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HOW ENVIRONMENTAL CONDITIONS AFFECT CANOPY LEAF-LEVEL PHOTOSYNTHESIS IN FOUR DECIDUOUS TREE SPECIES

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Abstract. Species composition of temperate forests vary with successional age (i.e., years after a major disturbance) and seems likely to change in response to significant global climate change. Because photosynthesis rates in co-occurring tree species can differ in their sensitivity to environmental conditions, these changes in species composition are likely to alter the carbon dynamics of temperate forests. To help improve our understanding of such atmosphere–biosphere interactions, we explored changes in leaf-level photosynthesis in a 60–70 yr old temperate mixed-deciduous forest in Petersham, Massachusetts (USA).

Diurnally and seasonally varying environmental conditions differentially influenced in situ leaf-level photosynthesis rates in the canopies of four mature temperate deciduous tree species: red oak (*Quercus rubra*), red maple (*Acer rubrum*), white birch (*Betula papyrifera*), and yellow birch (*Betula alleghaniensis*). We measured in situ photosynthesis at two heights within the canopies (top of the canopy at ~20 m, and in the sub-canopy of the same individual trees at ~14–16 m) through a diurnal time course on 7 d over two growing seasons. We simultaneously measured a suite of environmental conditions surrounding the leaf at the time of each measurement. We used path analysis to examine the influence of environmental factors on in situ photosynthesis in the tree canopies.

Overall, red oak had the highest photosynthesis rates, followed by white birch, yellow birch, and red maple. There was little evidence for a substantial midday depression in photosynthesis. Instead, photosynthesis declined throughout the day, particularly after 1600. Diurnal patterns of light reaching canopy leaves, leaf and air temperature, and vapor pressure deficit (VPD) contributed to diurnally varying photosynthesis rates. Large differences in these parameters through the growing season partly led to the seasonal differences observed in photosynthesis rates. Path analyses helped to identify the relative contribution of various environmental factors on photosynthesis and further revealed that species-specific sensitivities to various environmental conditions shifted through the season. Red oak photosynthesis was particularly sensitive to air temperatures late in the season when air temperatures were low. Further, red maple photosynthesis was particularly sensitive to high VPDs through the growing season.

Incorporating data on the physiological differences among tree species into forest carbon models will greatly improve our ability to predict alterations to the forest carbon budgets under various environmental scenarios such as global climate change, or with differing species composition.

Key words: Acer rubrum; Betula alleghaniensis; Betula papyrifera; canopy-tree photosynthesis; Harvard Forest (Petersham, Massachusetts, USA); leaf-level photosynthesis; path analysis; photosynthesis, seasonal and diurnal variation; Quercus rubra; temperate deciduous forests.

INTRODUCTION

Temperate-forest carbon cycles play a critical role in the global carbon cycle through photosynthesis, respiration, and biomass accumulation (Houghton 1991, Wisniewski and Lugo 1992). Our detailed knowledge of what controls the carbon cycle within these important ecosystems is still limited. For example, Goulden et al. (1996) demonstrated that there can be substantial

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variation between years in the various components of temperate-forest gas exchange; however, we still do not fully understand the mechanisms underlying these fluctuations and cannot predict the possibility for greater fluctuations in the future. Many forest carbon models have not yet adequately considered that different tree species can contribute differentially to carbon-cycle processes and that shifting environmental conditions may differentially affect different species. For many decades foresters have related stand productivity to species composition, by simply relating growth rate to diameter at breast height (dbh) for the principal species (e.g., Cooper 1981, Peet 1981 and references therein); however, very few studies have also quantified the in-

fluence of species-specific physiology on stand primary productivity or, more explicitly, the net ecosystem-level carbon exchange. This paper demonstrates that sensitivities to environmental conditions can significantly differ among co-existing tree species.

In contrast to the extensive information available for seedlings and small saplings, only limited data on photosynthesis rates exist for mature individuals of most canopy tree species (e.g., Dougherty et al. 1979, Jurik 1986, Pereira et al. 1986, Jurik et al. 1988, Marek et al. 1989, Weber and Gates 1990, Reich et al. 1991, Hanson et al. 1994). This ignorance hurts modeling efforts. The data that do exist show that the upper-canopy levels have high photosynthetic rates, in part due to the higher light levels there. The greater distribution of leaf area in the upper canopy may also be an important factor. Plants, or even plant parts, grown in high incident-light levels can acclimate to the high irradiance, and thus improve carbon, water, and heat balance of the plant or plant module (e.g., Boardman 1981, Givnish 1988, Lei and Lechowicz 1990).

In temperate deciduous forests, seasonality profoundly influences leaf physiology (e.g., Dougherty et al. 1979). In the canopy, large diurnal and seasonal variation in physiological activity exists in part because temperature, humidity, light levels, and vapor pressure deficit (VPD) all vary through the course of the day and through the course of the season, often on different scales. Physiological response to environmental conditions (e.g., temperature optima of photosynthesis) may also shift seasonally (e.g., Dougherty et al. 1979). This variation is likely to affect canopy-tree photosynthesis rates.

To quantitatively describe the patterns of diurnal and seasonal photosynthesis in a mixed deciduous stand, we measured in situ leaf-level photosynthesis rates of four dominant tree species. To understand the factors affecting these photosynthesis rates, we also simultaneously measured a suite of environmental conditions surrounding the leaf during the measurements to quantify the species-specific sensitivity to environmental conditions as they change throughout the day and the growing season. These measurements were performed at two different heights within the canopy, over the course of several days, and over two growing seasons.

We focused on four tree species: red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britton), and white birch (*Betula papyrifera* Marsh.). These species are important components of forests in the northeastern United States, and they cover much of the successional gradient for tree species in these forests (Burns and Honkala 1990). Mature individuals of all four species are frequently found together and collectively form >80% of the canopy at our study site, the Harvard Forest, Petersham, Massachusetts, USA.

We used path analyses to quantify the relative effects of both diurnally and seasonally varying micro-envi-

ronmental conditions on in situ leaf-level photosynthesis. This was done both within each day across the seasons to quantify the impacts of diurnal variation, and across all days to quantify the impact on photosynthesis of seasonal variation in environmental conditions. Further, we used path analyses to quantify the direct and indirect effects of light levels, air temperatures, and VPD on in situ leaf-level photosynthesis.

The data set described in the present paper represents the first attempt to measure simultaneously at two heights within the canopies of several trees the in situ leaf-level photosynthesis. It also is the first attempt to use path analysis to interpret this type of data set. The simultaneity of observations obtained using several gas-analysis systems allows us to quantitatively compare the photosynthetic performance of the four species' leaves at the two canopy heights.

The goals of this paper are to address the following questions: (1) What is the nature of the diurnal and seasonal differences in the in situ photosynthesis rates of co-occurring mature canopy trees? (2) Can we explain these differences based on the diurnally and seasonally shifting environmental conditions (i.e., light, VPD, temperature)? Does the relative importance of the environmental conditions to photosynthesis shift through the course of the season?

Answers to these questions will help improve understanding of atmosphere–biosphere interactions and facilitate incorporating biological processes in forest carbon-cycle models.

METHODS

Two canopy access towers, 20 m tall and ~40 m apart, were constructed in the Prospect Hill tract of Harvard Forest (42°32' N, 72°11' W, elevation 340 m) in a 60–70 yr old mixed deciduous forest. The stand is in the transition hardwoods–white pine–hemlock zone (Spurr 1956, Westveld et al. 1956), and is comprised mainly of red oak (*Quercus rubra*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), white birch (*B. papyrifera*), beech (*Fagus grandifolia*), white pine (*Pinus strobus*), and hemlock (*Tsuga canadensis*). The towers reached the top of the canopy at ~20 m height. The towers provided access to various heights within the canopies of 1–3 individuals of the four studied species. One canopy tree of each species, red oak, red maple, and yellow birch, were selected and accessible from Tower 1 (T1); and one canopy tree of each species, red oak, red maple, and white birch, were selected and accessible from Tower 2 (T2). To differentiate the individual oak and maple trees, they are hereafter termed "T1" or "T2" trees.

These towers allowed us to repeatedly measure the same individual tree canopies through the course of two years. We chose this sampling scheme to minimize additional variation introduced with the differences between individuals (Bassow and Bazzaz 1997). However, this meant we had to limit destructive sampling,

to avoid excessive damage that might alter the study trees. The towers also allowed us to simultaneously measure foliage at different heights within the same canopies. The two towers were located ~100 m from the Environmental Monitoring Station (EMS) Tower, which has been used to measure CO_2 and H_2O exchange between the forest and atmosphere (Wofsy et al. 1993, Waring et al. 1995, Goulden et al. 1996).

For the six selected trees the diurnal patterns of in situ photosynthesis were measured on seven days over two summer growing seasons. Measurements were also taken at two heights within the canopies. Only uniformly sunlit days were selected, to minimize sources of diurnal heterogeneity. We used four LiCor 6200 Photosynthetic Systems (LI-COR, Lincoln, Nebraska, USA) equipped with 0.25-L chambers. The gas analyzers were calibrated daily, and checked periodically throughout the measurement days. To make these observations, a group of eight people was divided into four teams, one person in each team operated the LI-COR 6200, and the other reached up to 1.5 m from the tower to clamp the chamber on the leaves. Two teams went to the top height of each of two towers, while the other two teams went to a sub-canopy height, as low as possible, while still having access to a substantial number of leaves of each target tree (corresponding to a height of ~12–16 m). The day was broken up into five 2-h periods. During each time period, teams measured the in situ photosynthesis rate of five randomly selected leaves of each of three target trees in no particular order. Between time periods the two teams positioned on one tower, along with their photosynthesis systems, switched canopy heights to avoid confounding machine operators with tower and canopy height. It was not feasible to switch machine-operator teams between the two towers, for safety and logistical reasons. This intense sampling scheme was necessary to capture a snapshot of the patterns of in situ photosynthetic rates at different canopy heights within multiple tree individuals and species.

We attempted to restrict photosynthetic measurements to ambient CO_2 concentrations (340–360 µL/L), and relative humidity levels (30–60%). The time that any leaf was enclosed in the chamber was limited to 60–90 sec to prevent excessive rise in leaf temperature (LI-COR 1990). We repeated the photosynthetic measurements on 7 d over two seasons: 16 July 1991, 22 August 1991, 28 September 1991, 12 June 1992, 10 July 1992, 21 August 1992, and 3 October 1992. On the last date only a portion of the measurements was taken.

Photosynthetic measurements were made from approximately ~0830 to 1800–1900 Eastern Standard Time, depending upon day length. The leaf chambers were manipulated so that leaves were in the same position (i.e., had the same angle and aspect) as before being clamped into the chamber.

Light-saturated photosynthesis rates

Light-saturated photosynthesis rate (P_{max}) was calculated as the mean photosynthesis rate of observations taken with incident light levels above 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD (photosynthetically active photon flux density). This light level was generally saturating for these species as determined from measurements of photosynthetic light-response curves on several leaves of the same trees (Bassow 1995), and from other studies (e.g., Jurik et al. 1988). For red oak that minimum light level corresponded to a photosynthesis rate that was ~80% of the maximally observed values (Bassow 1995). Data from the replicate trees are averaged for illustration purposes. For each date and species, the number of leaves that were used to determine the maximal photosynthesis rate is indicated (Fig. 3). There were insufficient light-saturated observations of leaves from the sub-canopy height for virtually all species (typically 0-3 leaves), so P_{max} estimates were not calculated for the sub-canopy leaf populations.

Data analysis

Tests of the analysis of variance (ANOVAs) and subsequent tests for differences between groups were performed in SuperANOVA (Abacus Concepts, Berkeley, California, USA). All data sets used in ANOVAs were tested for homoscedasticity and normality of residuals (Velleman 1992). Regressions of photosynthesis on conductance were performed in Data Desk v4.2 (Data Descriptions, Ithaca, New York, USA).

Following the procedures of path analysis as described by Li (1981), Sokal and Rohlf (1981), and Schemske and Horvitz (1988), we analyzed the dependence of in situ leaf photosynthesis on several microenvironmental factors. Path analysis is similar to multiple regression and is especially useful when additional causal or correlative information is known about the "independent" variables (Li 1981), such as environmental effects on leaf-level physiology and photosynthesis. Multiple regression is not appropriate when the independent variables are not truly independent or are correlated. To our knowledge, path analysis has not been used for physiological interpretation of in situ photosynthesis patterns, although path analysis has been widely used in ecological interpretation of plant population biology (e.g., Mitchell-Olds 1987, Schemske and Horvitz 1988, Thomas and Weiner 1989, Mitchell 1994), including the effects of inter-annual climate variability (e.g., Walker et al. 1994, Walker et al. 1995).

The path structure we used was created from physiological first principles (e.g., Jones 1992). In path analysis, the thickness of the arrow, or the path value, represents the relative strength of a given relationship. Because the path values are derived from the standardized partial regression coefficients, path values may be quantitatively compared. Thus in the present

case, path analysis will allow us to quantitatively compare the relative influence of the various environmental factors on in situ photosynthesis among species and through the season. While other paths may also be conceptually feasible, our intent was not to explore the relative goodness-of-fit of different models, but instead to identify seasonal shifts in the strength of components of the path diagram. Incident light levels (PAR) were log-transformed to meet the assumption of normality. Other parameters were normally distributed. To calculate values of the paths, we performed four multiple regressions (StatView 4.01, Abacus Concepts, Berkeley, California, USA). The path values for component paths of the multiple regressions were calculated as standardized partial-regression coefficients (photosynthetic rate regressed on conductance, ln(PAR), and leaf temperature; conductance regressed on ln(PAR), and vapor pressure deficit (VPD); VPD regressed on leaf and air temperatures and relative humidity; and leaf temperature regressed on ln(PAR) and air temperature).

Path diagrams were generated for each species, for each date through the season, as well as for all dates pooled together. The two canopy heights were pooled to get a sufficient range of light levels. Pooling dates introduced the seasonal component of variation, which was substantial for certain factors. For example, leaf temperature varied slightly across any given day, but only in certain temperature ranges may it have been particularly influential on photosynthetic rate. However, across the season, leaf temperature varied much more than it varied within a single day. The across-season path diagram can be used to contrast species' differences in the dependence of photosynthesis on specific environmental conditions that may vary seasonally. Leaf ontogeny is obviously confounded with the seasonally varying environmental conditions—a byproduct of this in situ approach.

In addition to the direct effects, we used path analyses to compute the strengths of the indirect influences of a given factor on another. The indirect effects of one factor on another is calculated as the compound path between two variables (see Li [1981] for general methodology for quantifying indirect effects). A compound path between two variables is one that is mediated through another variable (e.g., the compound path between ln(PAR) and photosynthesis rate was mediated by leaf temperature). The strength of a compound path was calculated as the product of the values of the constituent paths. In this path diagram, the indirect effects of light on photosynthesis included the following paths: (1) via leaf temperature, (2) via conductance, and (3) via leaf temperature, VPD, and conductance. The indirect effects of air temperature on photosynthesis were mediated (1) via VPD and conductance, (2) via leaf temperature, and (3) via leaf temperature, VPD, and conductance. The indirect effect of VPD on photosynthesis was simply the compound path via conductance.

RESULTS

Scatter of in situ photosynthesis rates

Photosynthesis rates within a species varied considerably across the day and across the season (Figs. 1–2). Through the course of each day, leaf and air temperatures and vapor-pressure deficits (VPD) varied systematically, reaching maxima at mid to late day. Fig. 1 illustrates the example of red oak; the other species showed slight differences. The light levels associated with each photosynthetic observation showed much greater variability, as would be expected. Particularly at the top of the canopy, the light levels varied from full illumination ($\sim$2000 μmol$\cdot$m$^{-2}\cdot$s^{-1}) to <500 μmol$\cdot$m$^{-2}\cdot$s^{-1}, depending on leaf angle and leaf-to-leaf shading. The pattern of incoming photosynthetic photon flux density (PPFD) set a diurnally and seasonally varying upper limit to the incident light levels reaching measured leaves (e.g., Wofsy et al. 1993). One notable period with reduced incoming PPFD during our observation days was on 29 September 1991, after $\sim$1600, when a thin cloud layer developed.

General trends across the season were also prominent: leaf temperatures, air temperatures, and VPD were all reduced late in the season in late September and early October. Not only did the mean environmental conditions vary through the season, but the pattern of diurnal variation also changed through the season. Early in the season, notably in July 1991, the diurnal variation in leaf and air temperatures and in VPD were quite substantial. For example, leaf temperatures at the top of the canopy of all four species increased through the course of the day by $\sim$6–10°C, and vapor pressure deficit nearly doubled on that day for all four species' top-canopy leaves. Late in the season, these diurnal fluctuations were reduced. In these trees, there was no strong evidence of midday photosynthetic depression (Figs. 1–2). Photosynthesis rates were generally highest in the early morning followed by a continuous decline throughout the day.

Trends in estimated light-saturated photosynthesis rates

Species differed in their light-saturated photosynthesis rates, P_{max} (Fig. 3): the two oak trees and the white birch had the highest P_{max} values, and this group had significantly higher rates than yellow birch, which was higher than the two red maples ($P < 0.05$, Fisher's protected LSD). There was also a significant trend through the seasonal course: all species had the lowest P_{max} values late in the season, and reached their maxima in either July or August of either year. In June P_{max} values were still relatively low, since leaves were presumably still maturing and had only $\sim$75% expanded (Table 1). There were also significant differences between the two years that differed by species.
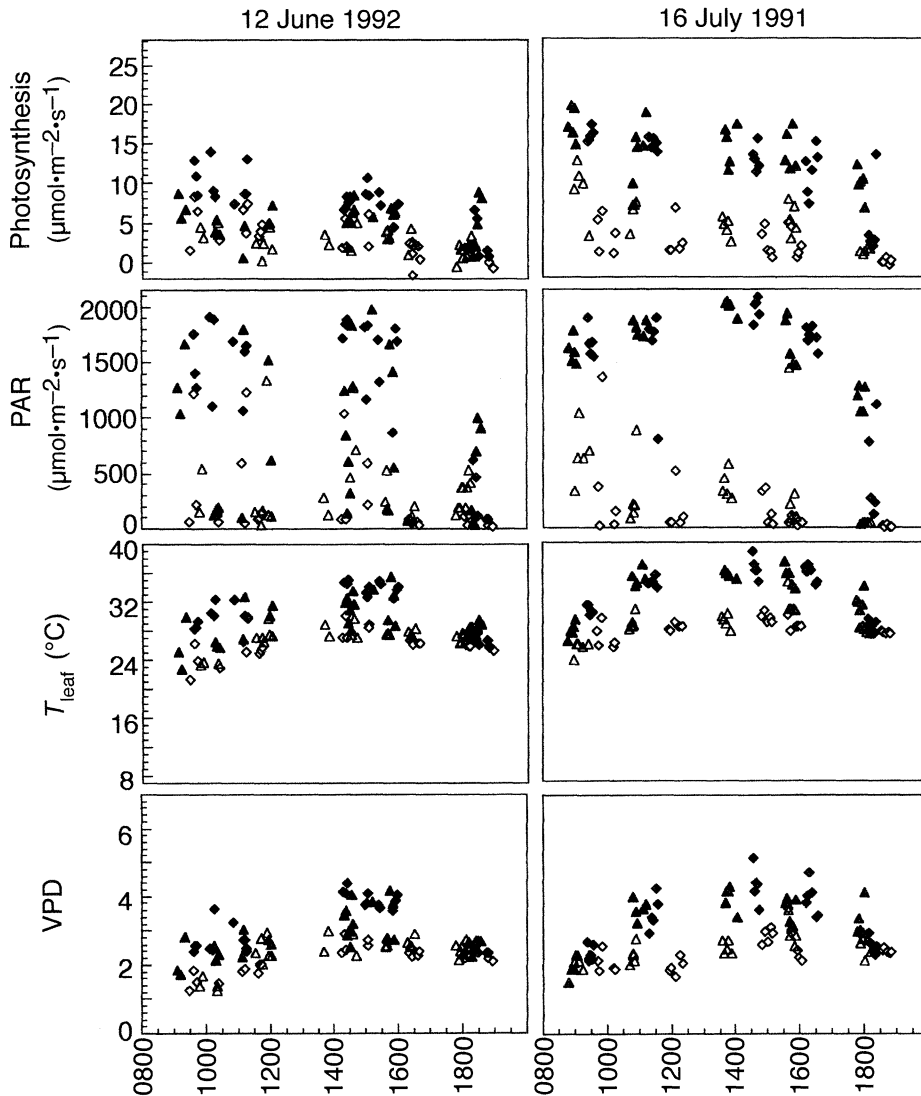
FIG. 1. Diurnal patterns of in situ red oak leaf-level photosynthesis rates at two canopy heights (μmol·m^{-2}·sec^{-1}). Closed symbols refer to canopy-top foliage, and open symbols are sub-canopy foliage. Data collected from both canopy access towers are included. Leaves sampled from the T1 tree are indicated by diamonds, and those sampled from the T2 individual are indicated by triangles. Also shown are light levels (levels of photosynthetically active radiation, PAR), leaf temperature, (T_{leaf}), and vapor-pressure deficit, (VPD). Only four of the seven sampling dates are shown graphically.

Relationship between photosynthesis rate and conductance

As autumnal senescence progressed, photosynthesis declined; stomatal conductance also declined through senescence. The degree to which photosynthesis declined faster than conductance through senescence would decrease a plant's water-use efficiency (WUE). Thus if the trees maintained a high conductivity to water (and CO_2), while the photosynthetic apparatus had declined, the WUE would decline.

To illustrate the relationship between stomatal conductance and in situ photosynthesis rate, we regressed leaf-level photosynthesis rate on conductance, sepa-

rately for each species and canopy height (Table 2). For all dates and both canopy heights for red oak, and virtually all dates for both canopy heights for red maple, the regressions were significant. Further, in most cases, the slopes of the regressions declined through the course of both seasons indicating lower WUE later in the season. Similar trends were evident in the birch canopies as well; however, more of the regressions were either not significant or marginally significant.

Path-analysis model: dependence of in situ photosynthesis rate on environmental factors

We used path analysis for simultaneously analyzing the dependence of photosynthesis on conductance and
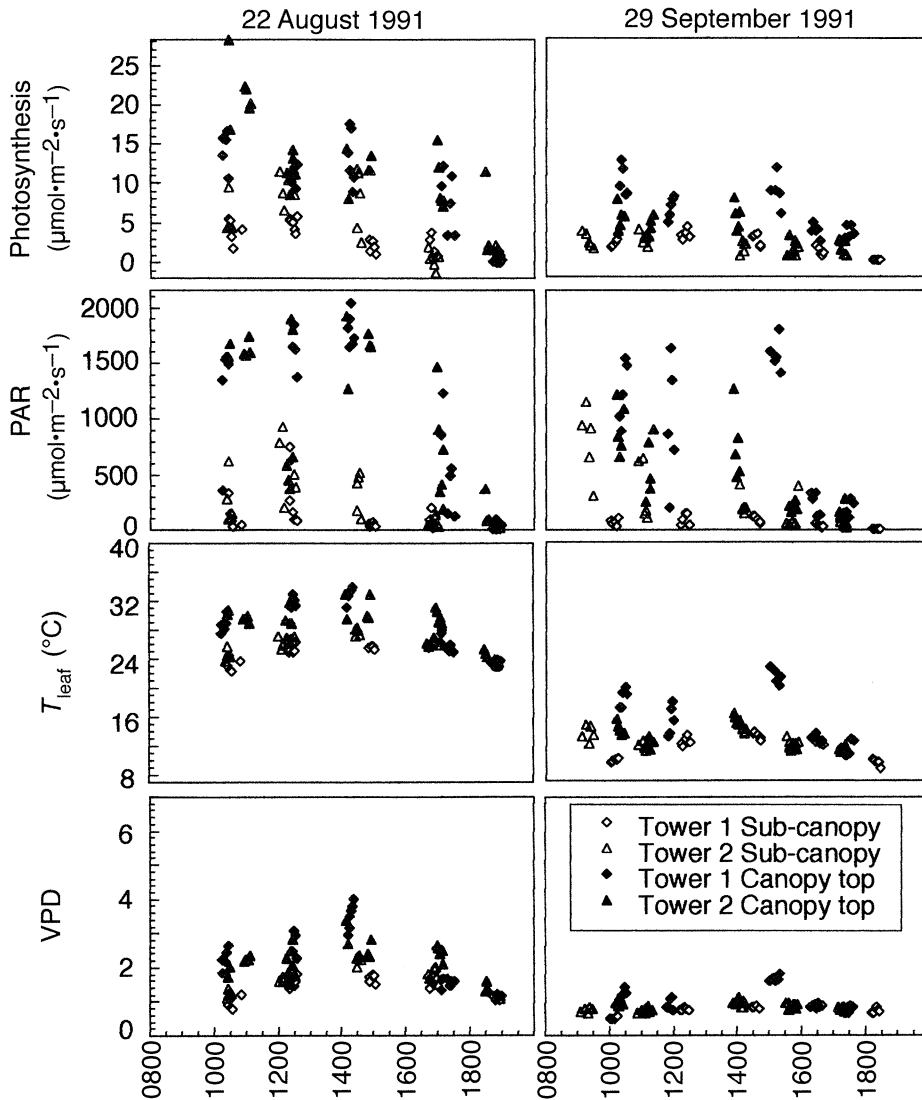
FIG. 1. Continued.

a suite of environmental parameters. Path strengths are illustrated separately for each species in Fig. 4 (only August 1991 is shown as an example). In each diagram, the strength of the path is illustrated as the width of each arrow. The paths were generally significant. While there are many similarities in these path diagrams among the four species (i.e., the very strong and predictable relationship among leaf and air temperature and VPD), there are also several subtle but significant differences among the species. For example, the light-loving, early successional birch species have stronger direct effect of light on photosynthesis than the later successional maple and oak. Conductance has a stronger positive effect on photosynthesis for red oak and maple compared with the birches. Light level has the weakest direct effect on leaf temperature for yellow birch, the most hirsute of the four species.

Fig. 5 illustrates for one species, red oak, the influence of seasonal variation. The first path diagram illustrates the strengths of the relationships of environmental factors to photosynthesis when all dates were considered simultaneously. Thus the first path diagram represents the influence of both the seasonally and diurnally varying environmental conditions on in situ photosynthesis rates. The remaining panels denote the influence of diurnally varying conditions on in situ photosynthesis rates for each date through the season. Only figures for June 1992 and for July, August, and September 1991 are shown.

In red oak the direct effects of leaf temperature on the photosynthesis rate for a single day were low through most of the season or even nonsignificant, until September 1991, when this path reached a maximum strength (Fig. 5). This date corresponded with the low-
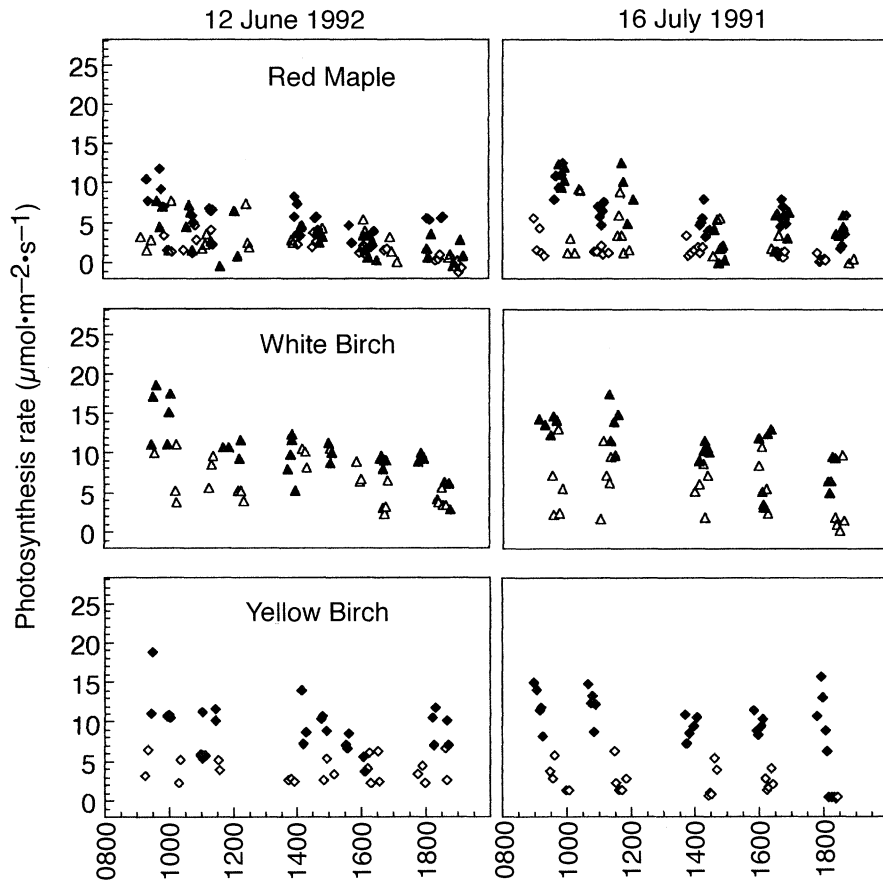
FIG. 2. Diurnal patterns of in situ leaf-level photosynthesis rates at two canopy heights for three tree species. Symbols are as described in Fig. 1.

est temperatures (Fig. 1). Consequently, across all dates, the strength of the leaf-temperature effect on photosynthesis in red oak was moderate. Yellow birch showed a similar pattern.

In red maple and white birch within any single date, the direct effect of leaf temperature on photosynthesis rate was generally either not significant or weakly negative (July 1991). Across all dates together, leaf temperature had a slight but significant positive effect on both red maple and white birch photosynthesis rate. Thus for these cases, the temperature range within any single date was not great enough for temperature to influence photosynthesis rate; only across the season was there sufficient range to result in a positive effect of temperature on photosynthesis.

In addition to examining the direct effects of the environmental parameters on in situ photosynthesis, we also calculated the total indirect effects of light levels, air temperatures, and VPD on photosynthesis. Fig. 6 illustrates the seasonal trends of the direct and indirect effects of incident light levels and the total indirect effects of air temperature and VPD on the in situ photosynthesis rate separately for each species. White birch showed the most consistent trends across the sea-

son in the magnitude of these direct and indirect types of effects: the direct effects of light on photosynthesis were the strongest throughout the season, while the indirect effects of VPD were uniformly the most negative across the season. For the other three species, the relative strengths of the effects varied. For all four species, on the dates when the direct effects of light on photosynthesis were relatively high, the indirect effects were relatively low, thereby making the total effect of light approximately constant and high across the season.

The total indirect effects of measured air temperatures on photosynthesis were generally lower than the direct or the indirect effects of light on photosynthesis (particularly when considering the total of direct and indirect combined effect of light). On the last date in 1991, however, oak was particularly sensitive to the cold temperatures, indicated by the relatively high total indirect effects of air temperature on photosynthesis (Fig. 6). In other words, the temperature was low enough to reduce oak's apparent photosynthesis rate. Similarly, but in the opposite direction, red maple was particularly sensitive to the air temperature in July 1991; on that day, the higher air temperature corre-
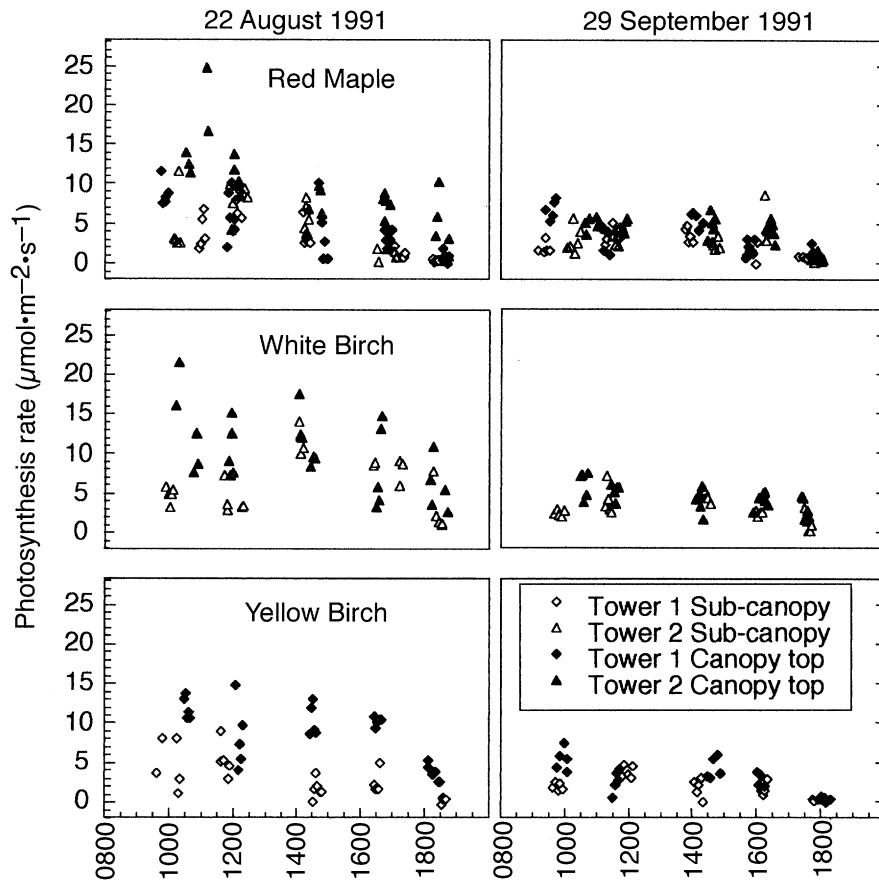
FIG. 2.   Continued.

sponded with lower photosynthesis rates for red maple leaves.

Across the season the birches had the highest total indirect effects of air temperature on photosynthesis (Fig. 7). Oak had a lower total indirect effect of air temperature, while red maple even had a negative effect of air temperature on photosynthesis across the season. This negative value implied that the higher the temperature, the lower the photosynthesis rate. Oak had the lowest direct effects of light (Fig. 7); however, it also had the highest indirect effects of light so that the four species had fairly similar total effects of light on in situ photosynthesis.

In most species and on most dates, the compound path relating VPD and in situ photosynthesis was negative, implying that higher VPDs were associated with lower photosynthesis rates (Figs. 6 and 7). Across the season, red maple had the greatest magnitude negative indirect effect of VPD on photosynthesis of the four species. Red maple had either the greatest negative, or second-to-greatest negative indirect effect of VPD on photosynthesis in all mid-growing season months.

DISCUSSION

In this paper, we used an extensive sample of in situ leaf-level photosynthetic observations to describe the complex physiological responses of a mixed deciduous forest canopy to daily and seasonal environmental variation. We found that leaf-level photosynthesis resulted from the interaction of various environmental factors and the species-specific sensitivity to these factors. The high replication of photosynthetic observations measured simultaneously at two heights in the canopies of several trees allowed us to quantify the relative magnitude of the effects of diurnally and seasonally varying environmental conditions on in situ photosynthesis. To our knowledge, no other single study has used this level of replication to simultaneously compare multiple tree species' canopy photosynthesis, across diurnally and seasonally varying environmental conditions. This approach is essential for describing how environmental conditions differentially influence in situ photosynthesis in different co-occurring tree species.

In situ leaf-level physiology: importance of species differences

This paper demonstrates the influence of environmental conditions on species-specific photosynthesis rates. Most temperate forests are mixtures of many different tree species. Global climate change or other major disturbance may lead to substantial shifts in species
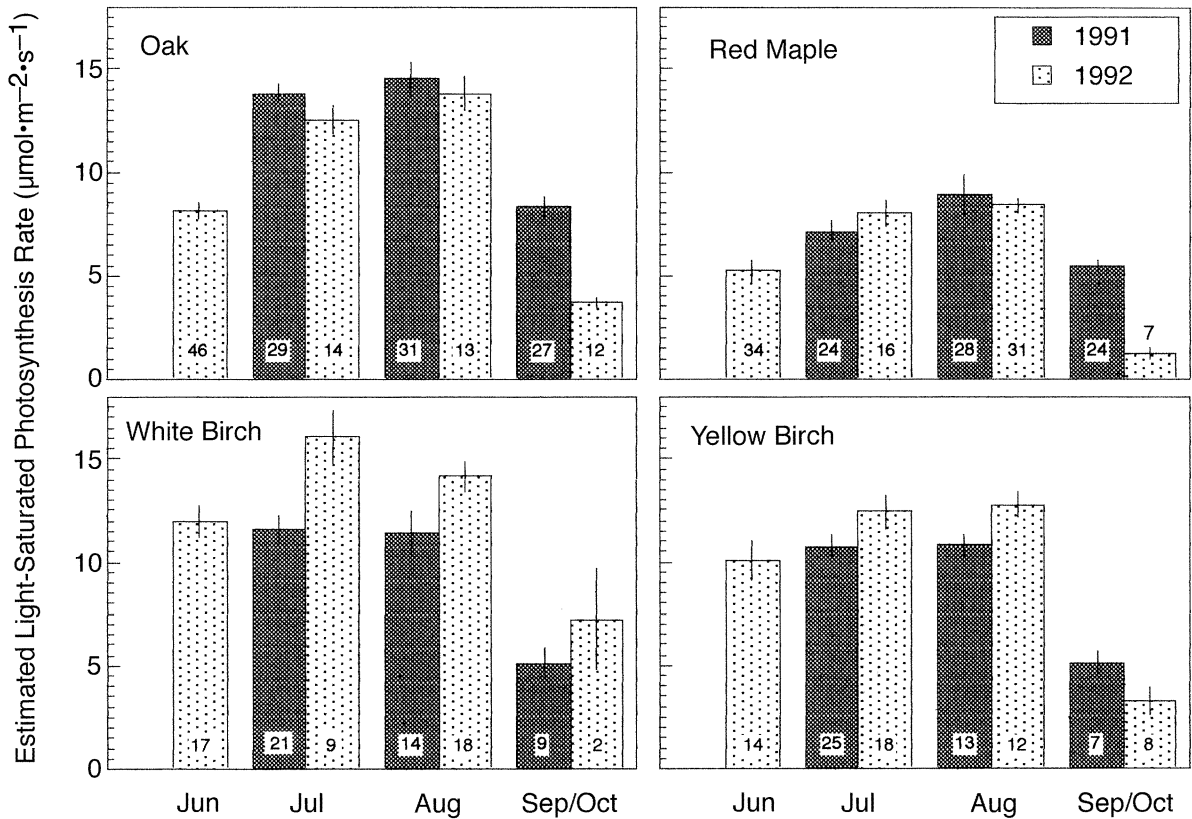
FIG. 3.   Seasonal patterns of light-saturated photosynthesis rates, P_{max}, indicated separately for each tree species. Observations from replicate oak and red maple trees are pooled together. Only the canopy-top foliage was considered for estimating P_{max}. The number of in situ leaf-level observations used to approximate the P_{max} values is indicated within each bar in the figure. Error bars represent ± 1 SE of the mean estimate.

composition, which in turn will have implications for forest carbon cycles (e.g., Bazzaz et al. 1996). Incorporating data on the physiological differences among tree species into forest carbon models will greatly improve our ability to predict alterations to the forest

carbon budgets under various environmental scenarios or with differing species composition.

Specifically, red oak and white birch canopy tops had the highest estimated maximal photosynthesis rates. The light-saturated photosynthesis rate (P_{max}) of

TABLE 1.   Leaf phenology of the four tree species for 1991 and 1992. Data were provided by John O'Keefe (Harvard Forest) and were collected by daily visual inspection at Harvard Forest, Petersham, Massachusetts, USA.

	Canopy development			Autumnal senescence		
Year	Bud break	75% leaf expansion	95% leaf expansion	Color-change onset	10–25% leaf drop	98% leaf drop
Red oak						
1991	8 May	23 May	4 Jun	25 Sep	20 Oct	3 Nov
1992	14 May	11 Jun	3 Jul	29 Sep	23 Oct	5 Nov
Red maple						
1991	3 May	22 May	31 May	13 Sep	3 Oct	11 Oct
1992	12 May	18 Jun	5 Jul	3 Sep	29 Sep	23 Oct
White birch						
1991	26 Apr	18 May	31 May	18 Sep	8 Oct	24 Oct
1992	11 May	12 Jun	26 Jun	23 Oct	23 Oct	5 Nov
Yellow birch						
1991	27 Apr	21 May	31 May	12 Sep	3 Oct	10 Oct
1992	11 May	12 Jun	27 Jun	16 Sep	⋯	23 Oct

TABLE 2. Regression coefficients of in situ leaf-level photosynthesis rate (μmol·m^{-2}·s^{-1}) regressed against conductance (mol·m^{-2}·s^{-1}).

	Sub-canopy				Canopy top			
Date	Intercept	Slope	R^2	P	Intercept	Slope	R^2	P
Oak								
16 Jul 1991	−0.26	36.56	0.63	****	3.73	31.22	0.73	****
22 Aug 1991	−0.29	34.17	0.79	****	0.19	37.79	0.78	****
28 Sep 1991	−0.12	19.24	0.50	****	0.79	26.77	0.29	****
12 Jun 1992	0.57	30.20	0.35	****	0.75	47.44	0.55	****
10 Jul 1992	0.82	19.73	0.24	***	3.36	30.07	0.44	****
22 Aug 1992	1.81	9.40	0.10	*	5.78	16.62	0.31	****
3 Oct 1992	···	···	···		1.98	30.15	0.27†	**
Red maple								
16 Jul 1991	−0.16	51.39	0.57	****	1.21	60.99	0.89	****
22 Aug 1991	1.35	20.09	0.30	****	−0.05	55.18	0.75	****
28 Sep 1991	0.96	18.34	0.27	****	1.23	24.83	0.13	*
12 Jun 1992	−0.02	37.68	0.52	****	−1.08	81.84	0.76	****
10 Jul 1992	1.56	21.94	0.41	****	1.41	62.64	0.71	****
22 Aug 1992	0.12	28.79	0.39	****	4.36	26.94	0.25	****
3 Oct 1992	−1.05	46.04	0.58‡	NS	0.20	15.90	0.23§	+
White birch								
16 Jul 1991	1.81	21.98	0.30	**	1.94	44.27	0.81	****
22 Aug 1991	1.43	17.77	0.24	*	2.72	25.23	0.44	***
28 Sep 1991	−1.04	20.53	0.34	**	−1.19	24.17	0.41	***
12 Jun 1992	4.93	8.68	0.07	NS	2.96	34.25	0.40	***
10 Jul 1992	3.59	11.55	0.22	*	10.39	10.40	0.07	NS
22 Aug 1992	1.89	14.30	0.21	*	6.52	17.70	0.23	**
3 Oct 1992	···	···	···		−1.29	52.57	0.83‡	*
Yellow birch								
16 Jul 1991	0.64	17.50	0.11	NS	4.09	27.90	0.67	****
22 Aug 1991	−0.91	33.10	0.48	****	0.94	25.06	0.23	**
28 Sep 1991	−0.21	19.53	0.46	***	0.73	10.95	0.17	*
12 Jun 1992	1.12	29.88	0.40	***	3.52	28.56	0.70	****
10 Jul 1992	3.60	4.48	0.01	NS	5.03	25.06	0.52	****
22 Aug 1992	−0.83	20.94	0.13	+	11.81	1.41	0.00	NS
3 Oct 1992	···	···	···		−1.10	30.19	0.20‖	+

Notes: Significance of each regression is indicated as follows: $+P < 0.10$, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, $****P < 0.0001$; NS, not significant. Sample size for each regression was 50 observations for oak and red maple and 25 observations for white birch and yellow birch, with exceptions for 3 October 1992, for which sample sizes are noted. Ellipses indicate that no data are available.
† 23 observations.
‡ 5 observations.
§ 17 observations.
‖ 15 observations.

the yellow birch canopy top was intermediate, and that of the red maple canopy tops was lowest of the four species considered. This ranking is the same as Jurik et al. (1988) observed in Michigan for red oak, white birch, and red maple. However, we found considerably higher light-saturated photosynthesis rates, particularly in some months, for red oak and white birch than did Jurik et al. (1988). This difference is likely explained by the canopy height of the measured foliage: we estimated P_{max} for canopy-top foliage only (~20 m), and Jurik et al. (1988) measured foliage at 2–14 m, only some of which corresponded to the canopy top.

Generally, early successional species within a system have higher P_{max} (often on an area basis, and especially on a mass basis) and lower leaf mass per area (LMA) than later successional species (e.g., Bazzaz 1979, 1996, Koike 1988, Reich et al. 1995). White birch is

the earliest successional, most shade-intolerant species of the four species in our study; red oak and yellow birch have intermediate shade tolerance and are considered mid- to late-successional species; and red maple is fairly shade tolerant and is considered a subclimax species (Burns and Honkala 1990). However, in the present study we found that the successional status only partially corresponded with the ranking of maximal photosynthesis rates on an area basis. Further, the strength of this association depended on the time of year and year-to-year differences in phenology, weather, and other conditions in the temperate forest.

In a separate study, using a larger sample size of individual trees of each species, and several other species as well, we also found a similar ranking of these species' maximal photosynthesis rates (Bassow and Bazzaz 1997). Moreover, and despite significant dif-
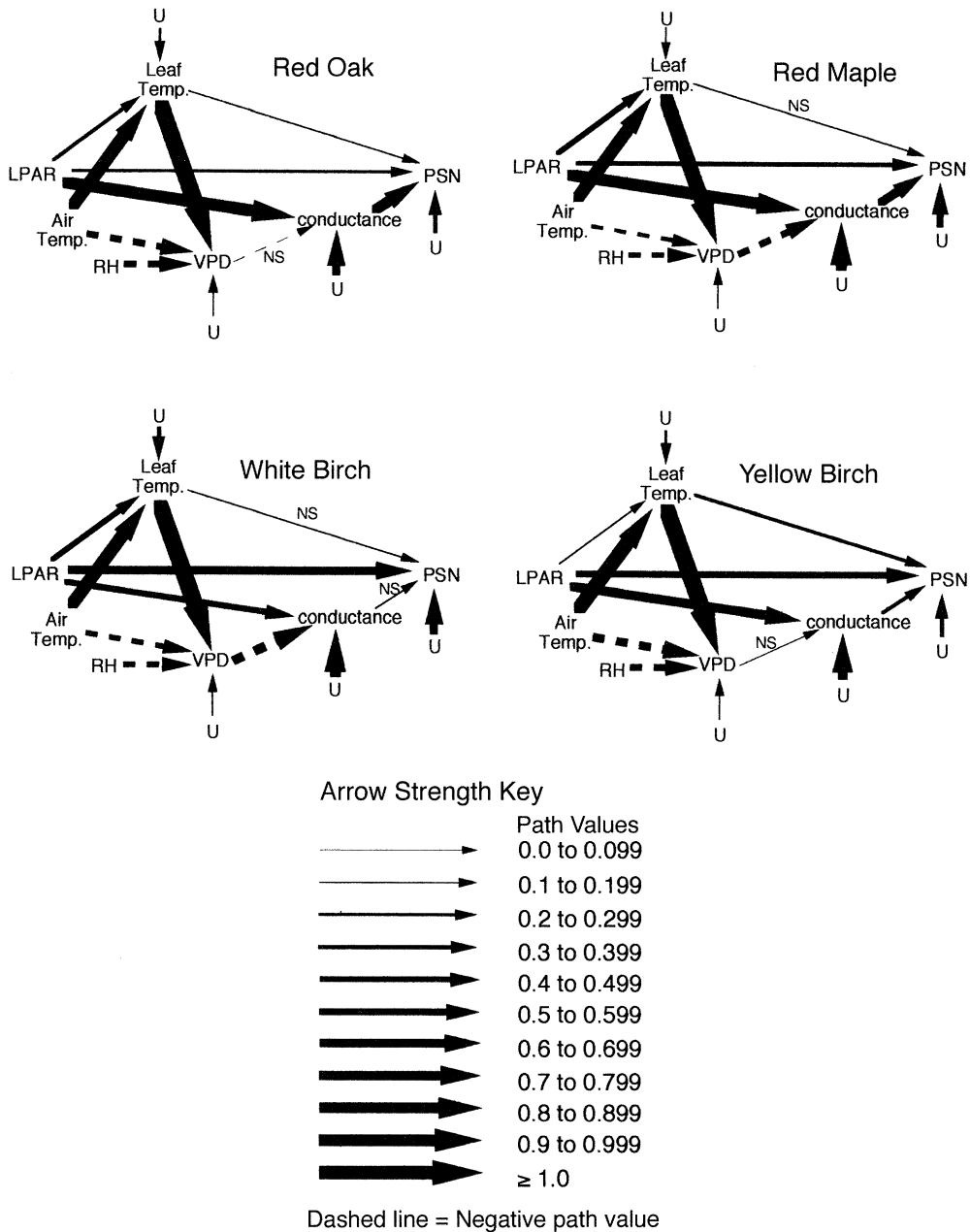
FIG. 4. Path diagrams for describing the dependence of red oak, red maple, yellow birch, and white birch in situ leaf-level photosynthesis on environmental conditions for August 1991. Both canopy heights are considered together. The thickness of the arrows represents the path value. Paths that are not significant at $P < 0.05$ are indicated as "NS"; all other paths are significant at the $P < 0.05$ level. Abbreviations are as follows: LPAR = ln(in situ light level) (μmol·m^{-2}·s^{-1}), Leaf Temp. = leaf temperature (°C), Air Temp. = air temperature (°C), RH = relative humidity (%), VPD = vapor-pressure deficit, conductance = leaf-level conductance (mol·m^{-2}·s^{-1}), and PSN = in situ photosynthesis rate (μmol·m^{-2}·s^{-1}); U represents the residual terms.

ferences among individual trees of a given species, differences were significantly greater between species than between trees within a species. Based on our other studies with extensive sampling of individual trees, we conclude that the few trees that were measured repeatedly through the course of two years for the present study, were indeed representative of other con-specific individual trees in the stand (Bassow and Bazzaz 1997).

In our present study we found that species' photosynthetic responses differed over the growing season. Light-saturated photosynthesis reached maximum values at different points through the growing season
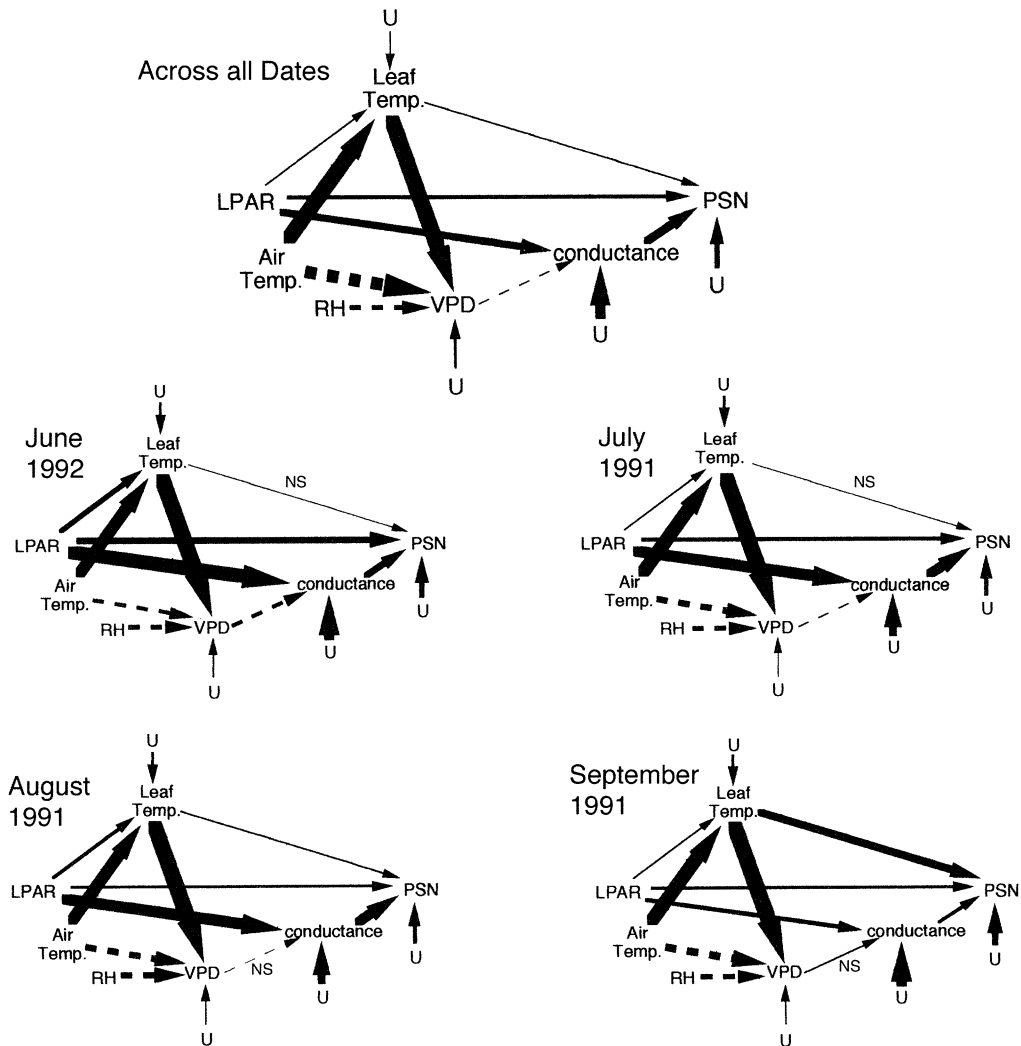
FIG. 5. Path diagrams for describing the dependence of red oak in situ leaf-level photosynthesis on environmental conditions. The top diagram is for all dates through the two seasons considered together. The other four diagrams illustrate the seasonal spectrum. Symbols and path arrow key are as in Fig. 4.

among the different species (Fig. 3). Notably, red oak did not reach maximal rates until late in the season in August; its P_{max} rates in June were still relatively low even though the leaves had expanded at least 75%, and in July red oak P_{max} remained sub-maximal even though the leaves had fully expanded (Table 1 and Fig. 3). In contrast, birch species reached near maximal P_{max} rates upon full expansion in June. For a number of deciduous tree species in Northern Michigan (including red oak and red maple), Jurik (1986) found that all species he measured reached their maximal P_{max} in early June near the completion of leaf expansion. Similarly for white oak, the highest maximal photosynthesis rate was observed at 100% leaf expansion in early June (Dougherty et al. 1979). However, in that study the date in June also corresponded with the last date of observation,

obscuring the possibility that P_{max} may have continued to increase after full leaf expansion.

Environmental influences on species-specific photosynthesis

In situ patterns of leaf-level photosynthesis consist of interactions between the suite of ambient environmental conditions and the species-specific sensitivity to the combination of those factors. In other words, the environmental conditions may have been similar surrounding the trees studied here, but the trees' photosynthetic responses were different. Path diagrams clearly demonstrate that environmental conditions had some similar and some different effects on different species. These different environmental effects on species, while relatively subtle, may have led to the sig-
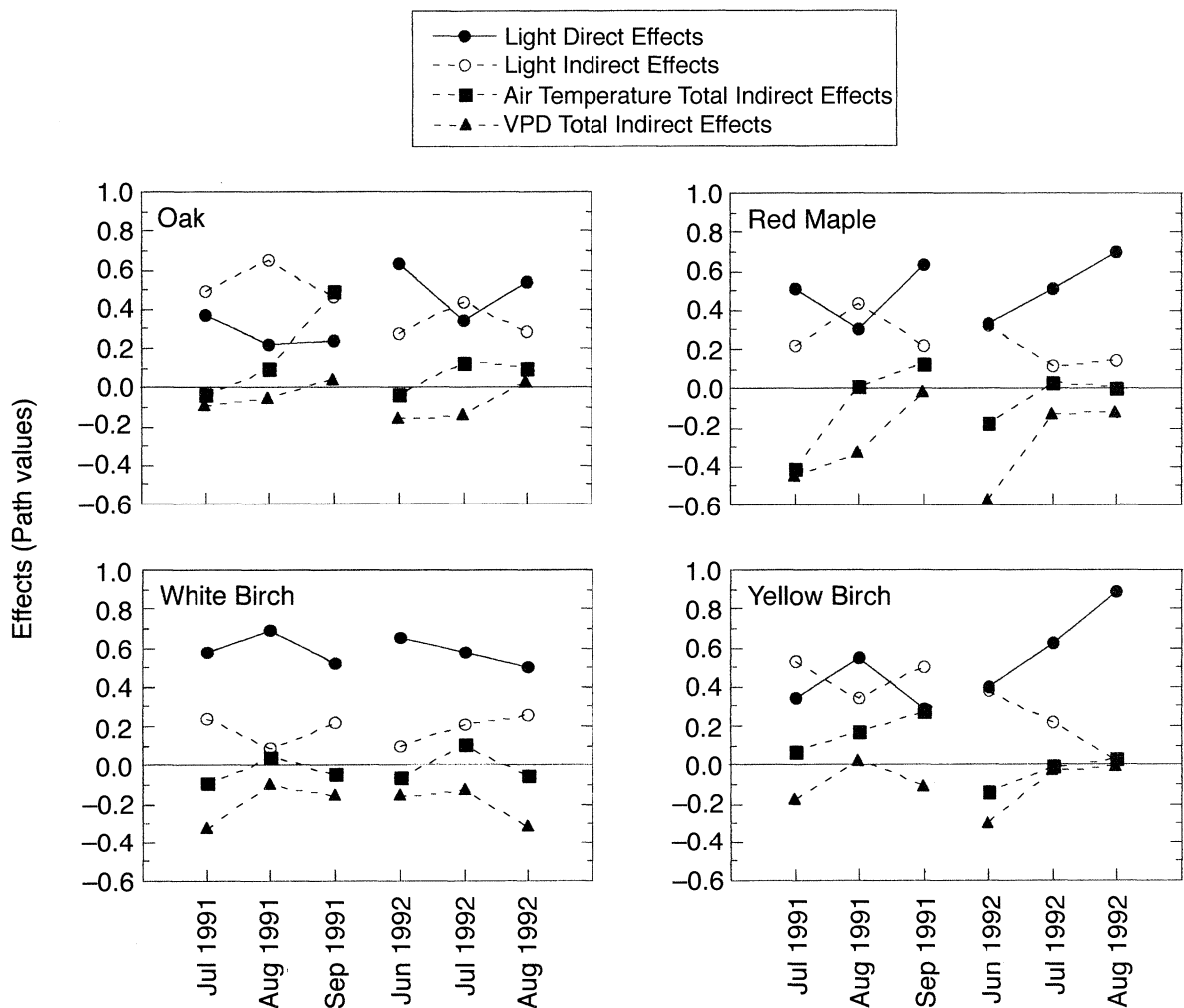
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FIG. 6. Summary of the seasonal patterns of the path values for the direct and indirect effects of light levels and the total indirect effects of air temperature and vapor-pressure deficit (VPD) on photosynthesis, for four tree species.

nificant variation found among years in forest carbon exchange (i.e., environmental factors altering net primary production [NPP] and soil respiration; Goulden et al. 1996). Species-specific responses to environmental factors may explain Goulden et al.'s (1996) finding that net ecosystem exchange of carbon (NEE) in Harvard Forest varied between 1.4 and 2.8 metric tons during the period 1991–1995. Goulden et al. (1996) explain the year-to-year variation simply as a result of climate variations. The extent to which species-specific sensitivities to these climate variations further explain annual differences in net ecosystem CO_2 exchange warrants further examination.

Path diagrams illustrate relationships that are both physiological and simply physical in nature. The strongest paths in many cases simply reflect the physical relationships between the parameters. For example, the relationship between leaf and air temperatures and VPD (vapor-pressure deficit) were very strong for all

species within a single date as well as across the season (Figs. 4 and 5). However, more interesting are the subtle physiological differences among the species. For example, the direct influence of light levels on leaf temperature, when calculated for the whole season, was very weak for all four species; obviously the seasonal variation in leaf temperature was more attributable to the seasonal variation in ambient air temperature than it was to the light levels. However, the diurnal influence of incident light levels on leaf temperature was stronger than the seasonal influence, particularly for red maple and white birch. For red oak, on the other hand, conductance tended to be the highest of the four species. High conductance may have been associated with high transpiration rates that cooled the leaves, thereby offsetting the influence of incident light levels on leaf temperature, particularly at some times of the season. Yellow birch had the weakest dependence of leaf temperature on incident light levels (Fig. 4). Yellow birch
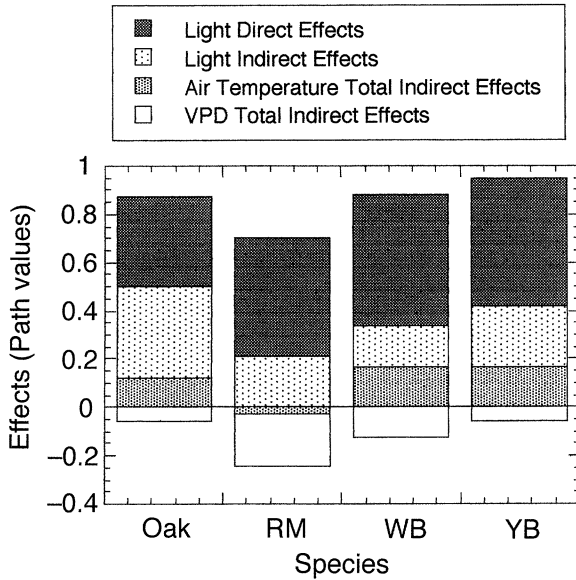
FIG. 7. The direct and indirect effects of light and the total indirect effects of air temperature and vapor-pressure deficit (VPD) on the in situ photosynthesis rates from path models across all dates together, for four tree species (RM = red maple, WB = white birch, YB = yellow birch).

is the most hirsute and textured of the four species, both features perhaps acting to reduce the leaf heating due to incident sunlight.

While many of the physical relationships are very strong, they should not draw attention away from the paths relating the physical environment to plant physiological responses. In red oak, the direct effects of measured leaf temperatures on the photosynthesis rate were very slight through most of the season, reaching a maximum strength in September 1991, when the temperatures were lowest (Figs. 1 and 5). When the temperature was in a relatively warm range, the leaf temperature had only a modest effect on the in situ red oak rate of photosynthesis; however, when the temperatures were low enough, the leaf temperature had a stronger positive effect on photosynthesis rate. However, aggregating across all dates, the strength of the leaf-temperature effect on red oak photosynthesis was moderate.

From the path analysis, we cannot conclude anything about seasonally shifting optimal temperatures for photosynthesis; we did not measure direct temperature response of photosynthesis with all other conditions held constant. However, we did observe natural diurnal ranges of temperatures through the growing season. Consequently, strong path values of temperature effects on photosynthesis late in the season indicate that the observed temperatures in September correspond with a steep portion of the temperature–photosynthesis response curve.

Species differed in the extent to which environmental conditions influenced the stomatal control of conduc-

tance. In all species in our study, the patterns of diurnal photosynthetic variation did not show substantial midday depressions, which often result from midday stomatal closure (cf. Tenhunen et al. 1987, Weber and Gates 1990). Rather photosynthesis rates declined fairly steadily following their morning maxima. In general, photosynthetic measurements were made on days that were not preceded by severe droughts, or other extreme weather, in which case we might have seen more pronounced midday reductions in photosynthesis.

While there was not a consistent and large midday depression in photosynthesis, all four species did exhibit a modest steady decline in canopy-top photosynthesis over the day, only in part due to slight declines in light levels (see Figs. 1 and 2). This reduction may have been due to any or all of the observed environmental conditions. Additionally, the daily accumulation of starch and carbohydrates may have led to a feedback inhibition of photosynthesis (cf. Herold 1980). This observed diurnal decline in photosynthesis rates in these trees corroborates our observation (Wofsy et al. 1993) that, at a given light level, the net ecosystem-level CO_2 uptake (NEE) was greater in the morning than in the afternoon. The reduced late-afternoon photosynthesis rates may also be explained by the higher respiration rates later in the day due to higher temperatures. Respiration generally is more temperature dependent than is photosynthesis (e.g., Amthor 1991).

Species–specific differences in the photosynthetic responses to conductance are visible in the path diagrams (Fig. 5). Among the four species, red oak and red maple had the strongest positive direct effects of conductance on photosynthesis, both across the season and within each day. Photosynthesis rates may have been limited by lower conductance in these two species. Additionally, red maple had some of the strongest negative relationships between VPD and conductance, both across the season and within each date. A high vapor-pressure deficit may have reduced conductance and then subsequently photosynthesis as well. This is quantified as the indirect effects of VPD on photosynthesis (Figs. 6 and 7). Red maple did indeed have the greatest negative effect of VPD on photosynthesis, both across the season and within each date (Figs. 6 and 7). Thus, the higher VPDs for red maple leaves did lead to reduced in situ photosynthesis rates, relative to the other three species studied.

Additionally, red maple had a negative value for the total indirect effect of air temperature on photosynthesis across the season (Fig. 7). That species' low conductance may have reduced its capacity for transpirational cooling. The reduced cooling capacity probably led to relatively higher leaf temperatures, which in turn may have led to reduced photosynthesis rates either directly or indirectly via VPD stress (Figs. 4 and 6). Incorporating these different physiological strategies into models of forest function would improve the models' predictive capacity.

It should also be noted that there was a high degree of leaf-to-leaf variation in in situ photosynthesis; not all leaves were contributing equally toward the net canopy CO_2 uptake. For all four species throughout the season there were obvious differences between the canopy heights in terms of light levels, leaf temperatures, and VPD experienced—although overall the variation observed in incident light level was greater than that observed in the other environmental factors (Fig. 1). We also observed significant differences in leaf structure, namely, leaf nitrogen content and LMA, between the canopy heights (Bassow 1995). Such vertical differences in leaf-level structure and function may also be necessary to incorporate into models of canopy photosynthesis in complex forest canopies (Ellsworth and Reich 1993).

We also observed a strong seasonal trend in leaf temperature and consequently VPD. Nevertheless, across all dates there was a much stronger combined direct and indirect effect of light than the total indirect effect of air temperature on in situ photosynthesis (Fig. 7). While air temperature had a strong effect on photosynthesis across the season, light levels had a stronger effect, particularly the direct effects of light.

Conclusion

The net photosynthesis in a mixed deciduous forest is largely determined by the canopy trees. We have shown that the component species of an ecosystem can contribute substantially differentially to the net ecosystem photosynthetic uptake: P_{max} (the light-saturated photosynthesis rate) is significantly different among canopy tree species. We have also demonstrated that in some cases co-occurring tree species' photosynthesis is differentially affected by environmental conditions that vary both diurnally and seasonally. This level of complexity is helpful to consider in models that hope to use physiological principles to predict ecosystem-level photosynthetic uptake and allows us to appreciate the importance of tree species composition and their differential sensitivities to environmental conditions on forest carbon exchange.

LITERATURE CITED

Amthor, J. S. 1991. Respiration in a future, higher-CO_2 world. Plant Cell and Environment 14:13–20.

Bassow, S. L. 1995. Canopy photosynthesis in a deciduous forest: Implications of shifts in species composition and rising concentrations of CO_2. Dissertation. Harvard University, Cambridge, Massachusetts, USA.

Bassow, S. L. and F. A. Bazzaz. 1997. Intra- and inter-specific variation in canopy photosynthesis in a mixed deciduous forest. Oecologia 109:507–515.

Bazzaz, F. A. 1979. The physiological ecology of plant succession. Annual Review of Ecology and Systematics 10: 351–371.

———. 1996. Plants in changing environments: linking physiological, population, and community ecology. Cambridge University Press, Cambridge, UK.

Bazzaz, F. A., S. L. Bassow, G. M. Berntson, and S. C. Thomas. 1996. Elevated CO_2 and terrestrial vegetation: implications for and beyond the global carbon budget. Pages 43–76 in B. Walker and W. Steffen, editors. Global change and terrestrial ecosystems. Cambridge University Press, Cambridge, UK.

Boardman, N. K. 1981. Comparative photosynthesis of sun and shade plants. Annual Review of Ecology and Systematics 28:355–377.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North American trees. Volume 2. Hardwoods. U.S. Department of Agriculture, Washington, D.C., USA.

Cooper, A. W. 1981. Above-ground biomass accumulation and net primary production during the first 70 years of succession in Populus grandidentata stands on poor sites in Northern Lower Michigan. Pages 324–338 in D. C. West, H. H. Shugart, and D. B. Botkin, editors. Forest succession: concepts and applications. Springer-Verlag, New York, New York, USA.

Dougherty, P. M., R. O. Teskey, J. E. Phelps, and T. M. Hinkley. 1979. Net photosynthesis and early growth trends of a dominant white oak (Quercus alba L.). Plant Physiology 64:930–935.

Ellsworth, D. S., and P. B. Reich. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. Oecologia 96:169–178.

Givnish, T. J. 1988. Adaptation to sun and shade: a whole-plant perspective. Australian Journal of Plant Physiology 15:63–92.

Goulden, M. L., J. W. Munger, S.-M. Fan, B. C. Daube, and S. C. Wofsy. 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. Science 271:1576–1578.

Hanson, P. J., L. J. Samuelson, S. D. Wullschleger, T. A. Tabberer, and G. S. Edwards. 1994. Seasonal patterns of light-saturated photosynthesis and leaf conductance for mature and seedling Quercus rubra L. foliage: differential sensitivity to ozone exposure. Tree Physiology 14:1351–1366.

Herold, A. 1980. Regulation of photosynthesis by sink activity–the missing link. New Phytologist 86:131–144.

Houghton, J. T. 1991. The role of forests in affecting the greenhouse gas composition of the atmosphere. Pages 43–56 in R. L. Wyman, editor. Global climate change and life on Earth. Chapman & Hall, New York, New York, USA.

Jones, H. G. 1992. Plants and microclimate: a quantitative approach to environmental plant physiology. Second edition. Cambridge University Press, Cambridge, UK.

Jurik, T. W. 1986. Seasonal patterns of leaf photosynthetic capacity in successional northern hardwood tree species. American Journal of Botany 73:131–138.

Jurik, T. W., J. A. Weber, and D. M. Gates. 1988. Effects of temperature and light on photosynthesis of dominant

species of a northern Hardwood Forest. Botanical Gazette **149**:203–208.

Koike, T. 1988. Leaf structure and photosynthetic performance as related to the forest succession of deciduous broad-leaved trees. Plant Species Biology **3**:77–87.

Lei, T. T., and M. J. Lechowicz. 1990. Shade adaptation and shade tolerance in saplings of three *Acer* species from eastern North America. Oecologia **84**:224–228.

Li, C. C. 1981. Path analysis: a primer. Third edition. Boxwood Press, Pacific Grove California, USA.

LI-COR. 1990. LI-COR operating manual for the LI-6200. LI-COR, Lincoln, Nebraska, USA.

Marek, M., E. M. Kratochvílová, P. Eliás, and D. Janous. 1989. Stand microclimate and physiological activity of tree leaves in an oak–hornbeam forest. II. Leaf photosynthetic activity. Trees **4**:234–240.

Mitchell, R. J. 1994. Effects of floral traits, pollinator visitation, and plant size on *Ipomopsis aggregata* fruit production. American Naturalist **143**:870–889.

Mitchell-Olds, T. 1987. Analysis of local variation in plant size. Ecology **68**:82–87.

Peet, R. K. 1981. Changes in biomass and production during secondary forest succession. Pages 324–338 *in* D. C. West, H. H Shugart, and D. B. Botkin, editors. Forest succession: concepts and application. Springer-Verlag, New York, New York, USA.

Pereira, J. S., J. D. Tenhunen, O. L. Lange, W. Beyschlag, A. Meyer, and M. M. David. 1986. Seasonal and diurnal patterns in leaf gas exchange of *Eucalyptus globus* trees growing in Portugal. Canadian Journal of Forest Research **16**:177–184.

Reich, P. B., D. S. Ellsworth, and C. Uhl. 1995. Leaf carbon and nutrient assimilation and conservation in species of differing successional status in an oligotrophic Amazonian forest. Functional Ecology **9**:65–76.

Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1991. Leaf age and season influence the relationships between leaf nitrogen, leaf mass per area, and photosynthesis in maples and oak trees. Plant Cell and Environment **14**:251–259.

Schemske, D. W., and C. C. Horvitz. 1988. Plant–animal interactions and fruit production in a neotropical herb: a path analysis. Ecology **69**:1128–1137.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Second edition W. H. Freeman, San Francisco, California, USA.

Spurr, S. H. 1956. Forest associations of the Harvard Forest. Ecological Monographs **26**:245–262.

Tenhunen, J. D., R. W. Pearcy, and O. L. Lange. 1987. Diurnal variations in leaf conductance and gas exchange in natural environments. Pages 323–351 *in* E. Zeigler, G. D. Farquhar, and I. R. Cowan, editors. Stomatal function. Stanford University Press, Stanford, California, USA.

Thomas, S. C., and J. Weiner. 1989. Including competitive asymmetry in measures of local interference in plant populations. Oecologia **80**:349–355.

Velleman, P. F. 1992. Data desk 4.2 handbook. Data Descriptions, Ithaca, New York, USA.

Walker, M. D., R. C. Ingersoll, and P. J. Webber. 1995. Effects of interannual climate variation on phenology and growth of two alpine forbs. Ecology **76**:1067–1083.

Walker, M. D., P. J. Webber, E. H. Arnold, and D. Ebert-May. 1994. Effects of interannual climate variation on aboveground phytomass in alpine vegetation. Ecology **75**:393–408.

Waring, R. H., B. E. Law, M. L. Goulden, S. L. Bassow, R. W. McCreight, S. C. Wofsy, and F. A. Bazzaz. 1995. Scaling gross ecosystem production at Harvard Forest with remote sensing: a comparison of estimates from a constrained quantum-use efficiency model and eddy correlation. Plant Cell and Environment **18**:1201–1213.

Weber, J. A., and D. M. Gates. 1990. Gas exchange in *Quercus rubra* (northern red oak) during a drought: analysis of relations among photosynthesis, transpiration, and leaf conductance. Tree Physiology **7**:215–225.

Westveld, M., R. I. Ashman, H. I. Baldwin, R. P. Holdsworth, R. S. Johnson, J. H. Lambert, H. J. Lutz, L. Swain, and M. Standish. 1956. Natural forest vegetation zones of New England. Journal of Forestry **54**:332–338.

Wisniewski, J., and A. E. Lugo, editors. 1992. Natural sinks of CO_2. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Wofsy, S. C., M. L. Goulden, J. W. Munger, S.-M. Fan, P. S. Bakwin, B. C. Daube, S. L. Bassow, and F. A. Bazzaz. 1993. Net exchange of CO_2 in a mid-latitude forest. Science **260**:1314–1317.