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Intra- and inter-specific variation in canopy photosynthesis in a mixed deciduous forest

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Abstract Within the same forest, photosynthesis can vary greatly among species and within an individual tree. Quantifying the magnitude of variation in leaf-level photosynthesis in a forest canopy will improve our understanding of and ability to model forest carbon cycling. This information requires extensive sampling of photosynthesis in the canopy. We used a 22-m-tall, four-wheel-drive aerial lift to reach five to ten leaves from the tops of numerous individuals of several species of temperate deciduous trees in central Massachusetts. The goals of this study were to measure light-saturated photosynthesis in co-occurring canopy tree species under field conditions, and to identify sampling schemes appropriate for canopy tree studies with challenging logistics. Photosynthesis differed significantly among species. Even though all leaves measured were canopy-top, sun-acclimated foliage, the more shade-tolerant species tended to have lower light-saturated photosynthetic rates (P_{max}) than the shade-intolerant species. Likewise, leaf mass per area (LMA) and nitrogen content (N) varied significantly between species. With only one exception, the shade-tolerant species tended to have lower nitrogen content on an area basis than the intolerant species, although the LMA did not differ systematically between these ecological types. Light-saturated P_{max} rates and nitrogen content, both calculated on either an area or a mass basis, and the leaf mass to area ratio, significantly differed not only among species, but also among individuals within species ($P<0.0001$ for both). Differences among species accounted for a greater proportion of variance in the P_{max} rates and the nitrogen content than the differences among individuals within a species (58.5–78.8% of the total variance for the measured parameters was attributed to species-level differences versus 5.5–17.4% of the variance was attributed to differences between individual trees of a given species). Furthermore, more variation is accounted for by differences among leaves in a single individual tree, than by differences among individual trees of a given species (10.7–30.4% versus 5.5–17.4%). This result allows us to compare species-level photosynthesis, even if the sample size of the number of trees is low. This is important because studies of canopy-level photosynthesis are often limited by the difficulty of canopy access. As an alternative to direct canopy access measurements of photosynthesis, it would be useful to find an "easy-to-measure" proxy for light-saturated photosynthetic rates to facilitate modeling forest carbon cycling. Across all species in this study, the strongest correlation was between nitrogen content expressed on an area basis (mmol m^{-2}, N_{area}) and light-saturated P_{max} rate (μmol m^{-2} s^{-1}, $P_{maxarea}$) ($r^2=0.511$). However, within a given species, leaf nitrogen was not tightly correlated with photosynthesis. Our sampling design minimized intra-specific leaf-level variation (i.e., leaves were taken only from the top of the canopy and at only one point in the season). This implies that easy-to-measure trends in nitrogen content of leaves may be used to predict the species-specific light-saturated P_{max} rates.

Key words Canopy access · Light-saturated canopy photosynthesis · P_{max} · Photosynthesis-nitrogen relationship · Variance partitioning

Introduction

Temperate forests play a substantial role in the global carbon cycle (Houghton 1991; Wisniewski and Lugo 1992). Nevertheless, we have a limited mechanistic understanding of the relative contribution of different species to forest carbon cycling, differences which could be substantial. For example, we do not fully understand the extent to which changes in species composition might alter carbon cycling within a forest. Decades of research within forest ecosystems have clearly demonstrated that species composition changes considerably throughout succession (e.g., Spurr 1964; West et al. 1981). Additionally, increasing concentrations of atmospheric CO_2, along with shifts in climate, may lead to substantial shifts in species composi-

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tion within communities (e.g., Leverenz and Lev 1987; Bazzaz and Fajer 1992). Will such shifts in species composition have the potential to dramatically alter the future carbon cycle within a temperate deciduous forest? Modeling approaches suggest that such species shifts can greatly influence biomass accumulation (Bolker et al. 1995).

Our ability to answer this question hinges on relating small-scale, biological observations to much larger regional scales. The general issue of "scaling" from the leaf to the ecosystem level has recently received considerable attention (e.g., Ehleringer and Field 1993; *Plant Cell and Environment*, vol. 18, 1995). Although this approach faces the risks of a reductionist "bottom-up" approach (e.g., Jarvis 1993, 1995), it may advance our understanding of the significance of succession, or merely the effect of different species compositions, on forest carbon cycling. Recent empirical measurements simultaneously taken at both the ecosystem level (with an eddy-correlation system) and at the leaf-level (measurements of leaf-level photosynthesis in the canopy of trees) have quantitatively demonstrated the linkage between these levels (Wofsy et al. 1993). While the soil compartment dominates the flux of CO_2 from the ecosystem to the atmosphere, the canopy tree foliage is responsible for the majority of net carbon uptake within the system. We need to understand how different tree species in the forest contribute to CO_2 uptake.

Here we examine the degree of variation in photosynthetic carbon uptake rates among different tree species. Within the same ecosystem, it has been demonstrated that earlier successional or shade-intolerant species often have higher maximal photosynthetic rates (P_{max}) compared to later successional species (e.g., Woods and Turner 1971; Bazzaz 1979; Jurik et al. 1988; Koike 1988; Walters et al. 1993; Sipe and Bazzaz 1994; Bazzaz 1996). However, these trends were largely seen for seedlings or saplings (Woods and Turner 1971; Koike 1988; Walters et al. 1993), or relatively short statured trees (Jurik et al. 1988), but rarely for adult trees. There can be substantial differences in photosynthesis and leaf structure between seedlings and mature trees of a given species (e.g., Koike 1988; Thomas 1993; Bassow 1995). Thus, in order to document variation among tree species in canopy photosynthesis and accomplish correct scaling, we need to measure leaf-level photosynthesis in mature canopy tree foliage of many species.

Measuring canopy-top foliage of an intact forest poses many logistical difficulties. Canopy research is increasingly being attempted using a variety of ingenious ways to physically place researchers into the tree canopies (e.g., a balloon-lofted raft, cranes, scaffolding towers, traditional tree-climbing techniques). The difficulties and expense of canopy access have often resulted in small sample sizes in terms of the number of individual trees (e.g., one tree in Zotz and Winter 1994). Here, using a construction-type aerial lift, we overcame many of these logistical and expense difficulties. By measuring a large sample of trees, we could determine statistically adequate canopy sampling regimes to best describe canopy photosynthesis. The second goal of this paper is thus methodological: to demonstrate the minimal sampling regimes useful for quantifying species-specific canopy tree photosynthetic rates while considering the logistic and expense concerns of canopy research.

An alternative to climbing trees for direct measurements of canopies is using remote sensing technology by satellite or aircraft. Our second methodological goal in this paper is to identify traits useful for predicting species-specific photosynthesis that may also be remotely sensed. Nitrogen content of foliage can be remotely sensed and in the future may be measured with greater precision (e.g., McLellan et al. 1991). Thus, it may be possible to use nitrogen content as a proxy for photosynthesis depending on the extent to which we can relate leaf nitrogen content to light-saturated P_{max} of canopy-top foliage.

Generally, leaf nitrogen content is related to P_{max} (Field and Mooney 1986; Evans 1989; Reich et al. 1994; Reich and Walters 1994; Schulze et al. 1994). This linear relationship is often stronger when both photosynthesis and nitrogen content are expressed on a mass basis rather than an area basis (e.g., Field and Mooney 1986); however, this may differ among species (Reich and Walters 1994; Reich et al. 1994).

In this paper, we report the species-specific P_{max} rates of canopy-top foliage from temperate canopy tree species, and consider the extent to which species' purported shade tolerance explains these differences. We compare the importance of variation among species, among individual trees within a species, and among leaves within the canopy of each tree for explaining the observed variation in P_{max} and nitrogen content. This is important for determining if we can sample more leaves from the canopy of a single tree, instead of ensuring a large sample size of individual trees in order to quantify species-level differences in photosynthesis. To examine whether foliar nitrogen content is an effective proxy for photosynthetic rate, we looked at the across-species, and the within-species relationships between P_{max} and nitrogen for ten canopy tree species.

Materials and methods

Site

We conducted this study at Harvard Forest, Petersham, Massachusetts, United States (42°32′N, 72°11′W, elevation 340 m) in a 60- to 70-year-old mixed deciduous forest. The site is in the Transition Hardwoods-White Pine-Hemlock zone (Westveld et al. 1956), and the stand is composed mainly of *Quercus rubra* (red oak), *Acer rubrum* (red maple), *Betula alleghaniensis* (yellow birch), *B. papyrifera* (paper or white birch), *Fagus grandifolia* (beech), *Fraxinus americana* (white ash), *Pinus strobus* (white pine), and *Tsuga canadensis* (hemlock). There are also several additional species at lower densities.

Methods

We used a gas-powered, four wheel drive, construction-type aerial lift, which reached a full extension height of 22 m (Shaughnessy Aerialifts Inc.). The base of the machine was kept within 5° of level, as was necessary, by positioning the base along a 200 m stretch of unimproved road bed. The tree canopy was uninterrupted across this infrequently traveled road. The angular rotation, vertical extension, and basket tilt allowed smooth access to leaves in the top of tree canopies located up to ~10 m away from the edge of the road. The motor was turned off during measurements, and was used only to position the basket for easy access to canopy foliage. The operation of the aerial lift was quite easy, allowing for generous access to foliage throughout the canopy, with very minimal disturbance to branches lower in the canopy.

This easy access allowed us to randomly select accessible trees, from a number of species, along this stretch (Table 1). For the commoner species, we randomly selected individual trees through the area. For some species, we only encountered one individual in the vicinity, which we sampled. The trees were randomly distributed spatially, and there was no spatial segregation of the trees of each species. All trees were canopy individuals, with the exception of the *Acer pensylvanicum* (striped maple) and *Castanea dentata* (chestnut). Striped maple is very shade-tolerant, and is commonly an understory tree (Burns and Honkala 1990). Chestnut trees generally do not survive to maturity and attain canopy height due to the chestnut blight (e.g., Kricher 1988). The striped maple trees measured were ~12–15 m tall, and the chestnut was ~6 m tall, though the leaves were in full sun at the time of the measurement due to a canopy opening above them. Removing either species from all analyses does not alter results significantly.

Leaf selection and photosynthetic measurements

All observations were made in a span of 4 days (19–22 July 1994). The weather was sunny, winds were calm, and the air temperature at the canopy-top was between 29 and 36°C, with no significant drought prior to the measurements. Photosynthesis was measured using a Licor 6200 Photosynthetic System (LICOR, Lincoln, Neb.), equipped with a quarter-liter chamber. The infra-red gas analyzer (IRGA) was calibrated daily, and checked periodically throughout the day. All observations were made between 0730 and 1500 hours, before the late-day decline of photosynthetic capacity in this forest (Bassow 1995). Five to ten leaves from each tree were randomly selected from the tops of the canopies. Leaf orientation was maintained while being enclosed in the chamber, and all observations were taken when photosynthetic photon flux density (PPFD) was above 1000 μE m^{-2} s^{-1}, which is saturating for the majority of the studied species. For red oak that minimum light level corresponds to a photosynthetic rate that is ~80% of the maximally observed values (Bassow 1995). We restricted photosynthetic measurements to the ambient CO_2 concentrations (330–360 μl l^{-1}), and humidity levels (40–60%). Leaves were enclosed in the chamber for less than 60–90 s to prevent excessive rise in leaf temperature (LICOR Manual, 1990).

Table 1 Species and the number of individual trees included in this study. Shade tolerance is indicated (Burns and Honkala 1990; Spurr 1956)

Common name	Scientific name	Number of trees	Shade tolerance
White birch	*Betula papyrifera*	5	Very intolerant
Black cherry	*Prunus serotina*	1	Inntolerant
Ash	*Fraxinus americana*	4	Intolerant/ Intermediate
Red oak	*Quercus rubra*	7	Intermediate
White oak	*Quercus alba*	1	Intermediate
Chestnut	*Castanea dentata*	1	Intermediate
Elm	*Ulmus americana*	1	Intermediate
Red maple	*Acer rubrum*	6	Tolerant
Sugar maple	*Acer saccharum*	2	Very tolerant
Striped maple	*Acer pensylvanicum*	5	Very tolerant

After the light-saturated photosynthetic rate ($P_{\max}$) was measured, each leaf was collected, sealed in a plastic bag, and kept out of the sun, until they were brought back to the lab to measure leaf area using a Licor 3000 leaf area meter (LICOR, Lincoln, Neb.). Cut leaves were left no longer than 2 h before area was measured. The leaves were then dried to constant mass and weighed for calculating leaf mass per area (LMA, g m^{-2}).

Collected leaves were ground individually with mortar and pestle to a very fine powder. The nitrogen content of the ground tissue was analyzed using a Europa CHN Analyzer (Model ANCA-*nt*, Europa Elemental Instruments, UK). Internal standards were used to correct for any variations of the instrument between runs.

Data analysis

For species with multiple sample trees, we executed a nested MANOVA with species as the main plot term, and trees nested within species as the sub-plot level in Data Desk 4.2 (Data Descriptions Inc., Velleman 1992). Because we had sampled a number of traits for each leaf, a MANOVA was the appropriate analysis. Species were treated as a fixed effect and trees within species were considered random. Variance percentages were calculated based on the nested design with unequal replication (Sokal and Rohlf 1981). A single factor MANOVA was used to assess the significance of the differences between species for photosynthesis, nitrogen content and LMA. The variance explained by this model versus the variance explained by the error term was calculated. Regressions of $P_{\max}$ against the leaf nitrogen, both calculated on either an area or a mass basis, and LMA were performed using Data Desk 4.2.

Results

Species-level differences in $P_{\max}$

Species had significantly different photosynthetic rates (area and mass basis), nitrogen content (area and mass basis), and LMA (Table 2) (one-way MANOVA, Wilk's

Table 2 Summary of the results from a one-way MANOVA of species. The percentage of sum of squares attributed to the terms species and error are also indicated. The MANOVA was highly significant: Wilk's λ for the species term was 0.0061, $P<0.0001$. All species were considered. Significance levels: $^{*1}P<0.05$, $^{*2}P<0.01$, $^{*3}P<0.001$, $^{*4}P<0.0005$

	Species SS	*df*	Error SS	*F*	*P*	Percent of variance	
						Species	Error
$P_{\max_{\text{area}}}$ (μmol m^{-2} sec^{-1})	6471.75	9	2317.97	61.117	$<0.0001^{*4}$	73.63	26.37
$P_{\max_{\text{mass}}}$ (nmol g^{-1} leaf sec^{-1})	563593	9	302018	40.847	$<0.0001^{*4}$	65.11	34.89
Nitrogen content (area basis) (mmol lm^{-2})	352104	9	84725	90.966	$<0.0001^{*4}$	80.60	19.40
Nitrogen content (mass basis) (mmol g^{-1})	17.73	9	5.94	65.38	$<0.0001^{*4}$	74.92	25.08
Leaf mass per area (mg cm^{-2})	777.61	9	156.98	108.43	$<0.0001^{*4}$	83.20	16.80

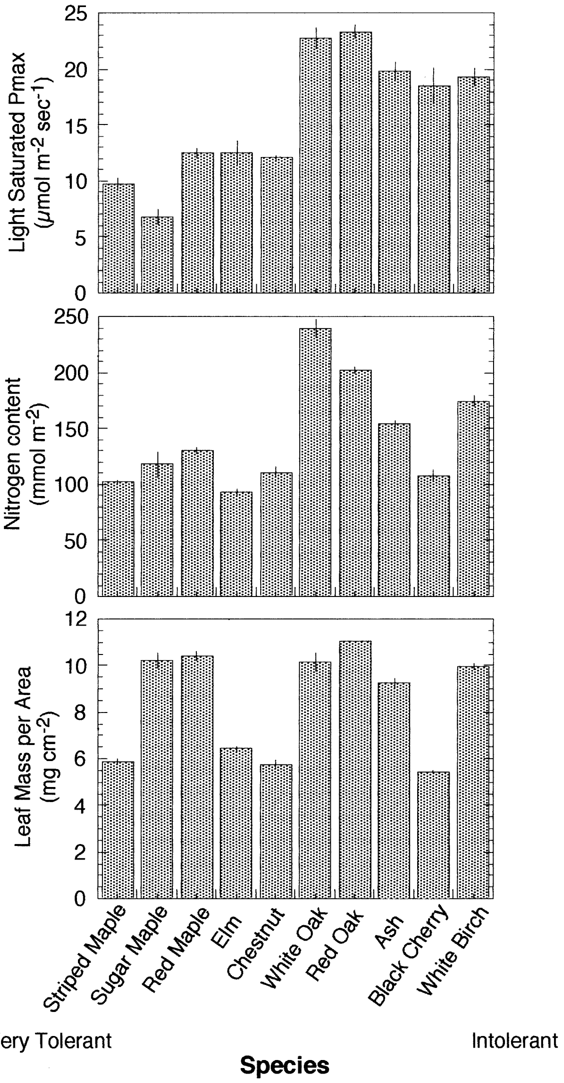

Fig. 1 Light-saturated P_{max} rates (µmol m^{-2} s^{-1}), nitrogen content (mmol m^{-2}), and LMA (mg cm^{-2}). *Values* are the means for each species across all replicate trees. Species are oriented along an axis from those classified as very *shade-tolerant* to those classified as shade *intolerant* (after Burns and Honkala 1990; Spurr 1956); however, shade-tolerance classification is inexact, so within a tolerance class, the order could be shifted. *Error bars* represent 1 SE of all leaf-level observations

λ criterion was 0.0061, $P<0.0001$). Furthermore, each factor's ANOVA was highly significant (all cases: $P<0.0001$). The species term accounted for 65–83% of the total variance for the parameters included in the MANOVA.

As illustrated in Fig. 1, red oak, the most dominant species in this system, had the highest maximal photosynthetic rate (23 µmol m^{-2} s^{-1}), as did white oak; these were followed by ash, white birch, and black cherry (all ~20 µmol m^{-2} s^{-1}). The maple species (sugar, striped, and red maple) had the lowest light-saturated photosynthetic rates (7, 10, and 13 µmol m^{-2} s^{-1}). In general, the more shade-intolerant species had higher light-saturated photosynthetic rates than the shade-tolerant species (Fig. 1), although there was considerable variation within a tolerance class.

Shade-intolerant species also had higher nitrogen content on an area basis than the tolerant species, with the exception of black cherry (Fig. 1). The oak species had the highest nitrogen content on an area basis (over 200 mmol m^{-2}). LMA was significantly different among the species, although there were no clear associations with species' shade tolerance (Fig. 1). All leaves sampled were canopy-top (sun-acclimated) leaves (with the exceptions discussed above for striped maple and chestnut).

Variation among species and within species

For species in which we had sampled multiple trees, we found that species and replicate trees within species had significantly different photosynthetic rates (on either an area or a mass basis), nitrogen concentration (on either an area or a mass basis), and leaf mass to area ratio. The nested MANOVA Wilk's λ criterion was highly significant for both species (main plot) and tree nested within species (sub-plot) terms (both $P<0.0005$) (Table 3). Further, each component ANOVA showed significant differences among species, as well as among replicate trees within species (all cases: $P<0.0005$) (Table 3).

To elucidate the relative contribution of species, trees within species, and leaves within a tree to the overall variance of photosynthetic rates, we calculated the percentage of the total variance explained by each level (Table 4). This analysis was also performed for the nitrogen content (on both an area and a mass basis) and the LMA data (Table 4). For all parameters (photosynthesis on an area and mass basis, nitrogen content on an area and mass basis, and LMA), the species term accounted for the majority of the variance, meaning that differences between species were much greater than those within species or within individual trees. Furthermore, for all parameters, with the exception of N content on a mass basis, the variance among leaves within a single tree (error SS%) was greater than the variance among trees within a species.

Photosynthesis-nitrogen relationship

Pooling all species together, the regressions of P_{max} on the nitrogen content, on both area- and mass-bases, were highly significant: area basis: $r^2=0.51$, $P<0.0001$; mass basis: $r^2=0.40$, $P<0.0001$ (Fig. 2). However, only striped maple and white birch exhibited significant regressions within species: $r^2=0.15$, $P=0.045$, and $r^2=0.14$, $P=0.042$, on an area basis, and $r^2=0.20$, $P=0.017$, and $r^2=0.16$, $P=0.030$ on a mass basis.

LMA was significantly and positively correlated with the P_{max} expressed on an area basis, although the coefficient of determination was low: $P_{maxarea}=4.887+1.25 \times \text{LMA}$, $r^2=0.17$, $P<0.0001$. In contrast, LMA was nega-

Table 3 Summary of the results from a nested MANOVA of species, and trees nested within species. Wilk's λ criterion was highly significant, so ANOVA results for each factor are shown. Only species for which we had sampled multiple trees are included in the analysis. Significance levels: $^{*1}P<0.05$, $^{*2}P<0.01$, $^{*3}P<0.001$, $^{*4}P<0.0005$

Source of variation	$P_{\max}$ (area basis) (μmol m^{-2} s^{-1})				$P_{\max}$ (mass basis) (nmol g^{-1} leaf tissue s^{-1})				Leaf mass per area (mg cm^{-2})			
	SS	*df*	*F*	*P*	SS	*df*	*F*	*P*	SS	*df*	*F*	*P*
Species	5440.4	5	39.583	0.0001*^{4}	350204	5	17.955	0.0001*^{4}	505.79	5	30.491	0.0001*^{4}
Trees (species)	632.24	23	2.752	0.0001*^{4}	89719	23	3.391	0.0001*^{4}	76.306	23	7.363	0.0001*^{4}
Error	1518.1	152			174860	152			68.493	152		

Source of variation	Nitrogen content (area basis) (mmol m^{-2})				Nitrogen content (mass basis) (mmol g^{-1})				Wilks λ criterion				
	SS	*df*	*F*	*P*	SS	*df*	*F*	*P*	λ	Prob	Approx *F*	*df*	Error *df*
Species	237454	5	25.956	0.0001*^{4}	11.558	5	16.589	0.0001*^{4}	0.0055	0.000*^{4}	8.83	25	72
Trees (species)	42083	23	7.369	0.0001*^{4}	3.205	23	8.313	0.0001*^{4}	0.0644	0.000*^{4}	4.76	115	731
Error	37742	152			2.548	152							

Table 4 The percentage of sum of squares attributed to the terms: species, tree nested within species, and error, in a nested MANOVA design. The MANOVA was significant at $P<0.0001$. Only species for which we had sampled two or more individual trees were incorporated into the analysis

	Percent of variance		
	Among species	Trees within species	Leaves within trees
$P_{\max_{\text{area}}}$ (μmol m^{-2} sec^{-1})	74	6	20
$P_{\max_{\text{mass}}}$ (nmol g^{-1} leaf sec^{-1})	59	11	30
Nitrogen content (area basis) (mmol m^{-2})	76	12	12
Nitrogen content (mass basis) (mmol g^{-1})	67	17	16
Leaf mass per area (mg cm^{-2})	79	10	11

tively correlated with $P_{\max}$ expressed on a mass basis with an extremely low coefficient of determination ($P_{\text{max-mass}}$=243.18 –6.697×LMA, r^2=0.048, P=0.0014). This means that LMA may not be a good proxy for predicting photosynthetic rates for sun leaves in this context.

The nitrogen content on an area basis (mmol m^{-2}) was significantly correlated with LMA for the entire population of leaves (r^2=0.47, $P<0.0001$), as well as within most species [white birch r^2=0.12 (P=0.063), black cherry r^2=0.78 (P=0.0195), ash r^2=0.66 ($P<0.0001$), red oak r^2=0.30 ($P<0.0001$), white oak r^2=0.95 ($P<0.0001$), chestnut r^2=0.77 (P=0.22), elm r^2=0.89 (P=0.0045), red maple r^2=0.29 (P=0.0002), sugar maple r^2=0.71 (P=0.0006), and striped maple r^2=0.46 ($P<0.0001$)]. In contrast, nitrogen content on a mass basis (mmol g^{-1}) was weakly negatively correlated with LMA (r^2=0.028, P=0.17) across all species. Moreover within the species, only three cases were significant: white oak had a negative correlation r^2=0.61 (P=0.023), striped maple had a negative correlation r^2=0.17 (P=0.032), and sugar maple had a positive correlation r^2=0.52 (P=0.0083).

Discussion

We present here quantitative information on the range of $P_{\max}$ rates of ten co-occurring deciduous tree species in a stand at Harvard Forest. By understanding the relative contribution of these different species to the net carbon flux of a mixed deciduous forest, we can make predictions as to how carbon flux might differ if the stand comprised different species, a response expected because of natural succession and especially because of global change. Further, our data suggest that we may be able to use leaf nitrogen content, an easy parameter to measure compared with canopy photosynthesis, to predict a static description of photosynthesis over an area much larger than we could possibly sample from an aerial lift or other means of canopy access.

Species-level differences

Within the mixed deciduous canopy at Harvard Forest, tree species have significantly different top-canopy-foliage photosynthetic rates, nitrogen concentration, and LMA. This important result advances our understanding of the photosynthetic component of temperate forest carbon cycling because measurements were made within an intact forest canopy. We observe that one of the two most dominant species, red oak, has nearly twice the $P_{\max}$ rate of the second dominant species, red maple (red oak photosynthetic rate was ~23 μmol m^{-2} s^{-1}, while red maple photosynthetic rate was ~13 μmol m^{-2} s^{-1}). This great difference in adjacent trees implies that if the species composition were shifted, as may happen in response to climate change or other dramatic disturbance, we may

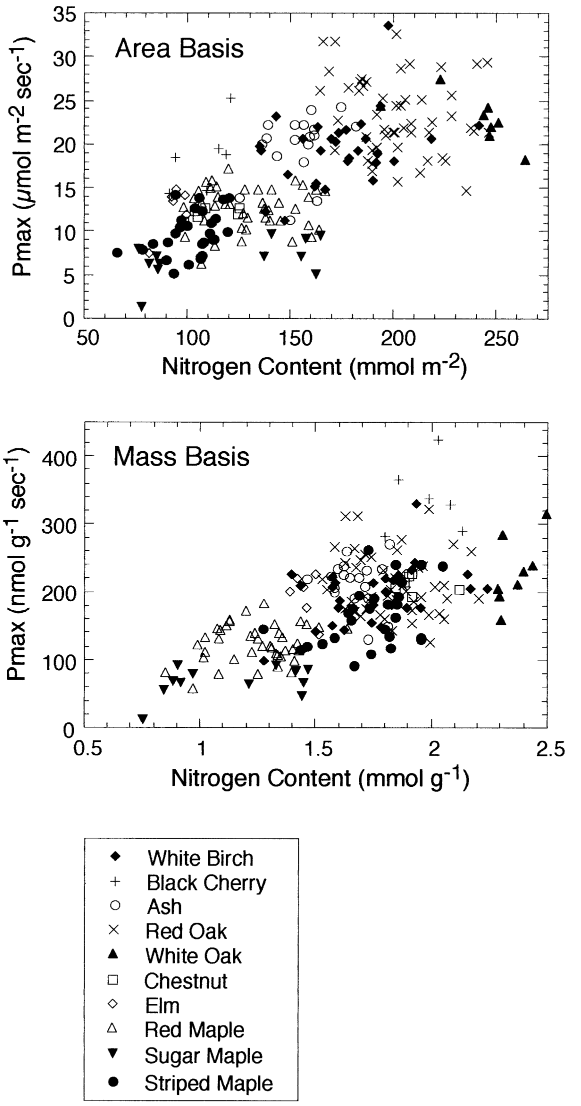

Fig. 2 P_{max} versus nitrogen relationship, graphed on the basis of area and mass. Species are indicated with different *symbols*. On an area basis, the regression is: $P_{maxarea}$=1.016+0.101×N_{area} , r^2=0.51, P<0.0001. On a mass basis the regression is: $P_{maxmass}$= −20.655 +121.63×N_{mass} , r^2=0.40, P<0.0001

expect a substantial alteration in the net carbon uptake by the stand. This link between the ecosystem's species composition and its carbon exchange has been both quantified (Wofsy et al. 1993), and modeled (Waring et al. 1995; Bolker et al. 1995).

Using a simple scaling model (cf. Norman 1993) based on leaf area index (LAI, the amount of leaf area above a given area of ground), leaf-level photosynthetic rates of the two dominant tree species (red oak and red maple), and a system-level respiration term, we compared the diurnal and seasonal patterns of the scaled leaf-level observations with the eddy correlation estimates of the net ecosystem exchange of CO_2 over the same region (Wofsy et al. 1993). The quantitative similarity between these two approaches provides evidence that tree species composition is relevant to the net system-level CO_2 exchange. Using the present data on P_{max}, it is evident that an early successional stand of white birch and black cherry, or a mid-successional stand of red oak and red maple, similar to that analyzed in Wofsy et al. (1993), would have a considerably greater photosynthetic uptake of CO_2 than a late successional stand of sugar and striped maple. The P_{max} values of the shade-intolerant species and the oak species were so high that even a moderately higher LAI in a late successional stand would not compensate for the photosynthetic differences. Only through such a species-specific understanding of photosynthesis in the forest canopy are we able to predict carbon flux consequences to environmental changes such as succession and global change.

To what extent can we relate the observed species patterns in photosynthesis to a well-recognized ecological classification? In seedlings and saplings of deciduous trees, late successional, shade-tolerant species generally have lower photosynthetic rates and lower leaf mass-to-area ratios than early successional, shade-intolerant species (e.g., Koike 1988). However, the micro-environmental conditions in which seedlings grow may alter the species' rankings of light-saturated photosynthetic rates. For example, growth in different locations within gaps created by canopy openings (e.g., the sun-exposed north side of the gap or the shadier south side of the gap) shifted the three maple species' rankings of light-saturated photosynthetic rates (Sipe and Bazzaz 1994). In most locations the shade-tolerance order was the inverse of the ranking of light-saturated photosynthetic rates; however, on the south side of large gaps the order was not maintained. In the present study, the shade-tolerant (later successional) species do tend to have lower P_{max} than the more shade-intolerant species, even though the leaves are all sun-adapted. With the main exception of black cherry, the shade-intolerant species also tend to have higher nitrogen contents on an area basis than the tolerant species. In contrast, although there is a wide range in LMA among species (~5.5–11 mg cm^{-2}), there is no clear pattern of LMA between tolerant and intolerant species. This lack of pattern may be due to the fact that virtually all leaves in this study were top-of-canopy, sun-adapted leaves.

If rapid warming results in extensive forest mortality, we can expect an increase in the dominance of early successional species relative to later successional species (Bazzaz et al. 1995). After an initial increase in carbon released to the atmosphere when the dead trees decompose, the predominantly early successional stand of trees may take up carbon at a faster rate, particularly at the onset of canopy closure. The extent to which we can describe the successional status of component species in a forest following a disturbance regime will improve our ability to use this species-specific photosynthetic information.

Sampling issues in canopy research

Canopy research in tall forests is often quite difficult, dangerous, and/or expensive. For these reasons, we must carefully consider exactly what level of replication is necessary for making accurate statements about species-level physiological and ecological differences in a forest. Since large trees have many leaves, we can, in part, make up for low sample sizes in the number of trees measured by sampling several leaves within one tree.

In this site, we found that replicate trees within a species did have significantly different photosynthetic rates, nitrogen contents (on both area and mass bases), and LMAs. However, the proportion of the variance in these factors associated with replicate leaves within a single canopy was greater than the proportion of variance associated with different trees within a species. If we had sampled only one leaf from each of several trees of a given species, we would have wrongly attributed this additional within-tree variance to differences between trees. Furthermore, both of these "error"-associated variance terms were dwarfed by the magnitude of the species-level differences. In other words, we can statistically differentiate among species, in spite of the significant differences among trees within a species.

We suggest that sampling additional leaves within a single canopy may in part substitute for sampling additional trees. Pseudo-replication is still a problem (Hurlbert 1984), and inference should be restricted in such cases. However, canopy research can be well justified even when sample sizes of individual trees are low if the inter-specific differences in traits are considerably greater than the differences among individual trees within a species, which was the case in this temperate forest system.

Photosynthesis nitrogen model

Alternatively, if we can relate the photosynthetic rate of canopy foliage to its nitrogen content, then we may be able to use nitrogen content, a trait easy to measure in tree canopy leaves, to predict canopy tree photosynthesis. For example, Schulze et al. (1994) used this approach to scale from leaf-level nitrogen content to estimate global patterns of CO_2 assimilation. In the present study, we find a significant regression of photosynthesis on nitrogen content, particularly on an area basis, indicating that such a model may be useful and accurate.

However, there are limitations to the predictions that can be made using nitrogen concentration. In this study the photosynthesis-nitrogen relationship was generally not significant, for either an area or a mass basis, within the individual species. This is not surprising since we sampled leaves only from the top of the canopy in one site, where all leaves were approximately the same age, and had acclimated to the same high light levels and soil fertility. The vertical gradient, differing leaf ages, the seasonal course of time, and additional sites with differing fertility would add other sources of variance in leaf nitrogen and photosynthesis within a species, and may lead to significant correlation (e.g., Field 1983; Reich et al. 1991; Hollinger 1992; Ellsworth and Reich 1993; Bassow 1995). The fact that in the canopy-top foliage the correlation between nitrogen and $P_{\max}$ is significant only across species, and not within species, implies that this model is useful only in a mixed species stand. In other words, we have limited ability to predict within-species variation in canopy-top photosynthetic rates within one site. Furthermore, co-occurring tree species can also have substantially different diurnal patterns of leaf-level photosynthesis (Bassow 1995); the nitrogen-photosynthesis model across species, such as that described here, would have no sensitivity to this level of variation.

There is another potential limit to Schulze's approach. If the slope of the relationship between photosynthesis and nitrogen content changes over the course of the season (Reich et al. 1991; Bassow 1995), then the ability to predict canopy photosynthesis based on leaf nitrogen content alone would be restricted to a certain calibrated time period. The extent to which particular deciduous species are able to re-translocate leaf nitrogen prior to autumnal senescence (e.g., del Arco et al. 1991), while maintaining photosynthetic activity (e.g., Koike 1990; Amthor et al. 1990), would affect this relationship.

Because they were sampled at only one point in the season, leaves from this study were not affected by seasonal or leaf-age effects on LMA. Nitrogen content on an area basis was significantly related to LMA overall, as well as for most of the species considered individually (with one exception, white birch, P=0.21). This is not surprising: higher LMA implies "thicker" leaves, so nitrogen on a per area basis should be higher (Reich and Walters 1994). However, overall and in virtually all species, nitrogen calculated on a mass basis was not significantly correlated with LMA (with one exception: striped maple, P=0.0059). This may be because these leaves were approximately even-aged. This relationship may co-vary over the course of a season, because as leaves age, there can be a simultaneous decline in nitrogen on a mass basis, and an increase in LMA (Reich and Walters 1994).

Another useful proxy for predicting photosynthetic rate has been based on the correlation between LMA and photosynthetic rate (DeJong and Doyle 1985, Ellsworth and Reich 1993). LMA is easy to measure for a large number of samples. However, here we find only a weak relationship between LMA and photosynthetic rate (on either an area or mass basis). Using LMA to predict photosynthesis may only be an appropriate proxy when comparing photosynthetic rates through a vertical profile of the canopy (e.g., for sugar maple: Ellsworth and Reich 1993).

To summarize, this study has shown that species differ greatly in their light-saturated photosynthetic rates. We believe that it is important to understand species-specific differences in canopy tree photosynthesis quantitatively, because only this level of understanding will allow us to quantify the impact of species compositional shifts on the net ecosystem carbon flux. Furthermore, if we can develop well-supported relationships between leaf nitrogen content and photosynthesis, we can develop models which may more accurately link remotely sensed data for estimating leaf nitrogen content to ecosystem carbon exchange. The extent to which we can use such a model to explain within-species differences in canopy-top photosynthesis at a single site at one point in time, however, is quite limited, because within species we saw poor correlation between nitrogen and photosynthesis in canopy-top leaves. Finally, low sample size in canopy tree physiological studies may be less problematic in the future for two reasons: access to multiple trees is not difficult using an aerial lift of the type we have used for this study; and further, the bulk of the variation in leaf-level photosynthesis which we observed in this mixed deciduous stand was attributed to differences between species, secondarily to differences among leaves within a tree canopy, and finally to differences among individual trees.

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