

Estimates of net photosynthetic parameters for twelve tree species in mature forests of the southern Appalachians

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Received February 1, 1995

Summary Leaf gas exchange, temperature, and incident radiation were measured *in situ* for 20 mature trees of 12 deciduous species spanning a range of heights from 7.9 to 30.1 m and growing in the southern Appalachian Mountains. Air temperature, water vapor pressure, total radiation, photosynthetically active radiation, and carbon dioxide concentration were also measured. Estimated mean, light-saturated net assimilation rates ($\mu\text{mol m}^{-2} \text{s}^{-1}$) were: *Quercus coccinea* Muenchh. (10.3), *Q. prinus* L. (9.9), *Q. rubra* L. (8.9), *Betula lenta* L. (8.1), *Liriodendron tulipifera* L. (7.9), *Q. alba* L. (7.6), *Carya glabra* Mill. (7.2), *Acer rubrum* L. (5.6), *Nyssa sylvatica* Marsh. (3.9), *Cornus florida* L. (3.5), and *Acer pensylvanicum* L. (1.7). There were significant differences in both net assimilation rates and quantum yield efficiencies between species, with the understory species *C. florida* and *A. pensylvanicum* exhibiting lower net assimilation rates at saturation and higher estimated quantum yield efficiencies than the other species. Average temperature and light decreased from the canopy top to bottom, whereas ambient CO_2 concentration increased, and vapor pressure and vapor pressure deficits were inconsistent. We observed curvilinear effects of temperature and vapor pressure deficit on net assimilation response to light, and these effects varied by species. Errors in predicted net assimilation ranged from 1 to $3 \mu\text{mol m}^{-2} \text{s}^{-1}$ under the environmental conditions prevailing during the study.

Keywords: *Acer*, *Betula*, *Carya*, *Cornus*, gas exchange, *Liriodendron*, net assimilation, *Nyssa*, quantum yield efficiency, *Quercus*, radiation, solar radiation, temperature.

Introduction

During the past decade there has been much effort to develop and improve landscape- and regional-scale estimates of forest processes and productivity. Most estimates involve the coupling of detailed measurements of small-scale processes (e.g., respiration and photosynthesis) with spatially explicit estimates of both temporally stable and variable factors (temperature, soil water, atmospheric vapor pressure, forest composition and structure, and soil texture and depth) (e.g.,

Valentini et al. 1995). Scaling generally involves integrating a point-specific model of ecophysiology with appropriate spatial data, and the application of the model to the region of interest (Ehleringer and Field 1993). Process-based models have been developed for several spatial and temporal scales, including leaf- (Wang and Jarvis 1990) and stand-level models in coniferous forests (Running 1984, Hari et al. 1991, Korol et al. 1991, Webb 1991), leaf-to-plant-level models for clonal poplar (Rauscher et al. 1990) and oak-maple forests (Reich et al. 1990), and generalized models that encompass large regions (Aber and Federer 1992, Rutherford 1993, Running and Hunt 1993). Scaling requires aggregation, often across species, stands, and larger geographic areas, because of finite computational resources and limited knowledge of important physiological parameters. Accounting for inter-species variability in physiological responses results in extremely complex models (Bossel 1991); however, the guidelines for aggregation are often arbitrary because differences in physiological responses among species are poorly known. Most measurement and modeling efforts in mature forests have concentrated on conifers (Running 1984, Korol et al. 1991), particularly even-aged, single-species stands (Wang and Jarvis 1990). Physiologically based, large-scale models in mixed species forests have typically used lumped-parameter approaches (e.g., Aber and Federer 1992), where for example, the photosynthetic rate of the entire forest canopy is represented by a single equation.

Although direct physiological measurements in mature broad-leaved deciduous forests are limited because canopy access is difficult, studies have established within-crown variation in environmental factors and their effects on photosynthesis (Aubuchon et al. 1978, Caldwell et al. 1986), relationships of annual ontogeny to net carbon fixation (Dougherty et al. 1979), and physiology during water deficits (Weber and Gates 1990). However, functional ecophysiology in most mature deciduous forest species and canopies must be inferred through syntheses of several studies and approaches. Glasshouse and field studies employing seedlings and saplings have established relationships between net carbon assimilation (A_{net}) and leaf conductance, temperature, nitrogen, water, and other environmental factors, at least under controlled condi-

tions (Geis et al. 1971, Bacone et al. 1976, Hinckley et al. 1978, Bahari et al. 1985, Hanson et al. 1988, Parker and Pallardy 1988, Walters and Reich 1989, Mebrahtu et al. 1991, Ranney et al. 1991, Hollinger 1992, Kubiske and Abrams 1992, Masarovicova 1992, Epron and Dryer 1993, Walters et al. 1993, Abrams et al. 1994). Additional work has identified typical within-canopy environmental gradients (Geiger 1965, Rosenberg 1974, Aubuchon et al. 1978), and vertical variation in leaf area (Aber 1978, Hutchison et al. 1986, Vose and Swank 1990, Ellsworth and Reich 1993). However, little is known about (1) A_{net} in mature canopies, (2) the magnitude of interspecific differences in maximum A_{net} and quantum yield efficiency, or (3) how A_{net} differs among species with respect to environmental conditions (light, humidity and temperature). The objectives of this study were to: (1) measure *in situ* rates of net photosynthesis for several species in mature southern Appalachian forests across the range of light, air temperature, and humidity conditions typical for the region, (2) model the relationships between photosynthesis and these abiotic variables, and (3) identify species groups that may be functionally equivalent when modeling mature canopy productivity at stand and larger scales.

Methods

Sites and access

Research was conducted at the Coweeta Hydrologic Laboratory (35°3' N, 83°25' W) located in the southern Appalachians of western North Carolina. Four plots were established in control watersheds, undisturbed since harvesting before 1927. The area is occupied by mature mixed broad-leaved deciduous stands (Swank and Crossley 1988). Plots were arrayed along an elevational gradient, spanning a range from 740 to 1430 m, with a concomitant range of climatic conditions. Average annual temperature ranges from 8.2 to 13.1 °C and precipitation ranges from 1800 to 2200 mm within the Coweeta watershed (Swift et al. 1988).

We erected a canopy access tower at each plot. Towers were approximately 30 cm in cross section with cross-braces welded at intervals of approximately 25 cm, allowing continuous vertical sampling of leaves within approximately 2 m of the tower. Towers ranged from 18 to 28 m in height, and allowed access to the top of the canopy.

Table 1. Site data, based on 0.07-ha plots centered on canopy towers, at Coweeta Hydrologic Laboratory, NC.

	Site 1	Site 2	Site 3	Site 4
Elevation (m)	740	840	1070	1430
Aspect	East	Southeast	East	North
Slope (%)	52	29	24	35
Tree density (ha ⁻¹)	780	860	765	405
Mean DBH (cm)	19.7	15.3	21.3	27.3
Basal area (m ha ⁻¹)	33.51	21.39	36.15	32.06
LAI	4.56	4.58	4.94	5.35
Tower height (m)	24	17.8	26.8	21

Basic site-vegetation characteristics (Table 1) were determined from measurements made in March 1994 on 0.07-ha circular plots centered on the canopy access towers. Height and diameter of all trees greater than 6.3 cm in diameter (at 1.3 m height) were measured.

Nitrogen was measured in leaves collected from all canopy levels of the sample trees. Leaves were dried at 70 °C for 24 h, ground, and N concentration determined with a Perkin-Elmer CHN analyzer. Specific leaf areas were determined from fresh litter fall, sorted by species, and used to calculate nitrogen concentration on a per unit area basis.

Approximately monthly during the growing season, soil water was measured by time-domain reflectometry, using four pairs of 25-cm rods placed within each plot.

Sample tree descriptions

Twenty trees comprising 12 species were accessible from the four towers (Table 2). Diameters and heights ranged from 6.4 to 70.4 cm and 7.9 to 30.1 m, respectively. Six *Acer rubrum* L. individuals were distributed among three sites, three *Betula lenta* L. trees and two *Quercus prinus* L. trees were present at two sites, and the remaining species were represented by a single tree: *Cornus florida* L., *Fagus americana* Ehrh., *Nyssa sylvatica* Marsh., *Quercus alba* L., *Liriodendron tulipifera* L., *Quercus coccinea* Muenchh., *Quercus rubra* L., *Carya glabra* Mill., and *Acer pensylvanicum* L. Dominant individuals such as *Q. prinus*, *Q. rubra*, *Q. alba* and *L. tulipifera* were only accessible near the top of the towers. The shade-tolerant species *A. pensylvanicum*, *C. florida*, and *F. americana* were only accessible at low to intermediate heights (5 to 10 m). Branch retention and narrow crown form allowed sampling over a 10 to 12 m height range (from mid- to upper-crown positions) for *B. lenta*, *N. sylvatica* and *C. glabra*. *Acer rubrum* was accessible in various canopy positions. At the 840-m elevation plot, three small *A. rubrum* trees were accessible at heights between 5 and 8 m, at the 740-m elevation plot, one individual could be reached only in the upper-mid canopy (18 m height), and at the 1430-m elevation plot, subcanopy branching allowed access to *A. rubrum* from mid- to upper-canopy positions (10 to 18 m).

Carbon assimilation measurements

Estimates of carbon assimilation were based on gas exchange measurements with an open-flow infrared gas analyzer (IRGA, Model LCA III) and Parkinson Leaf Chamber (Analytical Development Corporation, Hoddesdon, England). Gas exchange measurements were conducted from May through September of 1992 and from June through September of 1993. Leaves were sampled from those accessible from the tower, and no effort was made to ensure or avoid repeat sampling of the same leaves on subsequent dates. Sampling was usually conducted between 1000 and 1400 h, although observations were made earlier and later on two days. Shaded leaves and, if possible, leaves in direct sunlight were measured at each sampling location. Leaves were maintained in their natural orientation during measurement to minimize disturbance and reduce variation due to light and temperature acclimation responses. Leaves were monitored until CO₂ entering and

Table 2. Characteristics of sampled trees. Abbreviations: D = dominant, CD = codominant, I= intermediate, and U = understory canopy position.

Species	Diam (cm)	Total height (m)	Min. sampling height (m)	Max. sampling height (m)	Canopy class
Site 1					
<i>Acer rubrum</i>	27.5	26.3	18.0	18.0	CD
<i>Cornus florida</i>	7.2	8.4	5.9	8.3	U
<i>Fagus americana</i>	6.4	7.9	5.9	5.9	U
<i>Nyssa sylvatica</i>	13.3	15.5	9.1	12.2	I
<i>Quercus alba</i>	47.6	24.1	19.4	21.0	D
Site 2					
<i>Acer rubrum</i>	8.7	9.1	5.6	8.2	I
<i>Acer rubrum</i>	5.4	8.6	4.6	7.2	U
<i>Acer rubrum</i>	9.3	9.5	4.8	7.4	I
<i>Liriodendron tulipifera</i>	23.7	21.0	13.6	16.6	D
<i>Quercus coccinea</i>	33.1	19.5	11.2	15.0	D
Site 3					
<i>Betula lenta</i>	21.0	22.1	14.5	23.7	CD
<i>Betula lenta</i>	25.8	24.4	12.7	24.1	CD
<i>Carya glabra</i>	17.9	24.6	10.4	21.0	CD
<i>Quercus prinus</i>	70.4	30.1	21.7	23.2	D
Site 4					
<i>Acer pensylvanicum</i>	12.0	10.8	4.1	5.2	U
<i>Acer rubrum</i>	25.8	20.3	15.8	18.8	D
<i>Acer rubrum</i>	24.4	18.3	10.0	18.0	CD
<i>Betula lenta</i>	26.5	17.3	7.5	16.6	CD
<i>Quercus prinus</i>	47.3	21.3	15.1	17.1	D
<i>Quercus rubra</i>	45.8	20.3	18.3	19.3	D

exiting the leaf chamber stabilized (30–45 s).

The IRGA and leaf chamber CO₂ sensors were calibrated at the start of each sampling date with a 349 ppm CO₂ standard. Relative humidity sensors were calibrated using columns of desiccant (CaSO₄) and humidifier (FeSO₄). Outlet air temperature sensors were calibrated with a thermocouple and meter. Microclimate was noted for each sample using the sensors housed in the leaf chamber. Photosynthetic photon flux density (PPFD) was measured with a selenium cell mounted on the leaf chamber, and PPFD readings were periodically compared to values obtained with a quantum sensor (Model LI-190SA, Li-Cor, Inc., Lincoln, NE) that had been calibrated by the manufacturer in February 1992. The air to leaf temperature gradient in the chamber was reduced by continuous mixing of the air during sampling (Long and Hallgren 1985), and leaf temperature (T_l) was assumed to be the same as the temperature of leaf chamber outlet air T .

Net assimilation (A_{net} , $\mu\text{mol m}^{-2} \text{s}^{-1}$) was estimated as described by Long and Hallgren (1985). Vapor pressure deficit (VPD, kPa) was estimated as:

$$\text{VPD} = X_s - \left(\frac{\text{RH}}{100} X_s \right)$$

$$X_s = 0.0061078 e^{\left[\frac{17.269 T}{237.30 + T} \right]}$$

where X_s (mol^{-1}) is saturation vapor pressure at the temperature of the air (T) in the leaf chamber and RH is percent relative

humidity (after Landsberg 1986).

Data analysis

Statistical summaries, simple linear regression, and non-linear regression (Johnson and Wichern 1982) were conducted with a PC-based software package (CRC-STATA, College Station, TX, CRC 1992). A Gauss-Newton nonlinear estimation routine was used to estimate the parameters α and A_{max} in models based on measured values for net carbon assimilation (A_{net}) and PPFD (after Landsberg 1986):

$$A = \frac{\alpha \text{PPFD} A_{max}}{\alpha \text{PPFD} + A_{max}}$$

where A_{max} is the modeled asymptotic maximum rate of assimilation and α is quantum yield.

Two empirical approaches were used to examine the influence of T and vapor pressure deficit (VPD) on assimilation rates. In the first approach, we examined the effects of T and VPD on residuals from the light response models. The residual analysis allowed us to evaluate the light response models using all observations across all temperatures, humidities, and irradiances and examine the nature of any observed lack-of-fit. The second approach examined T and VPD effects at saturating irradiances, i.e., at PPFDs greater than $750 \mu\text{mol m}^{-2} \text{s}^{-1}$, and where other factors limit photosynthesis (Nobel 1991). The results of subsetting the data in the second approach may have been affected by the correlations between PPFD, T , and

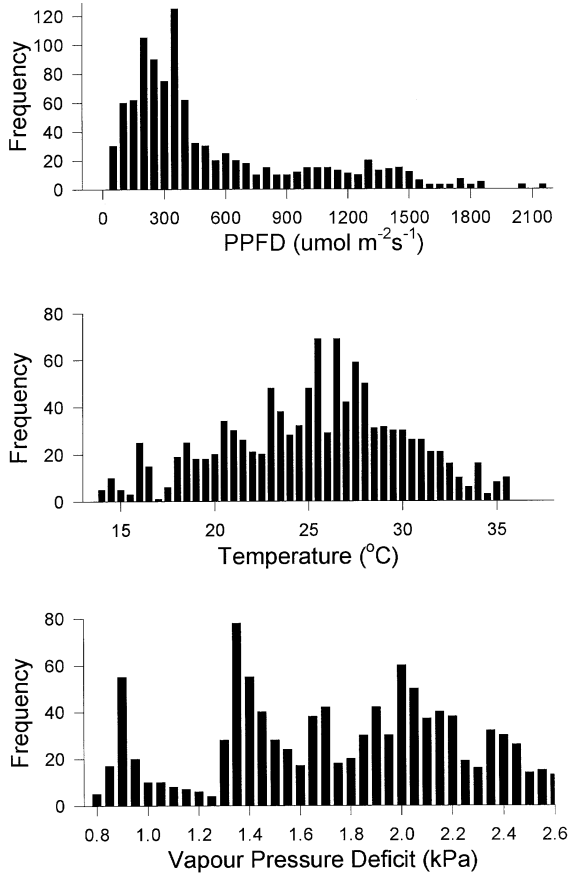


Figure 1. Distributions of leaf-incident light, air temperature, and vapor pressure deficit. Values are based on sensors attached to the leaf chamber.

VPD, i.e., observations under high light were more likely to be under high temperatures.

Results and discussion

Microclimate during sampling

Sampling under field conditions resulted in left-skewed distributions of photon flux densities (Figure 1), caused by sampling in lower- to mid-canopy positions and on overcast days. Temperatures (T) ranged between 13.8 and 36 °C with a mean of about 26 °C. Many low T observations were made in September when photosynthesis may also have been influenced by leaf senescence (Schaedle 1975), although we terminated sampling by mid-September, before color change and about five weeks before leaf fall. The VPD ranged from 0.8 to 2.8 kPa.

Significant vertical climatic gradients were observed on most sampling dates (Figure 2). In general, PPFD and T increased with increasing height in the canopy and CO_2 concentration decreased ($R^2 = 0.94, 0.50$ and 0.29 , respectively); however, there was no significant vertical VPD gradient (Figure 2c). Correlations between PPFD, T , and VPD constrained our ability to discern individual abiotic influences on CO_2 assimilation. In practice, separation of leaf T and VPD is impossible under field conditions (Aphalo and Jarvis 1991). In our study, T and VPD were significantly correlated ($R^2 = 0.43, P < 0.0005$) as were T and PPFD ($R^2 = 0.15, P < 0.0005$).

Soil water in the top 25 cm was generally high and varied little over the 1992 growing season. Mean percent soil water (and ranges) for Sites 1 to 4 were 23.3 (17.7 to 29.4), 26.8 (19.0 to 30.8), 27.3 (21.9 to 31.4), and 30.7 (26.1 to 31.2), respectively. Minima generally occurred in mid-July, and maxima in June and August.

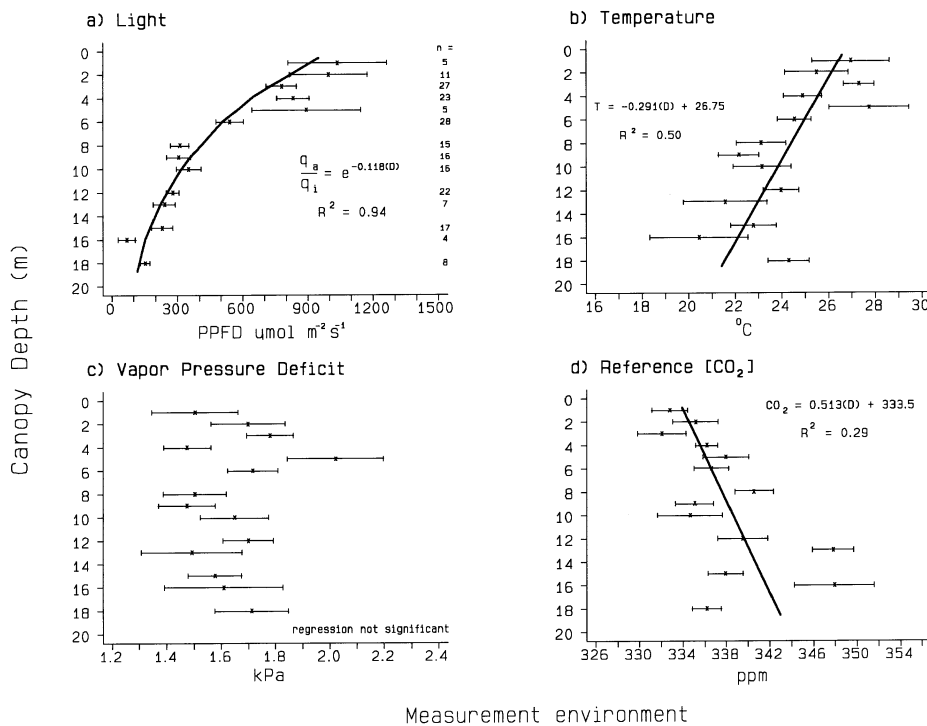


Figure 2. Distributions of light, temperature and vapor pressure deficit by canopy depth. For the nonlinear model of light extinction, q_a is the PPFD incident on the leaf and q_i is the maximum PPFD observed at the top of the tower during the sampling session.

Table 3. Summary of measured net photosynthesis (A_{net} , $\mu\text{mol m}^{-2} \text{s}^{-1}$), and incident light (PPFD, $\mu\text{mol m}^{-2} \text{s}^{-1}$) by three light categories: high (H) is ≥ 1000 , medium (M) is < 1000 and > 500 , and low (L) is ≤ 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Species	Irradiance	n	PPFD	A_{net}		
				Mean \pm SE	Min	Max
<i>Quercus coccinea</i>	H	41	1296 \pm 25.5	10.26 \pm 0.465	0.99	14.14
	M	30	756 \pm 24.6	7.83 \pm 0.324	4.16	11.52
	L	13	323 \pm 33.3	3.52 \pm 0.377	1.64	5.54
<i>Quercus prinus</i>	H	37	1348 \pm 40.6	9.91 \pm 0.552	3.61	17.80
	M	18	660 \pm 22.3	7.22 \pm 0.601	4.25	13.78
	L	39	342 \pm 14.4	5.26 \pm 0.413	1.29	12.11
<i>Quercus rubra</i>	H	13	1403 \pm 74.1	8.87 \pm 0.918	2.63	13.53
	M	2	644 \pm 56.6	4.95 \pm 2.651	2.30	7.60
	L	12	297 \pm 28.6	4.38 \pm 0.788	0.56	7.88
<i>Betula lenta</i>	H	30	1389 \pm 63.4	8.09 \pm 0.580	4.00	14.45
	M	38	661 \pm 21.9	4.97 \pm 0.364	2.03	12.14
	L	222	256 \pm 7.7	2.63 \pm 0.097	0.00	7.91
<i>Liriodendron tulipifera</i>	H	37	1350 \pm 44.4	7.85 \pm 0.447	1.92	13.07
	M	25	665 \pm 26.0	6.67 \pm 0.336	3.85	9.83
	L	29	366 \pm 13.6	4.18 \pm 0.363	1.27	10.16
<i>Quercus alba</i>	H	7	1452 \pm 87.7	7.59 \pm 1.201	3.23	11.34
	M	8	703 \pm 47.0	6.14 \pm 0.544	3.27	8.51
	L	14	274 \pm 24.3	2.75 \pm 0.465	0.88	6.85
<i>Carya glabra</i>	H	15	1283 \pm 61.2	7.22 \pm 0.707	3.60	12.11
	M	16	687 \pm 39.3	5.46 \pm 0.570	2.34	10.49
	L	68	305 \pm 11.6	3.79 \pm 0.257	0.33	12.77
<i>Acer rubrum</i>	H	30	1373 \pm 51.5	5.58 \pm 0.478	1.29	10.26
	M	24	676 \pm 25.7	4.52 \pm 0.334	0.97	7.36
	L	167	243 \pm 9.4	2.52 \pm 0.131	-0.56	10.16
<i>Nyssa sylvatica</i>	H	1	1400	3.91	3.91	3.91
	M	2	649 \pm 33.9	5.54 \pm 1.902	3.64	7.44
	L	29	242 \pm 18.4	2.91 \pm 0.213	0.93	5.94
<i>Cornus florida</i>	H	2	1501 \pm 41.0	3.58 \pm 0.657	2.93	4.24
	L	18	189 \pm 21.7	2.53 \pm 0.247	0.88	3.72
	L	36	107 \pm 14.7	1.13 \pm 0.121	0.19	2.66
<i>Fagus americana</i>	L	10	163 \pm 19.9	2.32 \pm 0.271	1.32	3.92

Net photosynthesis

Canopy trees, especially *Quercus spp.*, generally displayed the highest observed A_{net} and subcanopy trees generally had the lowest observed A_{net} (Table 3). Rates of A_{net} for individual observations ranged from 0.0 for *B. lenta* (minimum at lowest light category, < 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$) to 17.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for *Q. prinus* at high irradiances (> 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$). The mean A_{net} for PPFD values above 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ ranged from 1.7 (*A. pensylvanicum*) to 10.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (*Q. coccinea*). Rates of A_{net} declined with decreasing irradiance for all species, however the number of observations was low in certain light categories and species (e.g., *Q. rubra* and *N. sylvatica* at moderate irradiances and *N. sylvatica*, *A. pensylvanicum*, and *C. florida* at high irradiances).

Maximum observed net photosynthesis was strongly related to leaf nitrogen on a per unit area basis (Figure 3). Both A_{net} and leaf nitrogen concentrations were generally low for the subcanopy species *C. florida* and *A. pensylvanicum*, whereas intermediate values were observed for *B. lenta*, *A. rubrum*, and

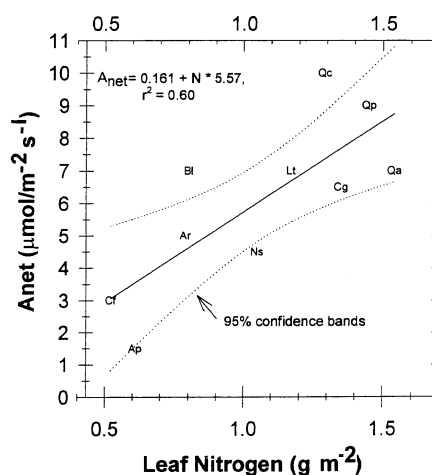


Figure 3. Relationship between mean light-saturated A_{net} and leaf nitrogen per unit area for the range of species included in this study. Ap = *A. pensylvanicum*, Ar = *A. rubrum*, Bl = *B. lenta*, Cf = *Cornus florida*, Cg = *Carya glabra*, Lt = *L. tulipifera*, Ns = *N. sylvatica*, Qa = *Q. alba*, Qc = *Q. coccinea*, Qp = *Q. prinus*.

Table 4. Comparison between observed CO₂ assimilation ($\mu\text{mol m}^{-2} \text{s}^{-1}$) in this and previous studies. Studies cited are: 1. Ranney et al. (1991), 2. Walters et al. (1993), 3. Kubiske and Abrams (1992), 4. Bahari et al. (1985), 5. Hinckley et al. (1978), 6. Weber and Gates (1990), 7. Dougherty and Hinckley (1981), and 8. Aubuchon et al. (1978).

Species	Source	Description			Net assimilation		
		Age	Light	Water status	Cited studies	Present study	
<i>Betula</i> spp.	1,2	Seedlings	Saturated	Drought	2 – 10	8.09	
	1,2	Seedlings	Saturated	Nondrought	7 – 16		
<i>Quercus rubra</i>	3	Seedlings	Saturated	Nondrought	5.5 – 7.5	8.87	
	2	Seedlings	Saturated	Nondrought	6.2		
	4	Saplings	Saturated	Nondrought	5.6		
	5	Saplings	Saturated	Nondrought	6.9		
	6	Saplings/mature	Saturated	Nondrought	13.0		
	6	Sapling/mature	Saturated	Drought	6.0		
<i>Quercus alba</i>	4	Saplings	Saturated	Nondrought	5.3	7.59	
	5	Saplings	Saturated	Nondrought	8.7		
	7	Mature	Saturated	Nondrought	> 8.8		
	7	Mature	Saturated	Drought	< 5.5		
	8	Mature	Low light	Site ambient	2.9		2.75
	8	Mature	Saturated	Site ambient	11.2 ¹		12.41 ²

¹ Maximum rate estimated by boundary-line analysis.

² Maximum rate estimated using nonlinear regression.

N. sylvatica. In our study, *B. lenta* was a subcanopy species and *A. rubrum* and *N. sylvatica* occupied the mid- to upper canopy, with a large portion of the leaf area occurring in mid-canopy positions (Vose et al. 1995). This may reflect a strategy for partitioning N, i.e., a low N content per unit leaf area, but a high leaf area per unit ground area. High rates of A_{net} were observed in association with high leaf nitrogen content for *L. tulipifera*, *Carya glabra*, and the three *Quercus* spp.

The assimilation values measured in our study are within the range of those observed for the same species in other studies (Table 4). We observed no seasonal trends in the maximum rate of A_{net} (A_{max}). Mean values were consistent through the growing season, even for subsets of data from similar conditions,

e.g., light-saturated conditions in early morning and from the upper canopy of selected species. Similarly, light-saturated A_{max} did not differ by canopy position, that is, light-saturated leaves had similar maximum photosynthetic rates regardless of canopy position. Because we did not purposefully resample the same leaves, leaf-to-leaf variation, even on the same trees and under similar environmental conditions, was greater than changes in A_{max} with leaf age.

Light response models

All nonlinear light response models were statistically significant ($P = 0.05$), both when fitted with pooled data and when fitted by species (Table 5). Model fits were best for *Quercus*

Table 5. Light response model parameters fit to measured data [$A_{\text{max}} = \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, α (quantum yield efficiency) = $A_{\text{max}}/\text{PPFD}$]. R^2 for all models adjusted for the mean and df. Both A_{max} and α were significant ($P < 0.001$ and $P < 0.05$, respectively) for all species except *C. florida* and *A. pensylvanicum*, where α was not significant ($P > 0.05$).

Species	<i>n</i>	A_{max}		α		R^2
		Estimate \pm SE	95% CI	Estimate \pm SE	95% CI	
<i>Quercus coccinea</i>	84	27.53 \pm 7.24	13.14 – 41.93	0.0133 \pm 0.0019	0.0095 – 0.171	0.576
<i>Betula lenta</i>	290	16.95 \pm 1.95	13.10 – 20.79	0.0115 \pm 0.0007	0.0100 – 0.0129	0.545
<i>Quercus prinus</i>	94	14.54 \pm 1.80	10.97 – 18.11	0.0234 \pm 0.0042	0.0151 – 0.0317	0.348
<i>Quercus rubra</i>	27	12.77 \pm 2.83	6.93 – 18.60	0.0213 \pm 0.0078	0.0053 – 0.0373	0.407
<i>Quercus alba</i>	29	12.41 \pm 3.03	6.20 – 18.63	0.0149 \pm 0.0039	0.0068 – 0.0229	0.533
<i>Liriodendron tulipifera</i>	91	10.18 \pm 1.10	8.00 – 12.36	0.0248 \pm 0.0054	0.0141 – 0.0355	0.281
<i>Carya glabra</i>	99	9.42 \pm 1.28	6.87 – 11.96	0.0217 \pm 0.0039	0.0139 – 0.0294	0.297
<i>Acer rubrum</i>	221	7.24 \pm 0.72	5.81 – 8.66	0.0167 \pm 0.0022	0.0124 – 0.0210	0.273
<i>Nyssa sylvatica</i>	32	5.62 \pm 1.16	3.25 – 7.98	0.0285 \pm 0.0093	0.0096 – 0.0474	0.271
<i>Cornus florida</i>	20	3.40 \pm 0.63	2.08 – 4.71	0.0662 \pm 0.0451	–0.0285 – 0.1610	–0.001
<i>Acer pensylvanicum</i>	41	1.63 \pm 0.22	1.18 – 2.08	0.0772 \pm 0.0427	–0.0092 – 0.1637	0.119
All samples	1038	14.19 \pm 0.73	12.75 – 15.63	0.0148 \pm 0.0007	0.0134 – 0.0161	0.513

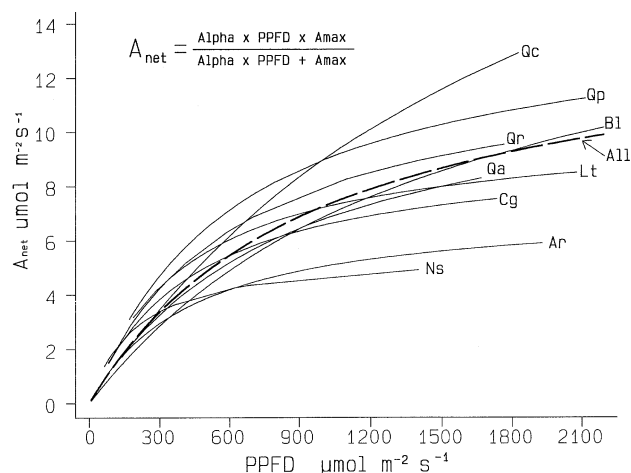


Figure 4. Non-linear light response models (Table 5) plotted for all species: *Acer pensylvanicum* (Ap), *Cornus florida* (Cf), *Nyssa sylvatica* (Ns), *A. rubrum* (Ar), *Carya glabra* (Cg), *Liriodendron tulipifera* (Lt), *Quercus alba* (Qa), *Q. rubra* (Qr), *Q. prinus* (Qp), *Q. coccinea* (Qc), *B. lenta* (B1) and all species pooled (All).

spp. and *B. lenta*, poorest for the subcanopy species, and intermediate for the remaining species. The pooled data model accounted for about 50% of the observed variation. The scarcity of observations at high irradiance may account for the poor fit for *A. pensylvanicum* and *C. florida*. Parameters for *F. americana* could not be estimated.

The estimated maximum assimilation values (A_{\max}) fall into the same general order as the measured maximum values (Figure 4, Table 5). One notable exception is that estimated A_{\max} of *B. lenta* is higher than that of *Q. prinus* and *Q. rubra*. Masarovicova (1992) determined A_{\max} values for two oak species of 27.2 and 20.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$ using the boundary line technique. Our estimated A_{\max} values are high for mature trees of some species (e.g., 27.53 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for *Q. coccinea*), probably because it is an estimate of an asymptote. The measured data best fit a model with a high asymptote; however, A_{\max} would not be approached under ambient light conditions. Un-

der high irradiance (2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$), the predicted A_{net} of 13.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ is similar to the observed A_{net} for *Q. coccinea*.

Based on 95% confidence intervals as the criteria (Sokol and Rohlf 1981), there are significant differences in A_{\max} and quantum yield among some species. For example, A_{\max} values for *Q. coccinea* and *B. lenta* (lower 95% CI = 13.1) are significantly higher than those for *L. tulipifera*, *C. glabra*, and *A. rubrum*. (upper 95% CI = 12.4). Abrams et al. (1994) divided 17 temperate species into three categories based on habitat characteristics (i.e., xeric, mesic and wet-mesic) in a comparison between wet and dry years. Our observations suggest a landscape-level model may also be simplified by grouping species into categories of similar ecophysiological response. However, these categories do not appear to correspond to typical habitat characteristics, e.g., *Q. coccinea*, a xeric species, appears to fall into the same category as *B. lenta*, a mesic species, and *Q. prinus* should, apparently, be grouped with *Q. rubra*.

Species with high estimated A_{\max} generally had lower estimated quantum yields than species with low A_{net} (Table 5). Conversely, species with generally low A_{net} as found in the subcanopy in this study (*N. sylvatica*, *C. florida*, and *A. pensylvanicum*), displayed more efficient use of light at low irradiances.

Temperature and VPD effects

Analyses of residual variation after fitting the light response models indicate about 10% of the variation in the residuals was related to squared T , VPD, and squared VPD (Table 6). These models of residuals are an attempt to understand the variation remaining after fitting the assimilation light response models (Equation 1) discussed above. A curvilinear response of T was expected (Lloyd and Woolhouse 1976, Kirschbaum and Farkuhar 1984, Nobel 1991) but the curvilinear VPD effect was unexpected and may have been due, in part, to the correlation between T and VPD, and, in part, to our assumption of equivalent chamber air and leaf temperatures. Some of the remaining unexplained variation may be related to differences in respiration rates among species. However, we have few data on leaf

Table 6. Models of residuals from the light response models of the influence of temperature and vapor pressure deficit (T and T^2 in $^{\circ}\text{C}$, VPD and VPD 2 in kPa). Significant differences denoted by: * = $P < 0.10$, ** = $P < 0.05$, *** = $P < 0.001$, and ns = not significant.

Species	n	T	T^2	VPD	VPD 2	y-Intercept	R^2
<i>Acer pensylvanicum</i>	41	ns	0.004***	-1.56***	ns	0.68*	0.25
<i>Acer rubrum</i>	221	0.919***	-0.021 ***	ns	0.23 **	-10.04 ***	0.16
<i>Betula lenta</i>	290	0.956 ***	-0.021 ***	1.20***	ns	-11.4 ***	0.16
<i>Cornus florida</i>	20	0.269**	ns	ns	ns	-6.66	0.34
<i>Carya glabra</i>	99	-0.305	ns	12.42 **	-2.68 **	-4.92	0.28
<i>Liriodendron tulipifera</i>	91	3.40 **	-0.061 ***	12.97 **	-3.65 ***	-57.21 ***	0.27
<i>Nyssa sylvatica</i>	32	ns	0.006***	-9.78 **	2.69 **	4.93	0.45
<i>Quercus alba</i>	29	ns	ns	-34.67*	11.22*	25.5*	0.07
<i>Quercus coccinea</i>	84	4.50 **	-0.079 **	16.12 ***	-4.24 ***	-78.02 **	0.32
<i>Quercus prinus</i>	94	ns	-0.005***	2.73 ***	ns	ns	0.11
<i>Quercus rubra</i>	27	21.71***	-0.504**	4.59**	ns	-306.17**	0.21
All samples	1028	0.43 ***	-0.011 ***	4.86 ***	-1.05 ***	-8.61 ***	0.10

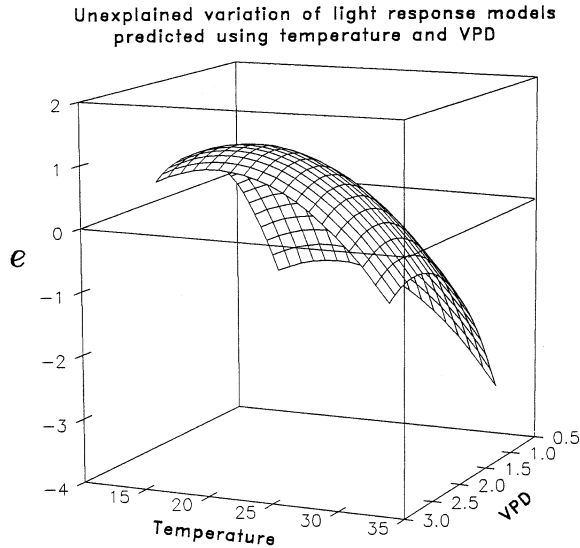


Figure 5. Three-dimensional surface plot of model residuals (e) in the pooled light-response function (Table 6).

respiration rate and our empirical approach cannot separate the influences of temperature on respiration and photosynthesis (Hari et al. 1991). Also, our data were not appropriate for discerning if species that spanned the elevation range acclimated to differing temperature regimes, resulting in differing optimum temperatures (Rada et al. 1992).

Analysis of residuals indicates small but statistically significant effects of T and VPD. For example, using the pooled-species model with a typical Coweeta climate (19 °C and 2 kPa VPD), our predicted A_{net} is about 1 $\mu\text{mol m}^{-2} \text{s}^{-1}$ below observed A_{net} (Figure 5). Under climatic conditions of 1 kPa VPD and 33 °C, we predicted A_{net} to be approximately 3 $\mu\text{mol m}^{-2} \text{s}^{-1}$ below observed A_{net} (Figure 5). However, the climatic conditions that cause these larger residuals were seldom observed while sampling (Figure 1).

The temperature and humidity response models for individual species varied in quality of fit (Table 6). For some species (*A. rubrum* and *B. lenta*) temperature alone was significant ($P < 0.0005$, $R^2 \approx 0.16$), T was not significant for *C. glabra* and *N. sylvatica* but VPD was significant ($P < 0.005$, $R^2 = 0.28$ and 0.46), and for *L. tulipifera* and *Q. coccinea* both T and VPD

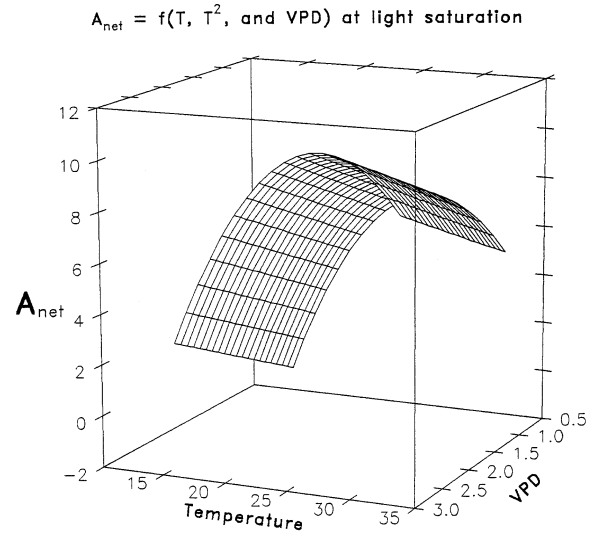


Figure 6. Three-dimensional surface of the residuals from the net photosynthesis model at light saturation (A_{net} at PPFD of $> 750 \mu\text{mol m}^{-2} \text{s}^{-1}$) as a function of temperature and vapor pressure deficit, all species pooled (Table 7).

were significant ($P < 0.005$, $R^2 = 0.27$ and 0.32). The lack of fit for some species could be because the species exhibited no response to T and VPD or because of the limited range of measured T and VPD values for each species.

Effects of T and VPD in saturating light

Temperature and VPD significantly influence A_{net} when light-saturated data for all species are pooled ($n = 266$, $P < 0.005$, $R^2 = 0.15$, Table 7, Figure 6). Squared VPD is not significant. The effects of T and VPD varied by species, and nonlinear models for *N. sylvatica*, *C. florida*, *A. pensylvanicum*, and *F. americana* would not converge. The T and VPD response model for all samples is plotted in Figure 6. Response across the VPD range is linear, 3.1 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ across all temperatures. Day et al. (1991) also observed increasing A_{net} with increasing VPD. The curvilinear response to T and VPD was greatest (10.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$) at 27 °C and 0.8 kPa, respectively, and least at 15 °C and 2.8 kPa (2.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$). The $A_{\text{net}}-T$ relationship increases to a maximum near 26 °C, and there is a

Table 7. Models predicting the influence of temperature (T and T^2 in °C) and vapor pressure deficit (VPD in kPa) on A_{net} above light saturation ($> 750 \mu\text{mol PPFD m}^{-2} \text{s}^{-1}$). Significant differences denoted by: * = $P < 0.10$, ** = $P < 0.05$, *** = $P < 0.001$, and ns = not significant.

Species	n	T	T^2	VPD	Intercept	R^2
<i>Acer rubrum</i>	37	2.31***	-0.046***	ns	-21.7	0.44
<i>Betula lenta</i>	39	2.59**	-0.050***	5.03**	-33.4**	0.29
<i>Liriodendron tulipifera</i>	44	10.22**	-0.174***	ns	-140.6	0.31
<i>Quercus coccinea</i>	55	5.72*	-0.093**	ns	-76.8**	0.20
<i>Carya glabra</i>	21	ns	ns	3.75***	ns	0.47
<i>Quercus alba</i>	10	ns	ns	3.75***	ns	0.43
All species	266	3.002***	-0.0559***	1.735**	-34.5***	0.15

rapid decline above that temperature. The $A_{\text{net}}\text{-VPD}$ relationship is more difficult to explain. Increasing VPD tends to reduce stomatal conductance, which in turn should reduce A_{net} . However, our model fits indicate a slight increase in A_{net} with an increase in VPD. Given the variation in the surface fit, revealed in scatter plots and R^2 values, this result may be an artifact of our sampling, measurement, or modeling procedures.

In summary, we found a broad range in observed maximum assimilation rate for twelve species of broad-leaved deciduous tree species. Differences in models of net assimilation versus light were statistically significant, particularly for typical understory versus overstory species. Small, although still significant, differences were found among overstory species, and species with similar site affinities did not always have similar light versus assimilation relationships. After accounting for the light response, we observed curvilinear effects of temperature and vapor pressure deficit on net assimilation.

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