake rates in June and August for red maple (light gray), red oak (dark gray), and hemlock (black) trees. Columns represent mean photosynthetic rates of three individuals of each species ±1SE. Means that are significantly different from one another between species but within a month ($p < 0.05$) share no letters in common, while means that are significantly different from one another between months but within a species ($p < 0.05$) are shown with boldface letters (sequential Bonferroni-adjusted means comparisons).

Discussion

Factors influencing leaf-level photosynthesis in tree canopies

As canopy microclimate is both spatially and temporally heterogeneous, many factors interact to influence the different leaf-level components of canopy photosynthesis (Norman and Jarvis 1975; Oker-Blom 1986). Leaves both respond to and modify their microenvironment, and these properties depend heavily on leaf characteristics. Among our study species, light availability was a major determinant of leaf-level photosynthesis. As expected, sunlit leaves had consistently higher rates of photosynthesis than shaded leaves for all species, and photosynthesis declined with decreasing height in the canopy for both sunlit and shaded leaves. Light has often been found to be the factor that varies most through tree canopies, and that most strongly influences leaf-level photosynthesis (Holbrook and Lund 1995). We did not directly relate photosynthesis to other environmental variables (e.g., air temperature and vapor pressure deficit), which may be additional determinants of canopy photosynthesis.

Species differed in their responses to canopy light environment. The broad-leaved species had significantly higher photosynthetic capacity than that of the conifer (15.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for red oak, 11.3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for red maple, and 7.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for hemlock). As a result, in the sun, the broad-leaved species had up to twofold higher rates of photosynthesis than hemlock. The A_{max} values for these species fell in the upper end of the general range for broad-leaved and coniferous species, respectively (Jarvis and Leverenz 1983; Holbrook and Lund 1995). Many studies have previously found that conifers have consistently lower photosynthetic capacities than broad-leaved species (Bond 1989; Reich et al. 1995), although the basis for the generality of this finding is still unclear. Differences in leaf structural properties and in stem conductance to water movement have both been proposed as possible explanations (Bond 1989). The greater sensitivity of the broad-leaved species to light availability (especially red oak), however, reduced these between-species differences for shaded leaves.

Ontogenetic constraints additionally influenced hemlock leaf-level photosynthesis. Early in the season, needles produced the previous year had higher rates of photosynthesis than either current-season needles or those produced at least 2 years before. The current-season needles, however, showed a dramatic increase in photosynthetic capacity through the season. Variation in needle nitrogen content and specific needle weight may have driven both the age-specific and seasonal changes in photosynthetic capacity (Field and Mooney 1986; Oren et al. 1986; Reich et al. 1991).

Species contributions to forest canopy carbon uptake

The large sizes of canopy trees present us with logistical problems for obtaining species-specific measurements of whole-tree carbon gain. In this study, we use a canopy aggregation model to scale leaf-level photosynthetic rates to total canopy carbon flux. The measurements were restricted

Table 4. Sensitivity of calculated total canopy carbon uptake (in both June and August) to varia-
tion in input parameters (A) for all species and (B) for hemlock only. Effects of each factor are
shown as changes in output relative to input.

(A) For all species	June			August		
Species	LAI	Sun–shade	Layer	LAI	Sun–shade	Layer
Red maple	0.807	0.314	0.106	0.778	0.401	0.148
Red oak	0.685	0.583	0.121	0.724	0.571	0.163
Hemlock	0.823	0.278	0.162	0.774	0.343	0.210

(B) For hemlock only		
Needle age (years)	June	August
0	−0.049	0.086
1	0.041	0.001
2+	0.002	−0.045

to sunny days during the peak growing season (June and Au-
gust) and thus do not fully represent the carbon dynamics
for each species. Despite these limitations, we did find clear
evidence that species differences in leaf-level photosynthetic
rates scaled up to create distinctions among species in mod-
eled canopy carbon uptake rates. These differences did not
fall simply along a leaf habit axis (evergreen coniferous vs.
deciduous broad-leaved), because of seasonal changes in
canopy photosynthetic rates (see Fig. 5). Earlier in the sea-
son, broad-leaved species had higher rates of total canopy
carbon uptake than hemlock (25% greater). The deeper can-
opy of hemlock (higher LAI) compensated to some extent,
but not completely, for its lower leaf-level photosynthetic
rates. Hemlock canopies have additional standing foliage
compared with broad-leaved species, but the approximately
one unit increase in LAI was not sufficient to offset the
lower photosynthetic capacity of its leaves. Moving down
through the canopy, leaves contribute less and less to total
canopy carbon uptake (Schulze et al. 1977a; Sprugel 1989;
Ellsworth and Reich 1993), because (i) a smaller proportion
of the leaves receive direct beam radiation (Norman 1993),
(ii) even leaves that do receive direct beam radiation receive
lower levels of PFD than leaves higher up (Oker-Blom
1986), and (iii) the lower canopy contains a greater propor-
tion of older needles. These phenomena may be particularly
important in hemlock stands, as canopies of hemlock trees
have very steep light attenuation curves (Canham et al. 1994),
so that additional foliage provides diminishing benefits.

Red oak and red maple achieved equivalent rates of total
canopy carbon uptake but did so in different ways. Because
red oak was particularly sensitive to changes in irradiance,
sunlit leaves in red oak contributed more to total canopy
photosynthesis than sunlit red maple leaves (80.5% for red
oak vs. 71.5% for red maple). Bassow and Bazzaz (1998)
found similar patterns for in situ photosynthetic rates of red
oak and red maple. We might have predicted these patterns
based on the species' life-history strategies (see Bazzaz
1979, 1996). Red oak is generally faster growing and, thus,
is likely to have higher light-saturated photosynthetic rates
than red maple but lower carbon assimilation in the shade.

Information on canopy photosynthetic rates from only two
points in time makes it difficult to draw many inferences

about seasonal trends in carbon flux. However, we found
that, at least between June and August, species' contribu-
tions to forest carbon uptake changed, even though air tem-
peratures and relative humidity were not different between
months. Hemlock showed a significant increase in modeled
total canopy photosynthesis, because of changes in photo-
synthetic competence of its current-season needles. These nee-
dles may compose up to 30% of canopy leaf area (see Fig. 4),
and thus, changes in their behavior will clearly influence total
canopy carbon uptake. In parallel with these changes, red ma-
ple canopy photosynthesis declined, so that red maple and
hemlock did not differ in their contributions to forest carbon
uptake later in the season. Declines in red maple photo-
synthetic capacity through the season may be related to re-
duced stomatal conductance in response to reduced soil water
availability and increased leaf-to-air vapor pressure deficits.
Soil water content was particularly low in these stands by
August in this year (~0.18 $cm^3 \cdot cm^{-3}$; K.M. Newkirk, unpub-
lished data), and red maple may be more sensitive to water
deficits than oak (Abrams 1998; Tschaplinski et al. 1998).

These changes in canopy-level photosynthesis across the
season reduced differences in modeled canopy carbon up-
take rates between hemlock and red maple, whose overall
carbon uptake rates did not differ from one another. In con-
trast, red oak had consistently higher canopy photosynthetic
rates than either of the other species. On an annual basis,
hemlock carbon gain may be underestimated by our instanta-
neous measures of canopy carbon gain on sunny days during
the main carbon season. Hemlock's contribution to annual
forest carbon gain may eventually surpass that of red maple,
as hemlock may compensate to some degree for its lower
photosynthetic capacity on clear summer days with higher
carbon uptake on cloudy days and outside the main growing
season. Previous studies have come to differing conclusions
regarding the importance of winter carbon gain for conifer
productivity (Schulze et al. 1977b: Schaberg et al. 1995). We
are currently developing approaches for measuring year-long
carbon gain for hemlock.

Validity of bottom-up approach

Because of the large degree of heterogeneity and
nonlinearity inherent in canopy processes, forest canopy

models are a particularly challenging method of ecological scaling (Holbrook and Lund 1995; Jarvis 1995; Baldocchi and Vogel 1996; Kruijt et al. 1997). Our summation approach accounted for a large proportion of the heterogeneity by stratifying the canopy vertically and into sun–shade classes. This method has previously been found to describe canopy properties sufficiently well to accurately predict total canopy carbon uptake (Norman 1980). In contrast, our sensitivity analysis showed that direct scaling components are the largest source of error in bottom-up approaches. Leaf area index (LAI) was the principle scaling factor for the summations used in the present study, and outputs were particularly sensitive to perturbations in LAI estimates. In the present study, our LAI estimates were based on direct foliage sampling (litter traps and destructive branch sampling) and indirect analyses of canopy structure with a hemispherical lens, both of which should provide an accurate representation of canopy density for the stands sampled. Our sensitivity analysis suggests, however, that obtaining accurate LAI estimates for other stands within the region would be the first step for extending these model results. Models that have effectively scaled canopy photosynthesis to the landscape level have often incorporated remotely sensed data covering broad geographic regions (Potter et al. 1993; Berry et al. 1997).

Implications for community and ecosystem dynamics

We have documented clear differences in canopy-level photosynthetic rates between the dominant coniferous and broad-leaved species in mixed forests in New England. We found that red oak consistently had the highest modeled canopy photosynthetic rates of the species studied, while through the season, the relative contribution of hemlock to forest carbon flux increased and that of red maple decreased. A more complete analysis of species' contributions should include full annual carbon budgets for these species (e.g., woody tissue respiration and photosynthesis outside the main growing season), and a broader range of species (e.g., white pine and yellow birch). Annual carbon budgets are clearly the next step for a comparison between deciduous and evergreen species.

Changes in canopy composition are likely to occur in this region in the near future, as a result of both natural and anthropogenic disturbance processes (Foster and Motzkin 1998). Many of these perturbations may differentially affect coniferous and broad-leaved species and, thus, alter the balance between these two groups of forest trees. There is growing evidence that both rising levels of atmospheric CO_2 and increased nitrogen deposition may favor broad-leaved species over conifers (Ceulemans and Mousseau 1994; Magill et al. 1997; but see Saxe et al. 1998). In addition, hemlock is specifically under threat from an exotic pest (the hemlock woolly adelgid, *Adelges tsugae*), that has the potential to eliminate hemlock from the region (Orwig and Foster 1998). In the present study, we have demonstrated that many of these changes could have substantial impacts on forest carbon dynamics in the future, particularly if red oak is the primary broad-leaved species to expand at the expense of hemlock. Models of carbon sequestration for temperate forests should account for the different contributions that tree species make to ecosystem-level carbon uptake.

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