

# Coupling whole-tree transpiration and canopy photosynthesis in coniferous and broad-leaved tree species

S. Catovsky, N.M. Holbrook, and F.A. Bazzaz

**Abstract:** We used sap flow as a measure of whole-tree function to examine how coniferous and broad-leaved species in mixed temperate forests differ in canopy-level transpiration and photosynthetic rates. We used heat dissipation probes to measure whole-tree sap flow in three species throughout one full year and then combined these measurements with micrometeorological monitoring and leaf-level gas exchange to determine whole-tree carbon gain. Both broad-leaved species (red oak, *Quercus rubra* L.; red maple, *Acer rubrum* L.) had two- to four-fold greater annual fluxes of water and carbon on a ground area basis than did the conifer (eastern hemlock, *Tsuga canadensis* (L.) Carrière), with red oak trees additionally showing 60–80% higher fluxes than red maple. Despite fixing one-third of its carbon when broad-leaved species were leafless, hemlock was not able to compensate for its low photosynthetic rates during the growing season. Productivity measures derived from annual growth rings and eddy covariance confirmed that whole-tree sap flow provided a valuable estimate of both the magnitude of current forest fluxes and differences in individual species' fluxes. Our results indicate that the predicted loss of hemlock from mixed temperate forests could potentially increase whole-forest water loss and carbon gain by two- to four-fold, provided sufficient nitrogen and water remain available to support such a change.

**Résumé :** Nous avons eu recours au flux de sève comme mesure du fonctionnement de l'arbre pour examiner comment les espèces résineuses et feuillues des forêts tempérées mixtes diffèrent dans leurs taux de transpiration et de photosynthèse au niveau du couvert. Nous avons utilisé des sondes à dissipation de chaleur pour mesurer le flux de sève de trois espèces pendant une année entière. Nous avons ensuite combiné ces mesures avec celles d'un suivi micro-météorologique et des échanges gazeux au niveau du feuillage pour déterminer les gains en carbone à l'échelle de l'arbre. Les deux espèces feuillues (le chêne rouge, *Quercus rubra* L. et l'érable rouge, *Acer rubrum* L.) avaient des flux annuels d'eau et de carbone de deux à quatre fois supérieurs à ceux du conifère (la pruche, *Tsuga canadensis* (L.) Carrière) sur la base de leur surface au sol. De plus, les chênes rouges avaient des flux de 60 à 80% supérieurs à ceux des érables rouges. Même si un tiers du carbone est fixé par la pruche pendant que les feuillus sont sans feuillage, celle-ci n'arrive pas à compenser la faiblesse de ses taux photosynthétiques durant la saison de croissance. Les mesures de productivité dérivées des cernes annuels de croissance et de la méthode des corrélations turbulentes confirment que le flux de sève fournit un estimé précieux de l'ampleur des flux actuels de la forêt et des différences dans les flux de différentes espèces. Nos résultats montrent que la disparition prévue de la pruche dans les forêts tempérées mixtes pourrait potentiellement augmenter la perte en eau des forêts et les gains en carbone par un facteur de deux à quatre, si suffisamment d'azote et d'eau restent disponibles pour supporter un tel changement.

[Traduit par la Rédaction]

## Introduction

Temperate forests currently represent an important sink in the contemporary global carbon cycle (Fan et al. 1998; Houghton et al. 1998) and may serve to slow continued increases in atmospheric CO<sub>2</sub> related to human activities (Woodwell et al. 1998). These forests, however, are threat-

ened by a suite of human-induced environmental perturbations that may affect their ability to function as a future carbon sink, e.g., changes in atmospheric composition, increased incidence of exotic pests, and increased influence of natural and human disturbances (Bazzaz 1996; Foster et al. 1997). To examine the potential influence of such changes, we address how the species composition of mixed temperate forests influences whole-ecosystem function. Changes in community composition could represent an important mechanism by which environmental perturbations affect future ecosystem functioning (Bolker et al. 1995; Wedin and Tilman 1996; Saleska et al. 1999) but have not been adequately addressed in forest systems to date, as our ability to take large-scale species-based measurements on whole ecosystems is still limited. In the present study, we take advantage of a physiological technique that provides a simple measure of whole-tree function and, thus, contributes detailed species-level information. Whole-tree transpiration

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can now be monitored relatively easily and continuously using sap flow measuring devices (Granier et al. 1996; Wullschlegel et al. 1998), which provide information on very short time scales but which may be maintained over the long term. As photosynthesis and transpiration are connected through the activity of stomata (Farquhar and Sharkey 1982), there is potential to use whole-plant sap flow to estimate annual patterns of total canopy carbon uptake.

We examine links between ecosystem structure and function in mixed temperate forests, which contain two distinct groups of tree species (evergreen coniferous and deciduous broad-leaved) (Pastor and Mladenoff 1992). These two groups of trees have evolved distinctive traits over time and exhibit numerous biological differences, e.g., leaf habit and water transport capacity (Bond 1989; Smith and Hinckley 1995). Differences in basic physiology could ultimately scale up to influence species' contributions to ecosystem-level processes, such as forest carbon gain and nutrient cycling (Baldocchi and Vogel 1996; Reich et al. 1997; Catovsky and Bazzaz 2000). As a result, basic forest ecosystem properties could be directly influenced by the relative abundance of different canopy tree species. Our ability to monitor plant function for long time periods using sap flow becomes particularly important when comparing evergreen and deciduous species, because evergreen species can stay physiologically active outside of the main growing season when deciduous species have no leaves. If we wish to compare annual water fluxes for both kinds of tree species, we need to monitor transpiration for the whole year, not just at select points during the main growing season.

In the present study, we tested the hypothesis that the dominant coniferous and broad-leaved species in mixed temperate forests in New England differ in canopy-level transpiration and photosynthesis. We predicted that over the year, the main coniferous species (eastern hemlock, *Tsuga canadensis* (L.) Carrière) would lose more water and fix more carbon than would the major broad-leaved species (red oak, *Quercus rubra* L.; red maple, *Acer rubrum* L.). Conifers are often more productive as mature trees than broad-leaved species, despite their lower instantaneous leaf-level photosynthetic rates (Reich et al. 1995), as a result of their higher leaf area index (Schulze et al. 1977; Bond 1989) and their ability to fix carbon outside the growing season when broad-leaved species are leafless (Neilson et al. 1972; Waring and Franklin 1979). We combined measurements of sap flow taken throughout one full year with micrometeorological monitoring (air and leaf temperatures, relative humidity, wind speed) to calculate canopy conductance (Meinzer et al. 1997). Leaf-level gas-exchange measurements were then used to convert canopy conductance to whole-plant carbon gain throughout the year. Finally, we evaluated our estimates of tree productivity using sensitivity analysis and by comparison with net biomass growth rates calculated from tree ring widths and published dimension analysis values.

## Materials and methods

### Sap flow

In autumn 1998, heat dissipation probes were installed in trees at three sites within the Prospect Hill tract of Harvard

Forest (Petersham, Mass.; 42°32'N, 72°10'W, elevation 340 m a.s.l.). Stands in this area contain trees that are 50–100 years old, and consist of a mixture of red oak, red maple, yellow birch (*Betula alleghaniensis* Britt.), black birch (*Betula lenta* L.), eastern hemlock, and white pine (*Pinus strobus* L.) (in approximately decreasing order of importance). The sites were located 150–500 m west and northwest of the Environmental Monitoring Station (EMS) tower (Wofsy et al. 1993), so that the study trees would be part of the ecosystem carbon flux signal. At each site, one tree of each study species was chosen (Table 1), with all study trees at a site located within 5 m of each other. The study species represent the currently dominant conifer (hemlock) and broad-leaved (red oak, red maple) species both locally (Harvard Forest) and regionally (central Massachusetts) (Foster et al. 1998).

Heat dissipation probes (2 mm diameter, 3 cm length) were constructed following Granier's (1987) original design. To minimize errors resulting from variation in probe function in space and time, each study tree contained two pairs of probes, inserted radially at a height of 1.4 m on opposite sides of the trunk from each other. At each insertion point, the bark was removed, and two 2-mm diameter holes were drilled, one 10 cm above the other, for probe insertion. The upper (downstream) probe contained 60 cm of tightly coiled high resistance heating wire (0.005 mm diameter), used to heat the probe with a constant power of 0.2 W from a marine deep cycle battery. Each probe, whether downstream or upstream (reference), contained a T-type thermocouple junction embedded in blackened superglue. The thermocouples of each pair were connected in series at the constantan side, and the copper leads were connected to a 21X datalogger (Campbell Scientific, Logan, Utah) programmed to record the temperature difference between the probes. Once assembled, the probes were covered in a polystyrene housing and surrounded with silver bubble wrap to provide thermal insulation. The edges of each polystyrene holding were sealed with hardening foam to prevent water entry.

The probes were run for 1 week in the middle of every month in 1999, logging data every 1 s and storing the mean every 20 min during each measurement interval. We were careful not to vary the time each month when the measurements were taken, so that we obtained a representative sample of sap flux throughout the year. Data collected were rigorously screened for wound responses to ensure that temperature changes were smooth and consistent across probe pairs. In general, probe outputs were typically within 10% of one another (occasionally up to 20% at times of low flow). In these cases, sap flow calculated from each probe pair was then averaged to produce a single tree value. However, through the course of the experiment, five pairs of probes had to be replaced because of noticeable problems with the data from the previous month. At these times, values from just a single probe pair were used until probe replacement the following month.

Prior to insertion in the field, the heat dissipation probes were calibrated in the laboratory. Probes were inserted into excised branches (40–50 cm diameter, 25–40 cm long) of each study species (described above). Branches were clamped into a continuous flow system where they were perfused with water from a reservoir. After a period of

**Table 1.** Characteristics of trees used in the study, showing measured dimensions and positions relative to EMS tower.

Site	Distance to tower (m)	Direction from tower	Species	DBH (cm)	Height (m)	Projected canopy area (m <sup>2</sup> )	Sapwood area (cm <sup>2</sup> )
1	500	West	Hemlock	30.5	23	17.9	127.2
			Red maple	23.5	22	16.7	174.4
			Red oak	32.7	21	17.6	70.6
2	150	West	Hemlock	36.9	21	19.5	157.4
			Red maple	38.1	21	18.6	263.9
			Red oak	29.0	23	21.6	49.8
3	150	Northwest	Hemlock	29.6	18	12.2	123.0
			Red maple	23.3	23	16.4	172.5
			Red oak	23.5	22	7.4	33.0

15 min to allow water to reenter all the functional xylem vessels, flow rates of water through stems were determined by measuring mass increase of water collected after leaving the branch per unit time. Flow rates were varied by adjusting the water reservoir height, and temperature differences at zero flow were determined 2 h after flow was stopped. Provided the probes were fully in conducting sapwood (Clearwater et al. 1999), Granier's (1987) original empirical relationship between sap flux velocity ( $v$ , mm·s<sup>-1</sup>) and temperature difference between probes ( $\Delta T$ , °C) was supported, as follows:

$$[1] \quad v = 0.119k^{1.231}$$

where  $k$  is related to the temperature difference between probes at some flow rate compared with the temperature difference at zero flow ( $\Delta T_0$ ):

$$[2] \quad k = \left( \frac{\Delta T_0 - \Delta T}{\Delta T} \right)$$

Regressions of  $\log v$  against  $\log k$  produced slope coefficients that varied from 1.19 to 1.25 ( $r^2 = 0.90$ – $0.95$ ), and these did not differ significantly from the original coefficient of 1.231 ( $F_{[1,28]} < 0.01$ ,  $p > 0.05$ ). Using this perfusion method, all probes were checked for correct function before insertion into trunks in the field using the laboratory method mentioned

Based on this empirical relationship, continuous measurements of  $\Delta T$  on our study trees were used to calculate sap flux velocity over 20-min intervals throughout each measuring period. For calculation of  $k$ , the largest temperature difference from the previous night was used as  $\Delta T_0$ . Sap flux velocity measurements on the same tree were averaged and converted to whole-tree sap flow by multiplying by sapwood cross-sectional area (m<sup>2</sup>) in the tree's trunk (Granier et al. 1996), which itself was determined by measuring sapwood depth on increment cores taken in late 1999. Sapwood could be easily distinguished from the heartwood based on color differences, provided the measurements were taken immediately after the core was removed from the tree. Whole-tree sap flow was scaled to ground area by dividing by projected canopy area (m<sup>2</sup>), which was determined for each tree by locating the canopy edge in eight compass directions using a densitometer (Arneith et al. 1996).

At this point, we noted the short sapwood depth of the red oak trees in the study (1.0–1.5 cm), a feature that is typical of ring-porous species. As the heat dissipation probes were not fully in conducting sapwood in these trees, we applied the correction formulated by Clearwater et al. (1999):

$$[3] \quad \Delta T_{\text{actual}} = \frac{\Delta T_{\text{measured}} - (1-a)\Delta T_0}{a}$$

where  $a$  is the proportion of probe in conducting sapwood. This correction assumes that all the water moves through the sapwood, which is a reasonable assumption for ring-porous species, such as red oak (Clearwater et al. 1999). This basic correction increased maximal sap flux values by close to twofold but was only applied to sap flow for red oak, the only species with a sapwood depth shorter than our probe length (compare 3.0–3.5 cm for hemlock sapwood and 6–11 cm for red maple sapwood). This correction has been validated both theoretically and empirically (Clearwater et al. 1999) and is now a widely accepted correction for ring-porous species with short sapwood (e.g., Oren and Pataki 2001). The correction was not appropriate for the laboratory calibrations, as conducting sapwood filled most of the cross-sectional area of the branches (40–50 cm) for all species, including red oak.

### Micrometeorology

Canopy conductance was determined from sap flow rates using

$$[4] \quad g_c = \frac{F}{\text{VPD}}$$

where  $g_c$  is canopy conductance scaled to ground area (mol·m<sup>-2</sup>·s<sup>-1</sup>),  $F$  is sap flow scaled to ground area (mol·m<sup>-2</sup>·s<sup>-1</sup>), and VPD is vapor pressure deficit between the leaf interior and the bulk air (mol·mol<sup>-1</sup>), itself calculated as the difference between saturation vapor pressure at leaf temperature and the ambient vapor pressure (function of air temperature and relative humidity) (Percy et al. 1989). Leaf temperatures were measured with fine-wire copper–constantan thermocouples attached to leaves of all study species from two canopy access towers located within 500 m of all study sites (Bassow and Bazzaz 1998; Hadley 2000). Thirty thermocouples were placed in the canopies of each study species. Because of temperature differences between sunlit

and shaded leaves, tree canopies were stratified into two layers of approximately equal leaf area: the upper canopy containing mostly sunlit leaves and the lower canopy containing mostly shaded leaves. Thermocouples were divided equally between both strata, and temperatures were recorded separately for each stratum. Stratification based on sunlit or shaded leaf conditions often captures much of the variation in canopy processes (Norman 1993; Catovsky and Bazzaz 2000). We aimed to ensure good contact between thermocouple junctions and leaves. For hemlock, thermocouple junctions were positioned within a tight constantan loop slipped around each needle. For the broad-leaved species, thermocouple leads were attached to leaf petioles with cable ties and then thermocouple junctions were held to leaf undersides using small strips of medical tape, which permitted continued water loss from leaves. In addition, a CS500 sensor (Vaisala, Woburn, Mass.) was installed on the hemlock canopy tower to measure both air temperature and relative humidity.

All temperature or humidity sensors were connected to 21X loggers (Campbell Scientific, Logan, Utah), which recorded data over the same sampling interval as did those measuring sap flow (1-s sampling averaged every 20 min, 1 week every month for a year). No apparent time lags existed between sap flow near the base of the tree and VPD in the canopy (highest correlations between  $F$  and VPD were obtained with no time lag,  $r_{70} = 0.78\text{--}0.95$  vs.  $0.62\text{--}0.88$  with a 1-h lag), and so  $g_c$  could be calculated from  $F$  and VPD measurements taken over the same time intervals. Because of differences in temperature between upper and lower canopy leaves, canopy conductance values were calculated separately for each strata. Sap flow was divided between strata (equal leaf areas) based on differences in conductance ratios determined from in situ measurements of gas exchange (see next section and Table 5). Upper to lower conductance ratios were  $0.08:0.04 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for hemlock,  $0.09:0.09 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for red maple, and  $0.25:0.16 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for red oak. Thus, the ratio of sap flow through upper and lower strata was assumed to be 2:1 for hemlock, 1:1 for red maple, and 3:2 for red oak.

Stomatal conductance was calculated from canopy conductance using the following relationship:

$$[5] \quad g_s = \frac{1}{\left(\frac{1}{g_c} - \frac{1}{g_b}\right)}$$

where  $g_s$  is stomatal conductance and  $g_b$  is boundary-layer conductance, both scaled to ground area ( $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). Boundary layer conductances in the upper and lower canopies were determined from wind speed, measured using O14A anemometers (MetOne, Grants Pass, Oreg.) attached to the hemlock canopy access tower at two heights, and from leaf size, according to the relationship proposed by Nobel (1999):

$$[6] \quad g_b = \frac{255}{\sqrt{\frac{d}{w}}}$$

where  $d$  is mean leaf length/width (0.5 cm hemlock, 7.5 cm red maple, 10 cm red oak) and  $w$  is wind speed ( $\text{cm}\cdot\text{s}^{-1}$ ). The relatively large size of maple and oak leaves created smaller boundary layer conductance values ( $1.5\text{--}2.0 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) than for hemlock (mean  $10.0 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) and led to a larger correction for stomatal conductance (three to four times greater than canopy conductance for oak and maple, compared with 1.2 for hemlock). Nevertheless, this boundary-layer correction is a well-established physical property of leaves (Nobel 1999) and has been shown to work well for the most part for canopy stomatal conductance corrections (Martin et al. 1999).

### Gas exchange

To convert stomatal conductance values to carbon uptake rates, we took in-situ gas-exchange measurements in the canopies of each of our study species. Trees of all species were sampled in July and September 1999, with an extra sampling interval for hemlock in May (before broad-leaved species had leafed out). At each sampling time, gas-exchange measurements were taken throughout the day (08:00–18:00) over 4 consecutive days on trees that could be reached from the canopy access towers at Harvard Forest (four hemlock individuals, two individuals of both maple and oak). Eight to 10 leaves were sampled within each canopy layer (upper and lower) each day and, additionally, for different needle age-classes for hemlock (see details in Catovsky and Bazzaz 2000). In-situ leaf-level photosynthesis and conductance were measured using a LI-COR 6400 open gas-exchange system (LI-COR, Lincoln, Nebr.). The system was set up to match current environmental conditions as closely as possible. Ambient air was drawn in from a dry, empty carboy (to stabilize gas concentrations), so that temperature and  $\text{CO}_2$  or  $\text{H}_2\text{O}$  concentrations corresponded with those of bulk air. In addition, to make measurements under ambient light levels, the gas-exchange chamber was fitted with a clear lid, and its orientation was set to match that of each leaf. Because of the irregular shape of hemlock needles, sampled needles were scanned into the computer after measurement and their area determined using NIH Image software version 1.6 (National Institutes of Health, Bethesda, Md.).

### Scaling validation

Assumptions of our scaling approach were investigated using sensitivity analysis, where effects of variation (up to 50% in each direction) in basic scaling parameters on calculated canopy carbon uptake were evaluated (Catovsky and Bazzaz 2000). The parameters that were varied included (i) VPD, (ii) canopy stratification, (iii) boundary-layer conductance, and (iv) photosynthesis–conductance relationships for upper and lower parts of canopy.

In addition to examining assumptions of our scaling approach, we were able to compare our measurements of gross canopy carbon gain in 1999 with estimates of net above-ground biomass gain for our three study species over the previous decade. The tree cores taken to determine sapwood depth or area (see earlier) were mounted and sanded to reveal annual rings. The widths of rings produced in the last 10 years were measured using a Unislide tree ring measuring system (Velmex, New York) and a dissecting microscope.

**Table 2.** Allometric coefficients used to calculate annual aboveground biomass growth rates (eq. 7) for each species, showing means and SEs (in parentheses) from all published studies on each species (ter Mikaelian and Korzukhin 1997).

Species	<i>a</i>	<i>b</i>	No. of studies	Range of <i>n</i> *	Range of <i>r</i> <sup>2</sup> *	States and provinces included
Hemlock	0.11 (0.02)	2.32 (0.08)	3	21–36	0.96–0.99	Maine, New Brunswick, West Virginia
Red maple	0.13 (0.02)	2.38 (0.05)	8	22–150	0.97–0.99	Maine, Michigan, New Brunswick, Rhode Island, West Virginia, Wisconsin
Red oak	0.10 (0.02)	2.51 (0.07)	3	16–24	0.95–0.99	Michigan, West Virginia, Wisconsin

\*Range of sample sizes and *r*<sup>2</sup> values for published studies.

Annual growth increments were used to calculate annual aboveground biomass growth based on dimension equations specific to each of our study species. All equations were of the form:

$$[7] \quad M = aD^b$$

where *M* is the dry mass of the aboveground woody and foliar biomass together (kg) and *D* is DBH (cm). For the species-specific parameters, *a* and *b*, we used means of published values for each study species (ter Mikaelian and Korzukhin 1997), shown in Table 2. To compare our study trees with a more general sample from the stand, additional tree cores were taken for another set of sample trees at Harvard Forest: 62 more hemlock trees and 20 more red oak and red maple trees (data provided by J. Hadley, Harvard Forest, and H. Lux, Marine Biological Laboratories).

## Results

All species showed a clear diurnal signal in water flux during months when sap flow could be detected (April–November) (Fig. 1). Broad-leaved species had very low rates of sap flow in the months prior to leaf out and after leaf fall (April, May, November) but had much greater fluxes of water than hemlock during summer months (June–October). Sap flow remained low at night, typically began to increase around 07:00, hit a peak close to 12:00 (up to 6.8 mmol·m<sup>-2</sup>·s<sup>-1</sup> for red oak, 4.7 mmol·m<sup>-2</sup>·s<sup>-1</sup> for red maple, and 1.4 mmol·m<sup>-2</sup>·s<sup>-1</sup> for hemlock, during summer months), and then declined steeply after sunset (20:00 in summer), after which no measurable sap flow was recorded (Fig. 1).

Canopy photosynthesis was derived from sap flow rates using (i) measurements of VPD to determine canopy conductance, (ii) wind speed measurements to determine boundary-layer conductance, and (iii) gas-exchange parameters to determine photosynthesis for a given stomatal conductance. Linear models were used to examine the influence of sampling month, canopy layer, and leaf age-class (for hemlock only) on the relationship between stomatal conductance and in-situ leaf-level photosynthesis. For the broad-leaved species, the relationship differed between upper and lower canopy layers ( $F_{[1,125]} = 133.60$  for red maple, 62.17 for red oak, both  $p < 0.001$ ) but not among sampling months ( $F_{[1,125]} = 0.72$  for red maple, 0.67 for red oak, both  $p > 0.05$ ) (Figs. 2a–2d). In contrast, for hemlock, both canopy layer and sampling month influenced the photosynthesis–conductance relationship ( $F_{[2,437]} = 10.18$ ,  $p < 0.001$ ) (Figs. 2e–2j), but this relationship did not differ among needle age-classes ( $F_{[2,437]} = 0.81$ ,  $p > 0.05$ ). The actual parameters used to convert stomatal conductance to canopy carbon

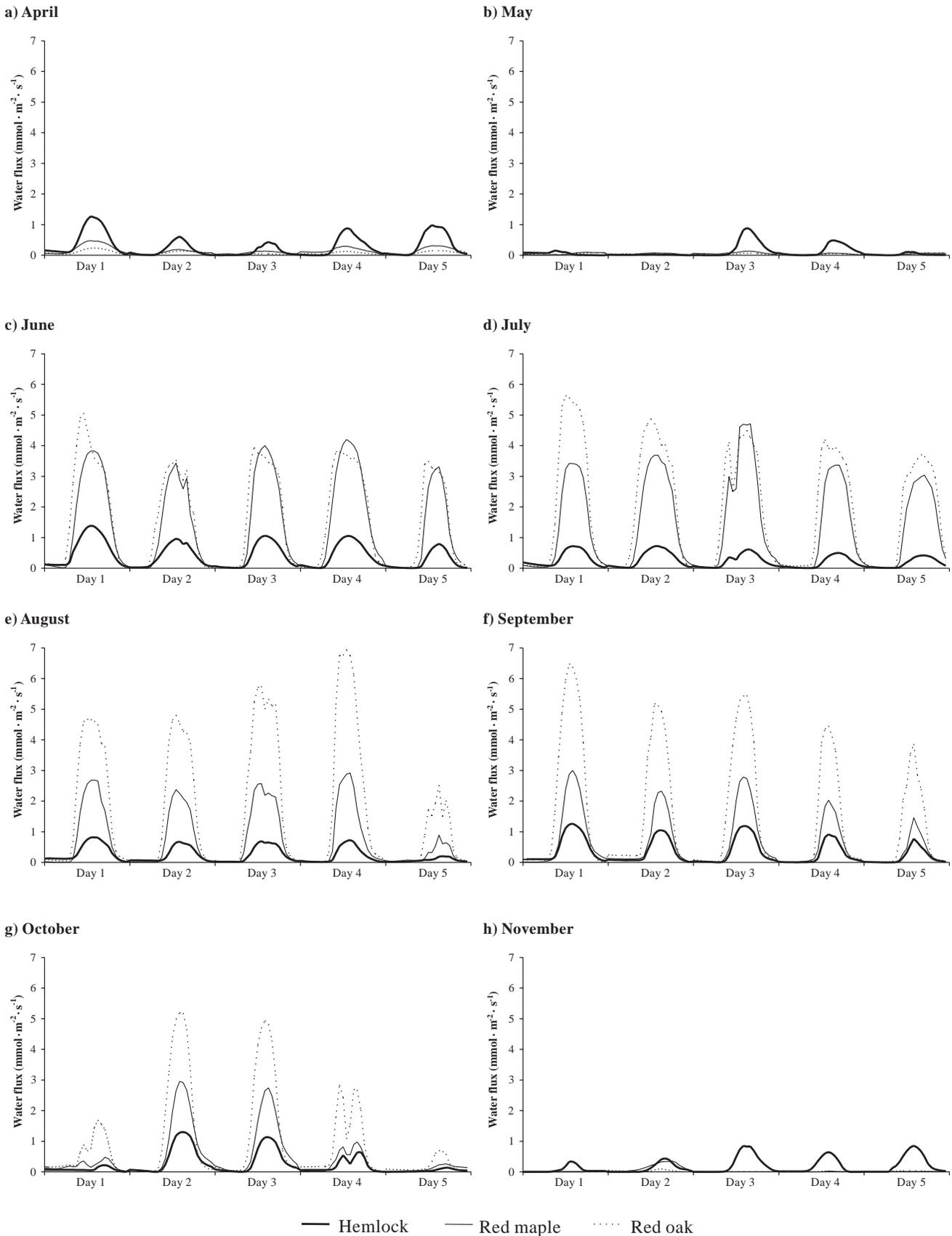
uptake rates were generated from model II linear regression analysis (Table 3) (Sokal and Rohlf 1995). As there was no seasonal variation in the relationship for either maple or oak, these parameters were used to scale sap flow across all months during which the trees were foliated (June–October). For hemlock, May parameters were used for both April and May, July parameters were used for June–August, and September parameters were used September–November.

Canopy photosynthesis showed similar diurnal trends to sap flow (Fig. 3), except that there was a more pronounced midday decline in photosynthesis for most species during the summer months. This trend arose as VPD often continued to increase after midday while sap flow leveled off, so that although the driving force for water movement was increasing, water flux did not increase as stomata closed and canopy conductance declined. Maximal instantaneous canopy photosynthetic rates ranged from 33 μmol·m<sup>-2</sup>·s<sup>-1</sup> for red oak, to 19 μmol·m<sup>-2</sup>·s<sup>-1</sup> for red maple, and 7 μmol·m<sup>-2</sup>·s<sup>-1</sup> for hemlock. Species-specific differences in water flux were matched in carbon gain patterns, with broad-leaved species having substantially greater rates of canopy photosynthesis than hemlock during summer months, and with hemlock compensating to some degree by fixing carbon in spring and late autumn (Fig. 3).

Sap flow, canopy conductance, and carbon uptake rates all showed distinct seasonal patterns for the different study species (significant species × month interactions in MANOVA,  $F_{[14,42]} = 26.9$  for sap flow, 238.6 for canopy conductance, 120.1 for canopy photosynthesis,  $p < 0.001$  for all). During the main growing season when all species had foliated canopies (June–October), the broad-leaved trees had significantly greater rates of water loss and carbon gain than did hemlock trees (2- to 10-fold greater for water loss, 3- to 12-fold greater for carbon gain) (Fig. 4). During the main summer months (July–September), the broad-leaved species also differed in canopy fluxes, with red oak showing significantly greater rates of water loss, canopy conductance, and carbon gain than red maple (e.g., water loss and carbon gain for red oak averaged 142.7 mol·m<sup>-2</sup>·day<sup>-1</sup> and 644.0 mmol·m<sup>-2</sup>·day<sup>-1</sup>, respectively, while equivalent values for red maple were 78.7 mol·m<sup>-2</sup>·day<sup>-1</sup> and 350.7 mmol·m<sup>-2</sup>·day<sup>-1</sup>, respectively; post hoc tests,  $p > 0.05$ ). Hemlock was able to maintain relatively constant rates of both water loss (~18.8 mol·m<sup>-2</sup>·day<sup>-1</sup>) and carbon gain (~85.7 mmol·m<sup>-2</sup>·day<sup>-1</sup>) from early spring (April) until late autumn (November). Hemlock compensated to some extent for its lower carbon gain during the main growing season by fixing carbon before and after the broad-leaved trees were foliated (April, May, November).

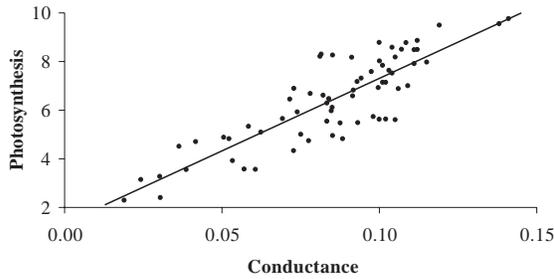
Canopy photosynthesis, as determined from whole-tree transpiration, represents species' contributions to forest gross

**Fig. 1.** Diurnal changes in sap flow (scaled to projected canopy area), shown for 5 days every month that sap flow could be detected, for hemlock (thick line), red maple (thin line), and red oak (broken line). Day numbers mark 12:00 on each day, and each line is the mean ( $n = 3$ ) for each species.

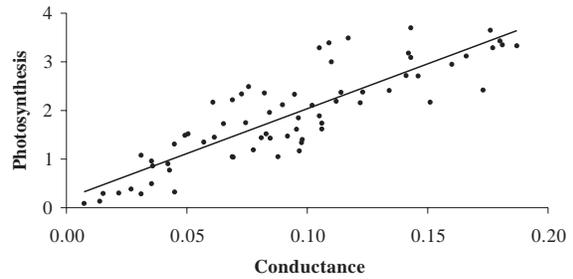


**Fig. 2.** Model II linear regression results for leaf-level photosynthesis ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) against conductance ( $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) for each study species, with different canopy layers and seasonal changes (for hemlock only) shown separately. Further details shown in Table 3.

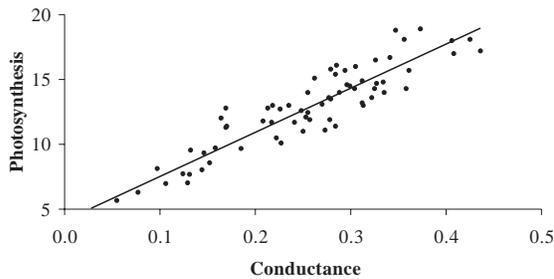
**a) Red Maple Upper Leaves**



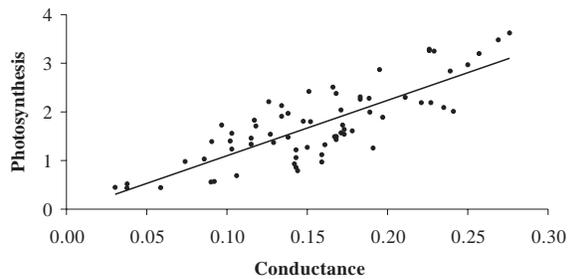
**b) Red Maple Lower Leaves**



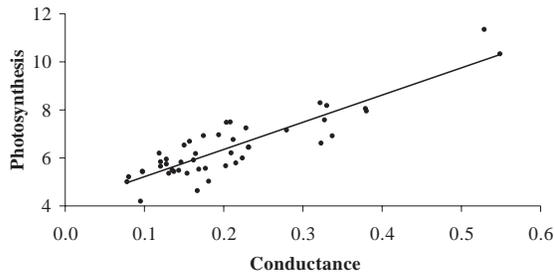
**c) Red Oak Upper Leaves**



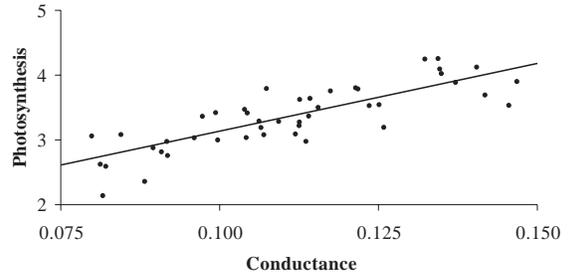
**d) Red Oak Lower Leaves**



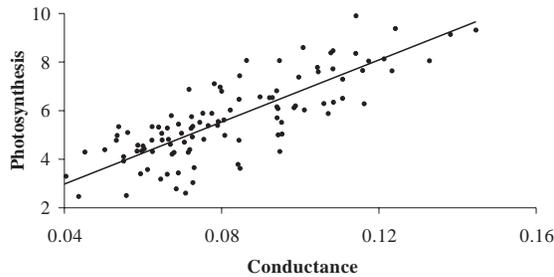
**e) Hemlock Upper Leaves, May**



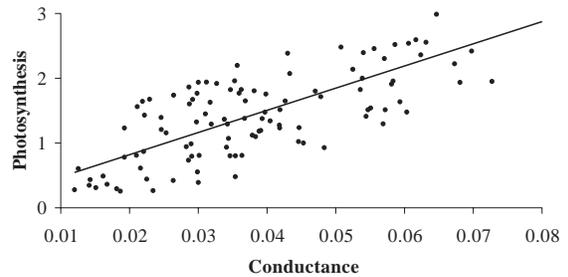
**f) Hemlock Lower Leaves, May**



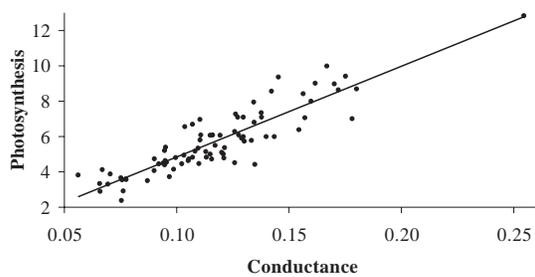
**g) Hemlock Upper Leaves, July**



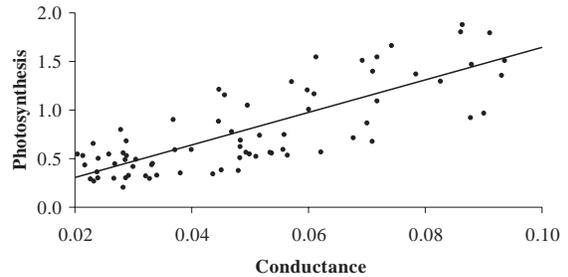
**h) Hemlock Lower Leaves, July**



**i) Hemlock Upper Leaves, September**



**j) Hemlock Lower Leaves, September**



**Table 3.** Model II regression coefficients for the relationship between measured leaf-level photosynthesis ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) and stomatal conductance ( $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) for different canopy layers and different species.

Canopy layer	Species	Month	<i>n</i>	<i>r</i> <sup>2</sup>	Slope*	SE*	Intercept	Mean conductance	Mean photosynthesis
Upper	Hemlock <sup>†</sup>	May	46	0.8	17.77	0.89	0.79	0.207	6.43
		July	108	0.7	77.89	4.34	-0.13	0.082	5.68
		Sept.	81	0.8	57.30	2.86	-0.10	0.117	5.72
	Red maple	—	69	0.8	68.28	4.06	0.62	0.085	6.40
	Red oak	—	69	0.8	46.99	1.77	0.39	0.249	12.61
Lower	Hemlock	May	48	0.7	25.69	1.97	0.63	0.110	3.35
		July	108	0.6	45.43	2.89	-0.20	0.039	1.47
		Sept.	81	0.7	20.43	1.32	-0.21	0.048	0.77
	Red maple	—	69	0.8	31.27	1.29	-0.07	0.094	1.92
	Red oak	—	69	0.7	24.07	1.01	-0.46	0.156	1.74

\*Slope and standard error of slope based on Model II geometric mean regression.

<sup>†</sup>As hemlock leaves exhibited significant seasonal variation in photosynthesis–conductance relationship, regression parameters were calculated for separate months.

primary productivity, since it does not account for plant, soil, or microbe carbon respiratory losses. In contrast, tree rings can be used to estimate net annual biomass increments. Using dimension analysis, we calculated aboveground woody and foliar biomass growth (scaled to projected ground area) for each study tree over the last 10 years (Fig. 5). There was a limited amount of interannual variation (significant year term in ANOVA,  $F_{[9,54]} = 2.41$ ,  $p < 0.05$ ), most notably with species having lower growth rates in 1993 than in 1999 (post hoc tests,  $p < 0.05$ ) but no other significant changes. These trends did not vary among species (no significant species  $\times$  year interaction in ANOVA,  $F_{[18,54]} = 1.27$ ,  $p > 0.05$ ). Overall, however, the species did differ in net primary productivity (species term in ANOVA,  $F_{[2,6]} = 8.70$ ,  $p < 0.05$ ), with red oak having significantly greater net biomass gains than hemlock (post hoc tests,  $p < 0.05$ ), but no significant difference between red maple and either of the other species.

Species differences in the scaling allometric exponent (*b*) used for this approach could play a substantial role in driving these differences. In this case, such effects likely arise from differences in wood density and foliar biomass. Species rankings for the exponent (oak > maple > hemlock) coincide well with species-specific differences in wood density (0.61, 0.49, and 0.38  $\text{g}\cdot\text{cm}^{-3}$ , respectively) (Panshin and de Zeeuw 1980). A given increase in basal diameter will translate into a greater biomass increase for species with higher wood density (e.g., oak). In addition, a species that maintains a larger foliar biomass because of its evergreen habit and shade tolerance (e.g., hemlock; Catovsky and Bazzaz 2000) may put on greater biomass for a given increase in basal diameter. These differences were reflected in a more general sample of trees from our study location. Our estimates of net aboveground productivity from our main study trees fall well within the range of estimates from a wider sample of trees within the stand (Fig. 6). All productivity estimates derived from our study trees were not significantly different from expected values produced from the regressions ( $F_{[1,18]} < 1.06$ ,  $p > 0.05$  in each case).

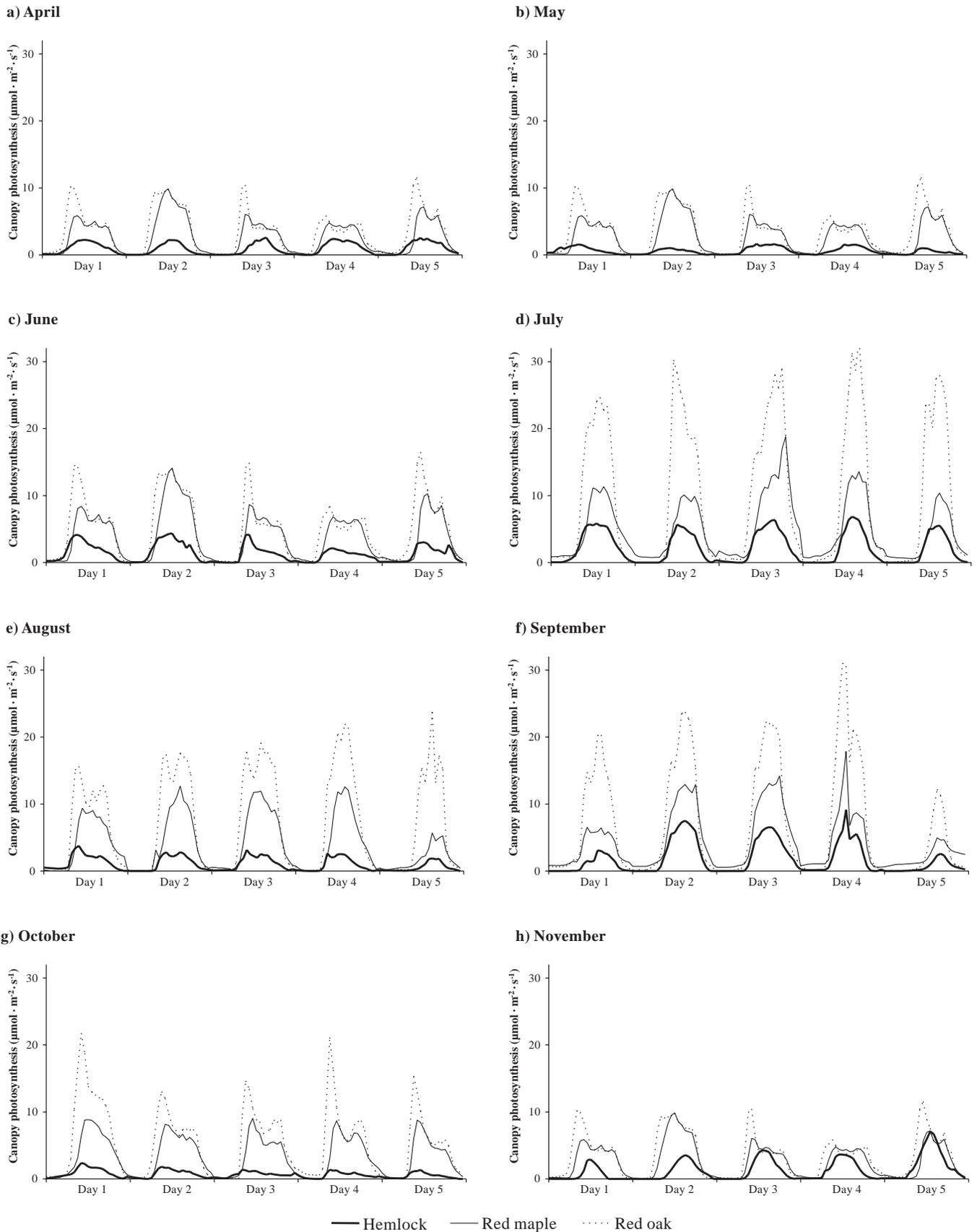
Species showed a consistent ranking in their annual totals for water loss, and gross and net carbon gain, all scaled to projected canopy area (species term in MANOVA,  $F_{[2,6]} =$

15.7–21.3,  $p < 0.01$ ) (Table 4). Most interspecific comparisons were significant (post hoc,  $p < 0.05$ ), except for oak–maple and hemlock–maple contrasts for net primary productivity. Red oak had 60–80% greater fluxes than did red maple, and three to four times greater fluxes than did hemlock, while red maple had a little over twice the fluxes than did hemlock. All species lost 200–250 times more water than they gained in carbon (on a mole for mole basis), and net aboveground primary productivity was typically 25–30% of gross primary productivity.

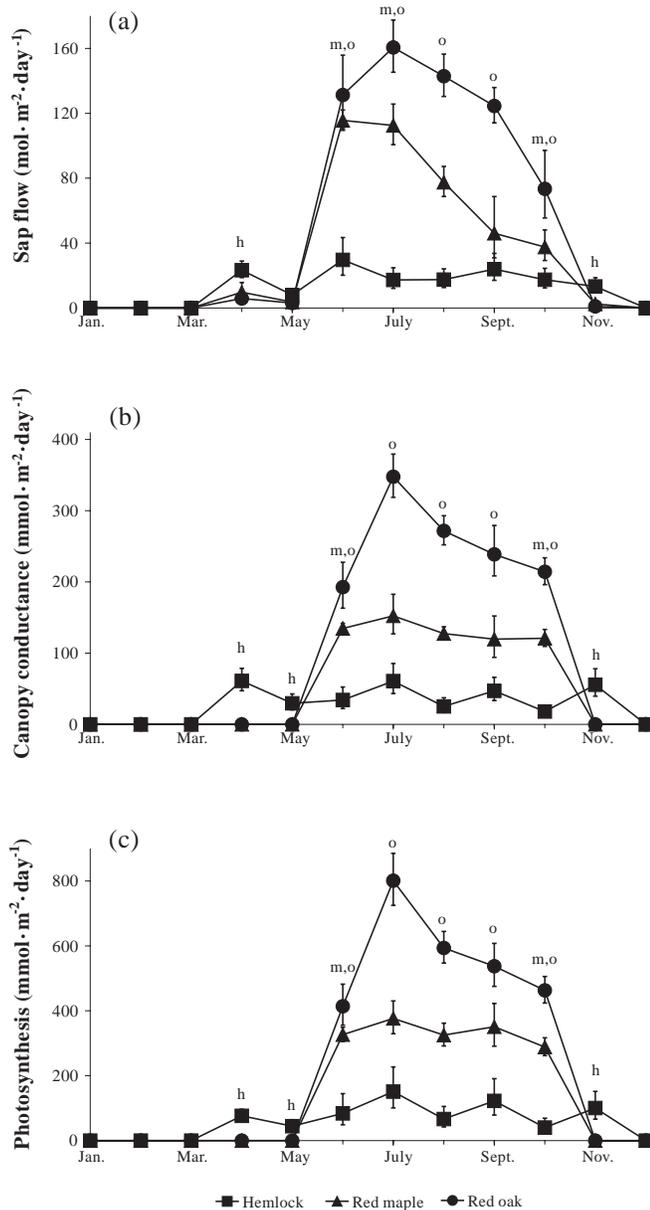
Sensitivity analysis showed that estimates of canopy photosynthesis were most sensitive to measurements of vapor pressure deficit (Fig. 7a) and the relationship between photosynthesis and conductance in the upper canopy (Fig. 7d). Boundary layer conductance measurements and the proportions of the canopy split between upper and lower leaves had relative small impacts on canopy photosynthesis calculations. Changes of up to 50% in each of these parameters typically produced less than 10% change in estimates of canopy carbon uptake rates (Figs. 7b and 7c). In contrast, even relatively small changes in VPD produced proportionally larger changes in canopy photosynthesis; for example, a 20% change in VPD produced a 20–30% change in photosynthesis (Fig. 7a). As VPD forms the driving force for sap flow, changes in this parameter directly scale to conductance estimates and, thus, canopy photosynthesis.

Canopy photosynthesis was also highly dependent on our leaf-level gas-exchange measurements (Figs. 7d and 7e), particularly in the upper canopy where changes in measured photosynthesis to conductance slopes mapped directly to changes in calculated canopy photosynthesis (e.g., 20% change in gas-exchange slope produced 18.7% change in canopy carbon flux). In the lower canopy, these gas-exchange relationships had about half the weighting on canopy photosynthesis compared with upper leaves (20% change in slope influenced carbon uptake by 7%). The 95% confidence intervals associated with these gas-exchange measurements (calculated from slope standard errors; Table 2) added 8–13% variation to our slope estimates for the photosynthesis–conductance relationships and provided a realistic indication of the magnitude of error inherent in our scaling approach. Gas-exchange measurements also gave us

**Fig. 3.** Diurnal changes in canopy photosynthesis (scaled to projected canopy area), shown for 5 days every month that sap flow could be detected, for hemlock (thick line), red maple (thin line), and red oak (broken line). Day numbers mark 12:00 on each day, and each line is the mean ( $n = 3$ ) for each species.



**Fig. 4.** Seasonal changes in sap flow (a), canopy conductance (b), and photosynthesis (c), all scaled to projected canopy area ( $n = 3$ ), for hemlock (squares), red maple (triangles), and red oak (circles). Canopy conductance and photosynthesis values were derived from sap flux measurements. Means ( $\pm$ SE) were calculated from natural logarithm transformed data and then back transformed. Letters above each month identify which species have the significantly highest rates at that time (Scheffé post hoc comparisons,  $p < 0.05$ ; h, hemlock; m, red maple; o, red oak).



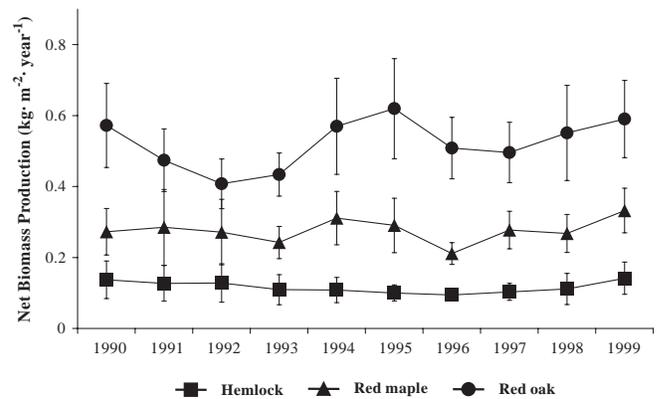
the opportunity to validate our model by comparison with the estimates of stomatal conductance produced from our sap flow scaling (Table 5). In every case, the two estimates produced similar values and remained consistent across species.

## Discussion

### Sap flow as a measure of whole-tree function

In the present study, we used sap flow as a measure of whole-tree function, determining species' canopy water and

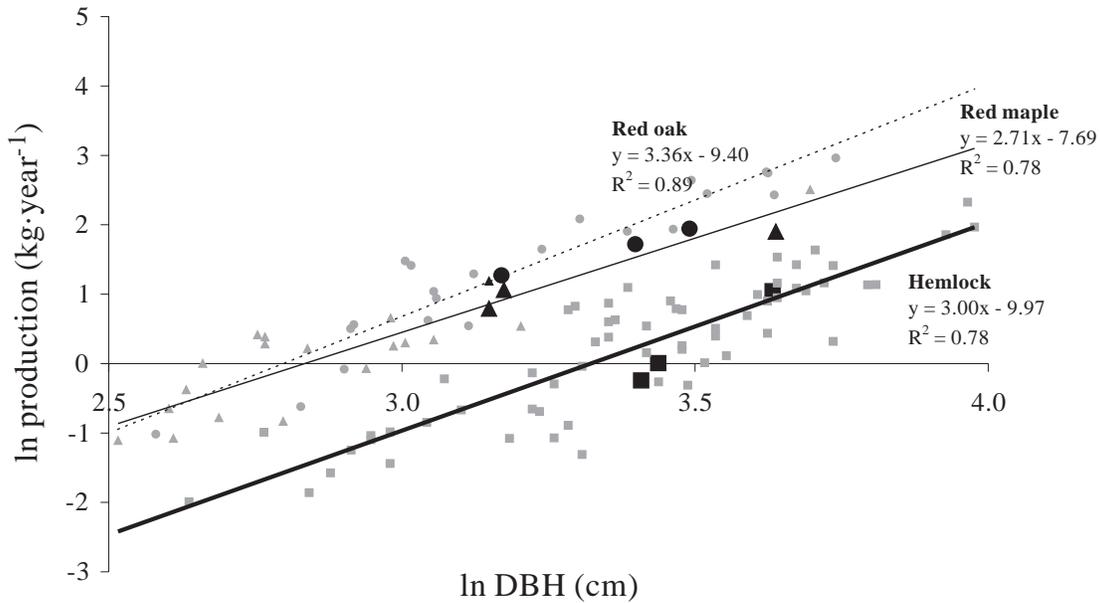
**Fig. 5.** Annual changes in net biomass production (mean  $\pm$  SE,  $n = 3$ ), scaled to projected canopy area, and determined from tree growth rings and allometric equations, for hemlock (squares), red maple (triangles), and red oak (circles).



carbon fluxes from measurements taken at the tree base. We were able to establish that the dominant broad-leaved species (red oak and red maple) in mixed temperate forests had substantially higher fluxes of water and carbon on an annual basis than did the coniferous species (hemlock). The large size of canopy trees has made it difficult to make physiological measurements at the whole-plant level. Most studies take some kind of scaling approach to measure whole-tree function (Jarvis 1995), either aggregating weighted leaf-level measurements (bottom-up) (Norman 1993) or using process-based measurements of leaf and canopy energy or nutrient budgets (top-down) (e.g., Jarvis and McNaughton 1986; Aber et al. 1996). Both kinds of approach, however, have problems arising from scaling between different spatial and temporal scales and, thus, may only be of limited use. Sap-flow measurements overcome some of these challenges by providing a whole-plant nondisruptive continuous measure of tree function on both short and long time scales (Granier et al. 1996; Wullschlegel et al. 1998).

Top-down approaches for understanding ecosystem function have the benefit of measuring integrated ecosystem-level processes over large spatial and temporal scales but only present a static picture of ecosystem properties for one forest over one particular time interval. In contrast, bottom-up scaling investigates ecological processes at smaller spatial and temporal scales and then aggregates these calculations to larger scales. Such approaches provide a more mechanistic understanding of controls on ecosystem function (Hollinger 1992) and contribute species-level data to ecosystem models (Bassow and Bazzaz 1998; Catovsky and Bazzaz 2000). As a result, bottom-up approaches can be used to determine how ecosystem function might respond to a change in environmental conditions or even community structure. The heterogeneous nature of plant canopies in space and time, however, requires that sampling schemes for bottom-up models are typically highly stratified and intense (Holbrook and Lund 1995; Jarvis 1995). In addition, the results of such approaches are extremely sensitive to the major scaling parameters used in the model, e.g., leaf area index (Catovsky and Bazzaz 2000). Thus, there is the potential for novel scaling techniques, such as sap flow combined with

**Fig. 6.** Log–log relationship between tree DBH (cm) and net aboveground productivity (kg·year<sup>-1</sup>), derived from last 10 years of annual growth rings, for an additional sample of trees from study site. For each species, additional sample trees are shown as small shaded symbols, study trees are shown as large solid symbols (hemlock, squares; red maple, triangles; red oak, circles), and regressions shown as equations and slopes (hemlock, thick line; red maple, thin line; red oak, broken line).



**Table 4.** Annual totals (1999) of water loss, gross (GPP) and net primary productivity (NPP) for each study species, scaled to projected canopy area, expressed as means (with SEs in parentheses,  $n = 3$ ).

Species	Water loss (kg·m <sup>-2</sup> )	GPP (kg C·m <sup>-2</sup> )*	NPP (kg C·m <sup>-2</sup> ) <sup>†</sup>
Hemlock	92.6 (32.6) <i>a</i>	0.301 (0.113) <i>a</i>	0.071 (0.023) <i>a</i>
Red maple	230.2 (30.7) <i>b</i>	0.630 (0.089) <i>b</i>	0.166 (0.031) <i>ab</i>
Red oak	359.4 (22.4) <i>c</i>	1.055 (0.107) <i>c</i>	0.295 (0.054) <i>b</i>

**Note:** Values with different letters are significantly different among species for a given column (Scheffé’s post hoc test,  $p < 0.05$ ).

\*GPP derived from sap flux measurements.

<sup>†</sup>Aboveground NPP (in units of carbon), calculated as 50% of aboveground net biomass gain (determined from tree ring growth).

**Table 5.** Comparison of mean daytime stomatal conductance values (mol·m<sup>-2</sup>·s<sup>-1</sup>) derived directly from gas exchange and from sap flow scaling for upper and lower canopy leaves during 5 days in July.

Canopy layer	Species	<i>n</i>	Gas exchange	Sap flow
Upper	Hemlock	235	0.082	0.073
	Red maple	69	0.085	0.080
	Red oak	69	0.249	0.227
Lower	Hemlock	237	0.039	0.042
	Red maple	69	0.094	0.092
	Red oak	69	0.156	0.194

gas exchange, which provide a bridge between both top-down and bottom-up approaches.

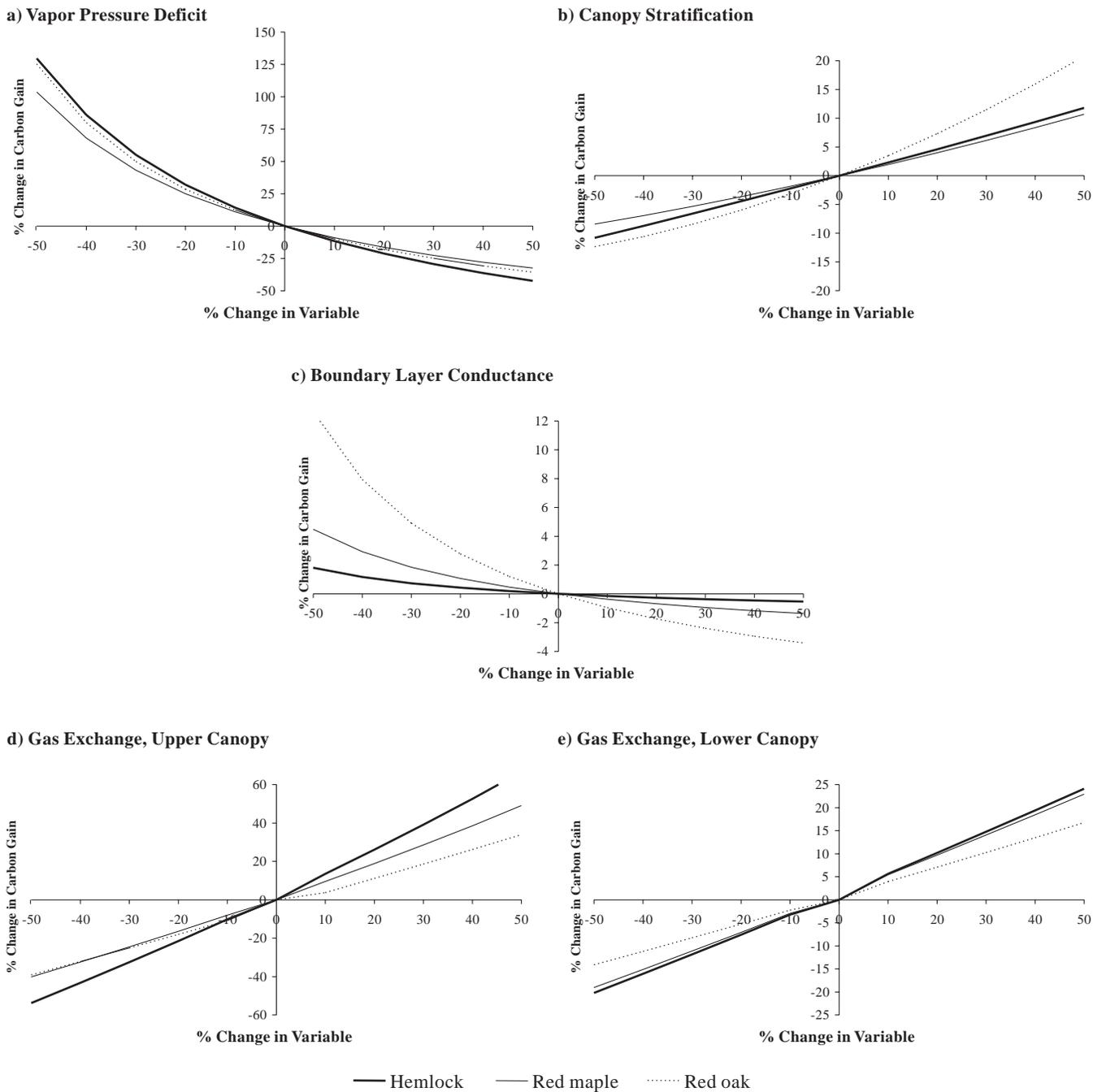
**Interspecific comparisons of water and carbon flux**

Although coniferous forests are typically more productive than broad-leaved forests (see survey in Jarvis and Leverenz 1983), recent work in boreal forests show opposite trends (Gower et al. 1997), matching current results of lower annual canopy photosynthetic rates for hemlock compared with broad-leaved trees. For coniferous species, thick leaf structure (so leaves survive more than one growing season) and limited water transporting capabilities through tracheids restrict their leaf-level photosynthetic rates (Smith and Hinckley 1995). Broad-leaved tree species that co-occur with hemlock typically have more than twofold greater rates of carbon uptake on a leaf level than hemlock itself (Catovsky and Bazzaz 2000). Often, however, conifers are able to compensate for their lower leaf-level photosynthetic

rates on the whole-tree level by maintaining deep canopies (Schulze et al. 1977; Bond 1989) and by fixing carbon outside the main growing season (Waring and Franklin 1979). For hemlock, however, neither of these traits was sufficient to compensate for its very low rates of canopy photosynthesis during the growing season.

The evergreen habit of hemlock did not benefit the species much in terms of increasing leaf longevity and thus producing a deeper canopy (compare with Schulze et al. 1977), as the planar arrangement of its needles keeps hemlock at a lower leaf area index (LAI of 4) than many coniferous species (LAI can be as high as 15) (Waring et al. 1978; Holbrook and Lund 1995). Nevertheless, hemlock was able to take some advantage of maintaining a fully foliated canopy year-round. In 3 of the 7 months when the broad-leaved species were leafless, conditions were favorable for hemlock to fix carbon and almost one-third of its annual carbon uptake was obtained during this time (Fig. 4). This additional carbon fixation, however, was still not sufficient to allow

**Fig. 7.** Sensitivity of calculated total canopy carbon uptake to the major scaling assumptions used in the model, with effects for each species (hemlock, thick line; red maple, thin line; red oak, broken line) shown separately.



hemlock’s canopy photosynthesis to match that of broad-leaved species on an annual basis. In eastern North America, the harsh winter conditions only allow conifers to fix limited amounts of carbon outside the main growing season (Jurik et al. 1988; Schaberg et al. 1998). Conifers are able to profit more from their evergreen habit in temperate forests in western North America, where the winters are mild (advantage for evergreen species) and the summers are dry (disadvantage for deciduous species) (Waring and Franklin 1979).

While hemlock consistently had lower fluxes of carbon and water than either red oak or red maple, there were also

significant differences in canopy photosynthesis between the broad-leaved species. In the study year, red oak fixed 60–80% more carbon annually than did red maple. Red oak was able to make a large contribution to ecosystem-level carbon flux by sustaining higher photosynthetic rates throughout the growing season. Oak (*Quercus*) typically exhibits the highest maximal photosynthetic rates of co-occurring species, both in New England forests (Bassow and Bazzaz 1997, 1998; Catovsky and Bazzaz 2000) and more generally (Reich et al. 1991; Morecroft and Roberts 1999). The substantial carbon uptake capacity of red oak may arise, in part,

from its ability for rapid water transport through its ring porous xylem vessel elements. To sustain high photosynthetic rates, trees must be able to deliver a constant supply of water to the leaves, so that stomata can stay open and maintain a high canopy conductance without causing cavitation (Sperry 1995). Low hydraulic conductance caused by differences in vascular architecture may limit maximal photosynthetic rates of tree species (Ryan and Yoder 1997). Mature red oak trees are also deeply rooted, which may allow them to access ground water and, thus, gain a relatively constant water supply that is unaffected by periods of low soil moisture availability (Cavender-Bares and Bazzaz 2000).

### Value of sap flow in scaling approaches

All scaling methods by their nature introduce some degree of uncertainty into our flux estimates, particularly when only a subset of trees from within the stand are sampled (three individuals for each species, in this case). Therefore, comparison with other measures of ecosystem-level productivity can prove a valuable way to assess the validity of our approach. In the present study, the estimates of total annual carbon uptake rates derived from sap flow were consistently about four times greater than species' net aboveground carbon gain determined from annual growth rings, and these growth ring results were validated for a wider sample of trees at our study site. Species typically retain 50% of their gross carbon gain as net biomass growth (Ryan 1991), approximately half of which will be allocated to aboveground parts. Thus, the consistent and realistic difference between gross and net productivity among species gives added support to the accuracy of our measurements. Both sap flow and growth ring methods produced identical species' rankings (red oak, red maple, then hemlock) and maintained the same magnitude of differences between species (Table 4). This analysis does make the implicit assumption that net productivity is a constant fraction (in this case, 50%) of gross canopy carbon uptake, but as this validation is not fully quantitative, this assumption is likely to be reasonable, especially as gross and net tree productivity match up consistently across species in this case. A second approach for validating our canopy photosynthesis results came from eddy covariance measurements taken during our sampling intervals (C.C. Barford and S. Wofsy, unpublished data; methods described in Wofsy et al. (1993) and Goulden et al. (1996)). Gross ecosystem productivity for the forest stand containing our study trees in 1999 was calculated as  $1.17 \text{ kg C}\cdot\text{m}^{-2}$ . This value was not significantly different from our calculated value of total annual carbon gain for red oak ( $1.10 \text{ kg C}\cdot\text{m}^{-2}$ ), the current stand dominant ( $F_{[2,2]} = 0.30, p > 0.1$ ).

Our laboratory calibrations and those of others (Clearwater et al. 1999) confirmed that heat dissipation probes give accurate estimates of sap flux velocities, suggesting that any errors are likely to have arisen only during the scaling process itself. Sapwood area and canopy projected area were both primary scaling factors in our approach (to calculate fluxes on whole-tree and ground area bases, respectively), and thus, the accuracy of our flux estimates depends strongly on the precision of these measurements (as demonstrated in Catovsky and Bazzaz 2000). In

addition, our sensitivity analysis highlighted the parameters that carried particular weighting in the scaling process. Some scaling assumptions had very small effects on calculated canopy photosynthetic rates, e.g., nature of canopy stratification (Parker and Brown 2000) and measurement of boundary layer conductance. In contrast, the high degree of coupling between leaf transpiration and the dryness of the air (Percy et al. 1989) emphasized VPD in scaling from water loss to carbon gain (Fig. 7). Calculation of leaf-to-air VPD is highly sensitive to accurate measurement of leaf temperature (Tyree and Wilmot 1990). Our sampling scheme incorporated leaf temperature in the upper and lower canopy strata but did not account for variation in leaf temperatures within each canopy layer. However, effects of variation in VPD on canopy photosynthesis are likely to be consistent across species and not influence the relative differences between species. In addition, our estimates of stomatal conductance obtained from sap flow fit well with those derived from instantaneous gas-exchange measurements, suggesting that our scaling approach was robust to these assumptions.

Our gas-exchange measurements played a major role in scaling from sap flow to whole-tree photosynthesis, with changes in the slope of the relationship between photosynthesis and conductance leading to equivalent changes in calculated canopy carbon gain. However, the magnitude of variation in gas-exchange parameters (8–13%) was still substantially smaller than the magnitude of differences between the species. Thus, the conclusions of the present study should be robust to most of these relatively small errors introduced during the scaling process. Annual growth rings (for study species and for a wider sample) and eddy covariance both confirmed that our scaling approach provides a good representation of the magnitude and direction of current fluxes. Overall, results of the present study suggest that a switch from a forest dominated by hemlock to one dominated by broad-leaved species (particularly red oak and red maple) could potentially increase canopy transpiration and photosynthetic rates by two- to four-fold, provided sufficient nitrogen and water remain available to support such a change.

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