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Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest

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Abstract. Canopy structure and light interception were measured in an 18-m tall, closed canopy deciduous forest of sugar maple (*Acer saccharum*) in southwestern Wisconsin, USA, and related to leaf structural characteristics, N content, and leaf photosynthetic capacity. Light attenuation in the forest occurred primarily in the upper and middle portions of the canopy. Forest stand leaf area index (LAI) and its distribution with respect to canopy height were estimated from canopy transmittance values independently verified with a combined leaf litterfall and point-intersect method. Leaf mass, N and $A_{\max}$ per unit area (LMA, N/area and $A_{\max}$/area, respectively) all decreased continuously by over two-fold from the upper to lower canopy, and these traits were strongly correlated with cumulative leaf area above the leaf position in the canopy. In contrast, neither N concentration nor $A_{\max}$ per unit mass varied significantly in relation to the vertical canopy gradient. Since leaf N concentration showed no consistent pattern with respect to canopy position, the observed vertical pattern in N/area is a direct consequence of vertical variation of LMA. N/area and LMA were strongly correlated with $A_{\max}$/area among different canopy positions ($r^2=0.81$ and $r^2=0.66$, respectively), indicating that vertical variation in area-based photosynthetic capacity can also be attributed to variation in LMA. A model of whole-canopy photosynthesis was used to show that observed or hypothetical canopy mass distributions toward higher LMA (and hence higher N/area) in the upper portions of the canopy tended to increase integrated daily canopy photosynthesis over other LMA distribution patterns. Empirical relationships between leaf and canopy-level characteristics may help resolve problems associated with scaling gas exchange measurements made at the leaf level to the individual tree crown and forest canopy-level.

Key words: *Acer saccharum* – Photosynthesis – Forest canopy – Sugar maple – Nitrogen

Forest canopies are spatially heterogeneous environments. The distribution, size and orientation of leaves in space determines the pattern of light availability within the canopy, controlling such processes as leaf development, leaf energy balance and water use, and photosynthesis (Norman and Campbell 1989). The presence of leaves to intercept light in upper portions of the canopy will have a strong effect on all these processes in descending portions of the canopy. These effects should be particularly profound for species displaying large, broad leaves, yet relationships among canopy structure, light interception, leaf morphology and photosynthesis are still poorly understood in broad-leaved forests (Eliás et al. 1989). Assessing vertical variation in leaf distribution and its relation to patterns of photosynthesis among different canopy positions should provide valuable insight into how carbon and nutrient resources are partitioned within forest canopies (Field 1991).

Measurements of the ratio of leaf dry mass to leaf area (LMA; leaf mass per area) and its relationship to variation in area-based photosynthetic capacity between different canopy layers may be an effective means of integrating influences of canopy structure and light environment on leaf photosynthetic performance (Jurik 1986; Oren et al. 1986). Leaves that develop in high light have high LMA as a result of increased leaf thickness and increased mesophyll cell density (Chabot et al. 1979; Witkowski and Lamont 1991). Previous studies have shown that LMA generally increases from the bottom to the top of the canopy in evergreen species (Hollinger 1989; Lewandowska and Jarvis 1977; Schulze et al. 1977). In controlled-chamber studies, photosynthetic capacity of leaves grown in different light levels varies with LMA (Björkman 1981; Nobel et al. 1975), but little such data is available for forest-grown deciduous trees (Reich et al. 1991)

Large variation in leaf nitrogen content per unit leaf area (N/area) has also been observed among different canopy positions (Hollinger 1989; Hirose and Werger 1987). Leaf N/area content is closely correlated with photosynthetic capacity per unit area in leaves within

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plant canopies (DeJong and Doyle 1985; Hollinger 1989). Hirose and Werger (1987) suggested that N/area varies with light availability in plant canopies in such a way as to optimize daily canopy photosynthesis. According to econometric and evolutionary arguments, N allocation patterns within a plant canopy should change according to the light extinction properties of a canopy so as to maximize the rate of photosynthetic carbon assimilation per unit N allocated to a leaf (Field 1983; Hirose and Werger 1987; Mooney and Gulmon 1979). These theories were derived from measurements in short-stature, herbaceous and open-canopy shrub communities where N is redistributed within the canopy throughout the growing season as leaf senescence in lower canopy layers occurs (Field 1983; Hirose and Werger 1987). In closed-canopy deciduous forests, though, leaf senescence occurs within a short period of time in the autumn for the entire canopy so that N cannot be reallocated during the growing season. Furthermore, previous models have not accounted for variation in LMA between different canopy layers as a source of variation in area-based photosynthetic capacity (Field 1983) or have confounded variation in mass-based leaf N with variation in LMA as causes of variation in area-based leaf N (Hirose and Werger 1987). Hence, it is not known to what extent canopy photosynthesis in closed forests is related to patterns in N allocation versus patterns in the allocation of leaf mass to leaf area within a canopy (Gutschick and Wiegel 1988).

The goal of this study is to integrate measurements of canopy structure (i.e. vertical patterns in leaf area), canopy light environment and leaf photosynthetic characteristics to address these issues in a hardwood forest canopy. We analyze interrelationships among LMA, N content and photosynthetic rate (both area- and mass-based measures), canopy position and radiation interception of different canopy layers and provide an example of how these empirical relationships could be useful in scaling vertical patterns in leaf structure and chemistry to predict potential canopy photosynthesis in broad-leaved closed forests. We use a model of canopy daily net carbon assimilation to determine if canopy photosynthesis is maximized by the observed distribution of mass and N allocation to leaf area among canopy positions compared to a set of alternate distributions.

Materials and methods

A deciduous hardwood forest in southwestern Wisconsin, USA (42° 59′N, 90° 07′W) was selected for study. The study site was located in a southward-facing, ridgetop forest stand (elevation 360 m) of relatively uniform second-growth hardwoods 60–80 years of age. Ridgetop sites in the region typically support mesic hardwood forests dominated by sugar maple (*Acer saccharum* Marsh.) with lesser components of white oak (*Quercus alba* L.) and basswood (*Tilia americana* L.) (Curtis 1979). The stand was dominated by sugar maple, which comprised more than 60% of the stand basal area and over 75% of stand litterfall leaf area index (see Results), so measurements of leaf morphology and physiology were made on trees of this species only. Average overstory tree height for the stand was 18 m.

A 50 m × 50 m plot near the center of the stand was used for all measurements presented here to minimize edge effects on leaf and canopy characteristics. Within this plot, 8 randomly- located 0.25 m^2 litterfall traps were emptied at 1 or 2-week intervals during periods of leaf fall. Green leaf area index was calculated from litterfall mass using a weighted mean of leaf mass per unit area (Jurik et al. 1985). A tower was constructed to provide access to three representative dominant sugar maple tree crowns in the center of the plot for detailed physiological measurements. Climbing ladders were used to access additional trees in the stand to examine vertical profiles in leaf traits.

Radiation transmittance and stand structure measurements

Measurements of canopy transmittance of direct-beam photosynthetically active radiation (400–700 nm wavebands) can be used to provide a non-destructive estimate of forest stand leaf area index (LAI) based on the theories developed by Lang and Xiang (1986), Lang (1987) and Norman and Jarvis (1975). We measured transmittance beneath the canopy of the stand in this study with a portable integrating radiometer (Model SF-80, Decagon Devices, Pullman, WA, USA) using techniques similar to Pierce and Running (1988) and Bolstad and Gower (1990). Transmittance was measured on two clear, cloudless days when the canopy was in full leaf (26 August and 10 September) between 1030 and 1400 h solar time. On both days, canopy-wide radiation transmittance to the forest understory was measured at 42 randomly-located points in the study plot, each covering approximately 10 m^2 ground area. At each point in the stand, a series of radiation measurements were made in a circle of 45° angle increments in the horizontal plane at 1.4 m above the ground. The radiometer sampled a linear array of 80 sensors at 1-cm intervals along a rod and instantaneously integrated data for all the sensors. Incoming radiation was measured nearby in a large clearing once prior to measurements in the stand and once during and after measurements. Canopy transmittance could then be calculated as the ratio of photosynthetically-active radiation beneath the canopy to radiation in the open and averaged geometrically for calculations of LAI (Lang and Xiang 1986).

Calculations of LAI based on canopy transmittance data have either used gap fraction methods (Norman and Campbell 1989) or a negative exponential relation between transmittance and LAI [e.g. Beer-Lambert law; see Lang (1987), Pierce and Running (1988)]. Either technique involves assumptions of the leaf angle distribution in the canopy and may not account for light scattering and penumbral effects in forest canopies (Jarvis and Leverenz 1983). Still, errors are typically only a few percent under these assumptions, and radiation measurements taken near solar noon will minimize penumbral effects (Norman and Campbell 1989). Thus we used canopy transmittance (τ) measurements to estimate LAI on the basis of the Beer-Lambert Law

$$\tau = \exp(-k \bullet \mathrm{LAI})$$

To solve for LAI using this equation we used sun zenith angles specific to each measurement day and time to compute a radiation attenuation coefficient (k) using calculations in Campbell (1986) and assuming a spherical leaf angle distribution. Models which account for foliage aggregation do not appreciably improve the accuracy of LAI estimates (Baldocchi et al. 1985; Caldwell et al. 1986). LAI calculations using a more complex model of radiation transmission and scattering based on the approach of Norman and Jarvis (1975) yielded values within 2% of those calculated using the Beer-Lambert relation (J. Norman, personal communication; data not shown).

Vertical profiles of canopy transmittance within the forest canopy were developed according to a sampling design similar to Bolstad and Gower (1990). Measurements of vertical variation in canopy transmittance were made from the tower at 1 m intervals within the canopy at mid-day (1100 to 1400 h solar time) on three sunny days in August and September when the canopy was in full leaf. On each day, transmittance was measured along the 80-sensor array for eight points at a given height for a total of 640 measurements per height and day. Stand-wide leaf area distribution at 1 m intervals was also measured independently using a point-intersect method (Aber 1979). The fraction of foliage at each canopy level from this method was multiplied by the total litterfall LAI to determine LAI at a given canopy level.

Gas exchange measurements

A combination of field and laboratory gas exchange measurements were used in this study to assess canopy photosynthetic characteristics by sampling leaf populations at four different canopy positions: 15 m high in the canopy, corresponding to the upper portion of dominant crown positions in the canopy; 12 m, corresponding to the main portion of the canopy; 9 m, corresponding to the lower portion of dominant tree crowns; and 5 m corresponding to subcanopy tree crowns (laboratory measurements only). Laboratory measurements were designed to measure the response of photosynthesis to photosynthetic photon flux density (PPFD) under controlled conditions for leaves from different canopy positions using a steady-state gas exchange system described in Bingham et al. (1980). In the field, leaves at arbitrarily-located canopy positions near the tower were tagged and the connecting branch was cut, recut under water, and taken to Madison, WI for laboratory gas exchange measurements. Branches were kept rehydrated and stored under dark, humid conditions until gas exchange measurements were made.

The laboratory gas exchange system consisted of a BINOS IRGA (Leybold-Heraeus, Inc., Hanau, FRG) and a leaf chamber and control circuitry (Bingham Interspace Model BI-2, Hyde Park, UT, USA). Water vapor content of the chamber air was measured using dew-point hygrometry (General Eastern Corp., Watertown, MA). Gas exchange measurements and calculations utilized null-balance techniques (Ball 1987) using equations based on the model of von Caemmerer and Farquhar (1981). Further details on the laboratory gas exchange techniques and instrumentation are provided in Ellsworth and Reich (1992). PPFD response curves were fitted to a non-rectangular hyperbola model using non-linear least-squares techniques (Hanson et al. 1987). The model generally described more than 95% of the variation in photosynthesis data for individual leaves. PPFD response curve parameters derived by the model are photosynthetic capacity at 364 μbars bar^{-1} partial pressure of CO_2 and $25.0 \pm 0.1°$ C (e.g. A_{max}/area), the point at which net photosynthesis compensates dark respiration (CP), and dark respiration rate (R_d). Upon completion of PPFD response curves, chlorophyll was extracted from disks from the leaves using dimethyl sulfoxide according to Hiscox and Israelstam (1979).

Gas exchange measurements were also taken in the field to establish relationships between photosynthesis measured under ambient conditions and LMA and N for leaves at different canopy positions. The field gas exchange system consisted of a portable IRGA and leaf chamber (Model LCA-2, Analytical Development Corporation, Hoddesdon, England) operated in the differential mode (Ellsworth and Reich 1992). Gas exchange measurements made with the field and laboratory systems under the same conditions showed close agreement for measurements of leaves varying widely in photosynthetic capacity (Ellsworth and Reich 1992; D.S. Ellsworth, unpublished data).

Field measurements of leaf photosynthetic CO_2 assimilation (A) and conductance to water vapor (g) were made for randomly-located leaves at three different levels in the stand canopy (15 m, 12 m, and 9 m) over the course of six sunny days from May–August 1989. Measurements were taken for leaves in their natural orientation located in sunflecks for 5+minutes in order to minimize effects of leaf induction state (Pearcy 1990). For measurements at light-saturation ($PPFD > 400$ μmol m^{-2} s^{-1}; see below) and low leaf-to-air vapor pressure difference ($VPD < 1.5$ kPa), we consider the three highest A measurements for a given canopy position and tree to indicate the maximum rate of photosynthesis at that position (A_{max}/area; Ellsworth and Reich 1992). Typically thirty A measurements for a given canopy position and tree were made per day. Predawn leaf water potential measured at two to three week intervals throughout the growing season using the pressure chamber technique always exceeded -0.5 MPa during the study. Daytime leaf water potentials less than -2.1 MPa were never observed in the canopy.

Leaves exhibiting high rates of photosynthesis during diurnal courses of photosynthesis measurements were tagged and the three leaves exhibiting the highest rates of photosynthesis (A_{max}/area) were harvested at the end of the day, stored on ice, and transported back to the laboratory for determinations of leaf area without petiole (LI-3000, Li-Cor, Inc., Lincoln, NE, USA) and dry mass (dried to a constant mass at 70° C). Total leaf kjeldahl N concentration was determined by the University of Wisconsin Soil and Plant Analysis Laboratory on a subset of the harvested leaves corresponding to the highest A_{max}/area measurement for a given canopy position, tree and sampling date.

Canopy modelling

Data from the present study were used to parameterize a simple empirical model of canopy photosynthesis in order to determine if the observed distribution of N and mass in the canopy maximizes whole-canopy daily carbon assimilation for the observed stand structure. We utilized a canopy carbon assimilation model based on Reich et al. (1990) which successfully predicted relative differences in primary productivity among seven deciduous forest stands in Wisconsin. The version used here incorporates a more complex radiation submodel using the approach of Norman (1980, 1993). In the present model, we assume the following: 1) radiation absorption by non-foliar surfaces is minimal, 2) light is attenuated by the canopy following ideal Lambertian principles, 3) all photosynthetic responses to PPFD reach steady-state within the 5-minute time scale of the model, 4) leaf photosynthesis is a function of leaf N content and stomatal limitations to photosynthesis are small, 5) vertical profiles in PPFD are considered the single most important environmental gradient driving canopy-wide photosynthesis, with limitations by other environmental factors (temperature, vapor pressure deficits, and CO_2) not considered. The model approximates the canopy by a series of horizontal layers, each comprised of leaves of homogeneous photosynthetic characteristics (e.g. "big leaf" approach).

Average net photosynthesis is predicted by the model for each level of the canopy over 5-minute intervals for an entire day. Required inputs (all of which were quantified in the present study) include: leaf N and LMA as well as LAI specific to each canopy level (Figs. 1 and 2), leaf light response curve characteristics (Table 1), and incoming PPFD at the top of the canopy. Above-canopy PPFD was measured with a quantum sensor (Model LI-190, Li-Cor, Lincoln,

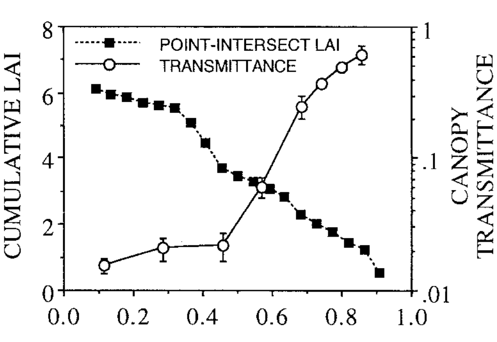

Fig. 1. Vertical pattern of cumulative leaf area index (*LAI*) determined by a combined point-intersect and litterfall method and pattern of canopy radiation transmittance (log scale) as a function of relative height in a deciduous forest canopy in Wisconsin. A relative height of 1.0 denotes the top of the canopy (lowest cumulative *LAI* values)

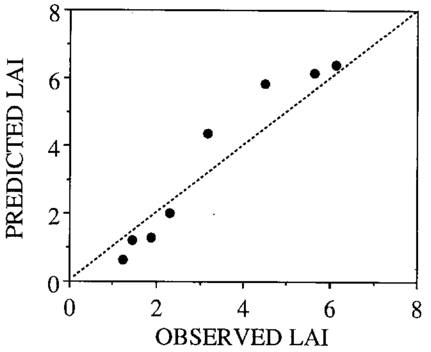

Fig. 2. Comparison of cumulative *LAI* using two independent methods: *LAI* predicted from canopy transmittance measurements using the Beer-Lambert Law (see text), and *LAI* measured at different levels of the canopy using a combined litterfall and point-intersect method ('observed *LAI*'). *Dashed line* – 1 : 1 relationship between predicted and observed LAI

NE) mounted on the tower above the canopy and continuously monitored at 5-second intervals with 5-minute averaging. PPFD within the canopy was also continuously measured at the same time periods using gallium arsenide phosphide photodiodes (Model G-1118, Hamamatsu, Japan) calibrated to agreement against a standard quantum sensor in natural and artificial light and mounted on leaves at appropriate canopy positions. We used the relationship between A_{max} and N specific to sugar maple (this study, see Results) to predict leaf photosynthesis at any point in the canopy based on LMA and N /mass. We predicted *A* at a given canopy layer using the fitted PPFD response curves developed for different canopy levels (see Results; Table 1) and incident PPFD estimated at that level by a radiation transmission submodel. An outline of the model structure and sample algorithms can be found in Reich et al. (1990). Although effects of water stress, ozone and mid-day stomatal closure can be simulated with the model, for our purposes here we have assumed no such limitations to *A*.

In the radiation transmission submodel, the average LAI at each canopy level that was sunlit (intercepting direct sunlight) or shaded (receiving only diffuse light) was treated separately as recommended previously (Norman 1993). Sunlit LAI at each canopy level was estimated using calculations of the projected LAI shading a given point in the canopy as a function of sun zenith angle from Norman (1980) and shaded LAI was taken as the difference between the total projected LAI of the level and sunlit LAI. Incident PPFD at a given canopy level was also separately predicted for sunlit and shaded leaves in each layer (Norman 1980) assuming that sunlit leaves received direct + diffuse PPFD and shaded leaves received only diffuse PPFD. Penumbral effects, which may be large under tall plant canopies, have been ignored in the present treatment due to inadequate data regarding the 3-dimensional distribution of individual leaves in the canopy and a lack of submodels that account for the complex geometry of forest canopies comprised of leaves with highly irregular shapes such as sugar maple. Maximum diffuse PPFD for the 15 m, 12 m and 9 m canopy levels was determined from PPFD data from the photodiodes according to protocol used previously (Ellsworth and Reich 1992). Diffuse PPFD incident on shaded leaves was then calculated for each 5-minute interval using the maximum diffuse PPFD and sun zenith angle at that time of day. Direct PPFD normal to the leaf plane was calculated as a function of the empirically-determined above-canopy PPFD data and sun zenith angle. Individual contributions of *A* from sunlit and shaded LAI were summed for each canopy layer and integrated over a 24-h period to represent daily canopy net carbon assimilation (daily *A*).

Daily *A* was modelled for each of four canopy layers corresponding to canopy positions where photosynthetic measurements were taken (18–15 m, 15–12 m, 12–9 m and 9–5 m) and averaged over four representative sunny summer days (21 June, 5 July, 18 July and 18 August) for which empirical data were available in order to estimate summertime daily canopy photosynthetic potential. We predicted daily canopy *A* for several alternative scenarios of mass distribution in the canopy using: 1) observed N and LMA distributions among canopy layers, 2) Uniform LMA and N distributions in the canopy corresponding to the LAI-weighted canopy average for these parameters, 3) A series in which the average LMA of each successive canopy layer was doubled relative to that of the remaining layers (e.g. LMA = 2 : 1 : 1 : 1 among the four canopy layers; LMA = 1 : 2 : 1 : 1; etc.). For all simulations, we assumed that LAI was distributed as observed in this study from the transmittance measurements and that canopy standing N was constant (5.9 g N • m^{-2} land area; calculated using LAI-weighted average of the data). Average leaf N /mass was considered constant in the simulations (18.8 mg g^{-1}; LAI-weighted average of different canopy levels) so that we could examine the implications of different N /area distributions in the canopy on vertical patterns in canopy carbon assimilation resulting solely from differences in LMA among canopy levels.

Table 1. Photosynthetic characteristics for sugar maple leaves at 15 m, 12 m, 9 m and 5 m height in the canopy of a forest stand in southwestern Wisconsin, USA. Parameters were derived from a non-rectangular hyperbola model (Hanson et al. 1987) fitted to data from steady-state responses of photosynthesis to PPFD for each leaf[1]. Within a row, means ± SE followed by a different letter are significantly different ($p < 0.05$, Studentized Range test)

Characteristic	15 m height	12 m height	9 m height	5 m height
A_{max}/area (μmol $m^{-2} s^{-1}$)	10.9 ± 1.2 a	8.5 ± 1.2 bc	6.4 ± 1.1 c	5.2 ± 0.2 d
A_{max}/mass (nmol $g^{-1} s^{-1}$)	136.5 ± 13.3 a	142.6 ± 14.9 a	152.9 ± 34.3 a	152.5 ± 6.7 a
$PPFD_{sat}$ (μmol quanta $m^{-2} s^{-1}$)	384 ± 62 ab	335 ± 34 ab	280 ± 5 b	184 ± 22 bc
$PPFD_{comp}$ (μmol quanta $m^{-2} s^{-1}$)	8 ± 2 a	5 ± 0 bc	4 ± 1 cd	3 ± 0 d
R_d/area (μmol $m^{-2} s^{-1}$)	0.83 ± 0.25 a	0.39 ± 0.04 bc	0.25 ± 0.01 c	0.20 ± 0.03 cd
R_d/mass (nmol $g^{-1} s^{-1}$)	10.7 ± 4.3 a	6.7 ± 0.9 ab	5.8 ± 0.4 c	5.9 ± 0.6 abc
chl/mass (mg g^{-1})	5.5 ± 0.4 a	7.4 ± 0.8 b	10.6 ± 0.6 c	12.3 ± 0.2 d

[1] Characteristics are based on laboratory measurements made on 2–6 leaves from different branches and trees at a given canopy position. A_{max} is the maximum photosynthetic rate under controlled conditions (leaf temperature = 25.0°C ± 0.1, leaf to air vapor pressure difference < 1.0 KPa, and ambient partial pressure of $CO_2 = 364 \pm 1$ μbar bar^{-1}) expressed on an area-basis (A_{max}/area) or on a dry mass-basis (A_{max}/mass) and $PPFD_{sat}$ is the PPFD level required to reach 95% A_{max}/area. $PPFD_{comp}$ is the PPFD required to balance photosynthesis and respiration, R_d is the dark respiration rate (area- or mass-based) of the leaf before receiving illumination, and chl/mass is the total chlorophyll content of the leaf per unit dry mass

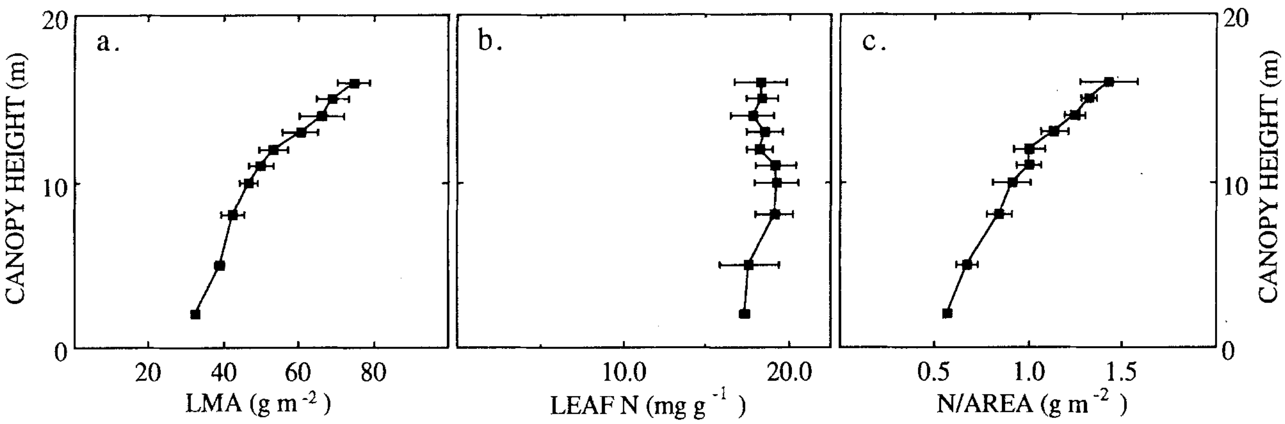

Fig. 3a–c. Vertical variation in leaf mass per unit area (*LMA*), mass-based leaf N concentration (*LEAF N*) and leaf N content per unit area (N/area) with canopy height. Error bars represent variation (± 1 SE) among 6 different locations within the stand

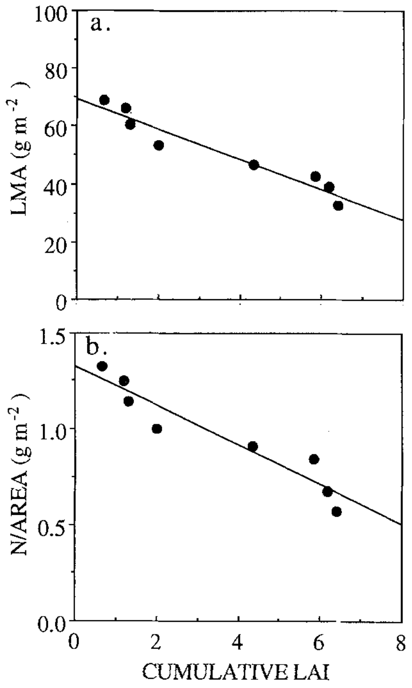

Fig. 4a, b. Linear regression of cumulative leaf area index (*LAI*) at different canopy positions versus LMA. **a** The regression relationship shown is $LMA = 69.4 - 5.20 \ast \mathrm{LAI}$ ($r^2 = 0.93$, $p < 0.0001$). **b** Regression between *LAI* and N/area. The regression relationship shown is $\mathrm{N/area} = 1.32 - 0.102 \ast \mathrm{LAI}$ ($r^2 = 0.90$, $p < 0.0001$)

Results

Total LAI for the deciduous forest in this study was 6.1 $m^2\,m^{-2}$ ground area from litterfall measurements and 5.7 (± 0.2) based on the stand-wide transmission measurements, indicating that the two measures agreed to within 10%. The vertical pattern in LAI showed a peak in LAI at approximately 7 m in the canopy (0.4 relative height, Fig. 1). An independent estimate of LAI distribution in the stand based on vertical patterns in transmittance yielded similar results for the overall pattern in LAI distribution, although the proportion of canopy radiation transmittance was lowest (highest LAI) at 8–10 m in the canopy (Fig. 1). The observed cumulative LAI (litterfall/point-intersect method) generally agreed with cumulative LAI predicted from the canopy transmittance measurements to within 10% but there was a tendency for overestimations in LAI based on transmittance for lower portions of the canopy (Fig. 2). The largest deviation from the 1 : 1 line shown in Fig. 2 corresponds to the 8 m height in the canopy, which also showed the largest variability in transmittance measurements (Fig. 1).

Both LMA and N/area varied continuously through the canopy from upper to lower canopy positions (Fig. 3). There was a strong trend toward higher LMA and N/area higher in the canopy ($p < 0.0001$, *F*-test). LMA decreased by nearly 50% from 75 $g\,m^{-2}$ near the top of the canopy at 16 m to 39 $g\,m^{-2}$ at 5 m height in the canopy (Fig. 3a). Similarly, N/area exhibited a 50% decrease from the top to the bottom of the canopy, whereas there was no difference in leaf N concentration ($mg\,g^{-1}$; N/mass) among upper and lower canopy positions ($p > 0.10$, *F*-test) (Fig. 3b, c). Thus, virtually all vertical variation in N/area could be explained by variation in LMA alone, since N/area = N/mass*LMA. Among different canopy positions, LMA and N/area were significantly correlated with the cumulative LAI above each position ($r^2 = 0.93$ and $r^2 = 0.90$, respectively; Fig. 4). Leaf N/mass within the canopy was not correlated with cumulative LAI overhead ($p > 0.05$, data not shown)

Leaf photosynthesis

Leaf photosynthetic traits varied appreciably along the vertical gradient from the top to the bottom of the canopy (Table 1). A_{max}/area under controlled conditions decreased by 50% from upper canopy to lower canopy positions, although there were no significant differences in A_{max}/mass among canopy positions ($p > 0.05$, Table 1). Both light saturation and compensation points showed continuous decreases from the upper canopy to shaded lower canopy positions. Dark respiration (R_d) also exhibited a strong decrease from the upper to lower canopy, with a four-fold decrease in area-based R_d and a two-fold decrease in R_d/mass (Table 1). Area-based leaf chlorophyll content was relatively constant among different levels in the canopy (0.44 ± 0.04 g chlorophyll • m^{-2} leaf area; hence data not shown). Chlorophyll per unit leaf dry mass was the only trait examined that showed an opposite trend, increasing in progressively deeper levels in the canopy (Table 1).

Trends in field A_{max} among canopy levels were consistent with those measured in the laboratory under controlled conditions: A_{max}/area was on the average higher for progressively higher canopy positions (Fig. 5a) while A_{max}/mass was essentially constant among canopy levels (data not shown). Across the vertical gradient in the canopy, A_{max}/area was significantly correlated with N/area ($r^2 = 0.81$, $p < 0.001$, Fig. 5). For *Acer saccharum*, relationships between A_{max}/area and leaf N/area have previously been observed, both across a leaf age and development sequence in mature trees (Reich et al. 1991) and across contrasting light regimes for seedlings (Ellsworth and Reich 1992). We tested whether the area-based A_{max}-N relationship in the present study was quantitatively similar to those published previously and found no significant differences ($p > 0.10$) among the overall regression equations or their slopes. However, the A_{max}-N relationship from the present study differs from the others in having a positive Y-intercept. To provide a more generic A_{max}-N/area relationship for *Acer saccharum*, we also combined the mature tree data (this study) with seedling data for sugar maple from the same stand (Ellsworth and Reich 1992) yielding a regression equation with a negative Y-intercept (A_{max}/area $= -0.63 + 5.98$*N/area, $r^2 = 0.89$, $p < 0.0001$). The lowest leaves from mature trees in this stand (at 1–2 m above the ground) exhibited LMA and N similar to those of seedlings and saplings at that level (D.S. Ellsworth, unpubl. data). Combined data for all three of the sugar maple A_{max}-N data sets under consideration (Ellsworth and Reich 1992; Reich et al. 1991 and the present study) yielded an area-based relationship with much the same slope (slope = 5.93, data not shown).

A_{max}/area was also significantly correlated with LMA ($r^2 = 0.66$, $p < 0.001$, Fig. 5b). Variation in LMA among the different canopy levels described 95% of the variation in N/area (Fig. 5c). Since leaf *A* and N per unit mass were both essentially constant among different levels in the canopy (Table 1, Fig. 3), variation in A_{max}/area and N/area can largely be ascribed to variation in LMA in the canopy rather than to variation in N concentration itself.

Canopy level

Predicted daily canopy *A* was highest for the hypothetical canopy in which LMA in the uppermost canopy layer was highest (2:1:1:1 scenario in Table 2). For simulations using the observed N and LMA distributions, predicted daily canopy *A* was similar to that of the former scenario (only 4% lower). For a hypothetical canopy in which leaf traits are constant through the canopy ('uniform'), predicted daily canopy *A* was 13% lower than for the canopy corresponding to observed N and LMA distributions. The model predicted the lowest daily canopy *A* when LMA was doubled in the lowermost canopy levels (i.e. 1:1:2:1 and 1:1:1:2 scenarios, Table 2). In general, foliage at the top of the canopy (> 15 m height) showed a large photosynthetic contribution to simulated daily canopy *A* relative to its proportion of stand LAI (Table 2). For the observed N and LMA distributions, predicted daily canopy *A* for the uppermost canopy level was 37% of the total predicted daily canopy *A*, although only 11% of the entire stand LAI was located at this level. The lowest canopy level (9–5 m) showed the lowest contribution toward predicted daily canopy *A* despite comprising nearly 30% of the stand LAI. Throughout the day, over 90% of the leaf area of lowest canopy level was

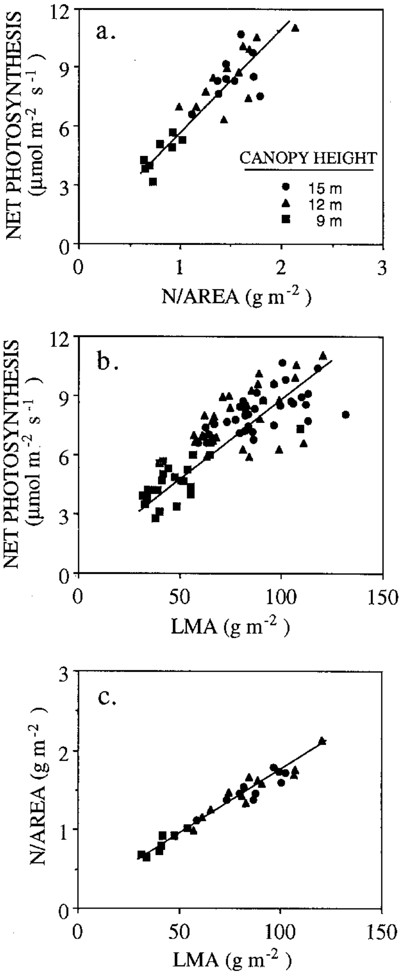

Fig. 5a–c. Relationship between maximum light-saturated net photosynthesis measured in the field (A_{max}/area) and leaf N/area for leaves from three different canopy positions. **a** The regression shown is A_{max}/area $= 0.847 + 5.026$*N/area ($r^2 = 0.81$, $p < 0.0001$). **b.** Relationship between maximum net photosynthesis (A_{max}/area) and leaf mass per unit area (*LMA*) for leaves from three different canopy positions. The regression shown is A_{max}/area $= 2.31 + 0.065$*LMA ($r^2 = 0.66$, $p < 0.0001$). **c.** Relationship between area-based leaf N (N/area) and leaf mass per area (*LMA*) for leaves from three different canopy positions. The regression shown is N/area $= 0.192 + 0.015$*LMA ($r^2 = 0.95$, $p < 0.0001$)

Table 2. Integrated daily PFD and daily canopy carbon assimilation results for alternate scenarios of LMA (and hence N/area) distribution among different canopy levels (see text). Average leaf N/mass was kept constant at 18.8 mg g^{-1} for all canopy levels in the simulations. Field measurements of daily integrated PFD made for leaves at the bottom of the canopy level (e.g. at 15 m, 12 m and 9 m) were averaged over the four sunny days (June–August) for which daily canopy carbon assimilation was modelled. Daily carbon assimilation is expressed as a percentage of the whole-canopy value for different canopy levels, or as a total for the entire canopy (mmol CO_2 m^{-2} day^{-1})

Canopy level	% stand LAI	Integrated PFD (mol m^{-2} day^{-1})	Observed	LMA and N/area distribution Uniform	2:1:1:1	1:2:1:1	1:1:2:1	1:1:1:2
			% total daily carbon assimilation					
18–15 m	11	24.6 ± 1.1	37	33	45	24	27	31
15–12 m	22	12.2 ± 2.2	31	33	26	40	34	36
12–9 m	38	2.7 ± 0.5	22	24	21	25	25	32
9–5 m	29	n.d.	10	9	8	11	14	1
			Total canopy carbon assimilation (mmol CO_2 m^{-2} day^{-1})					
			434	377	463	389	308	304

shaded (e.g. received predominately diffuse shade light over the 5-minute averaging interval). The photosynthetic contributions of lower portions of the canopy cannot be fully evaluated in the absence of quantitative data on the importance of penumbral effects on photosynthesis in the forest canopy, although even at 9 m in the canopy the total daily integrated PFD measured on four sunny summer days was an order of magnitude less than at 15 m (Table 2).

Discussion

Leaf area index and its distribution in forest canopies are important attributes influencing canopy energy and water exchange with the atmosphere (Jarvis and Leverenz 1983). In this study, stand LAI measured indirectly using canopy radiation transmittance (Fig. 1) was similar to LAI obtained directly from litterfall measurements (Figs. 1 and 2). Canopy distribution of LAI was also similar for the two methods, although dense, mid-canopy positions with LAI approaching 1 m^2 m^{-2} over a short vertical distance such as at 7–8 m showed the largest differences between the two methods. This discrepancy may have resulted from differences in the vertical pattern of LAI among different portions of the stand where LAI was estimated or may indicate a limitation of the canopy radiation transmission technique when leaf area is dense or clustered over a short vertical distance. Although LAI was not measured at the same location within the stand because of difficulties in access with the radiometer, the similar LAI values from independent measurements suggest that the theory and assumptions underlying radiation interception methods to predict LAI in a closed forest canopy can be considered valid at least as rough approximations. The major assumption of this technique is that leaves are randomly positioned in the canopy with respect to angle and azimuth (Norman and Campbell 1989, Norman 1993). Data from another deciduous forest indicates that this assumption may only be approximately true, however (Baldocchi et al. 1985).

Radiation transmission within the canopy is largely a function of leaf properties and canopy structure or LAI distribution (Ross 1981; Campbell and Norman 1989). Because of the high LAI and foliage density in this stand, there was a strong gradient in light through the canopy from full sun at the top of the canopy to less than 2% of incoming radiation at the forest floor (Fig. 1). A number of leaf traits were responsive to this gradient in light availability including LMA, N/area, A_{max}/area, R_d (mass and area-based) and chl/mass (Figs. 3 and 4; Table 1). Photosynthetic characteristics such as photosynthetic PPFD response parameters typically vary along a gradient from sun to shade such as is found in the forest canopy (Oberbauer and Strain 1986). Photosynthetic acclimation to shade is expected to result in lower canopy leaves that can be characterized by low A_{max}/area and R_d but high chlorophyll contents thereby reducing the respiratory cost of maintaining the leaf in the shade while increasing light-capturing capabilities (Björkman 1981; Ellsworth and Reich 1992). Acclimation of the photosynthetic apparatus also typically involves a shift in the relative importance of carbon-fixing to light-harvesting components and N partitioning among these components (Björkman 1981; Evans 1989). An increase in leaf chlorophyll per mass with increasing shading in the canopy for sugar maple may reflect the high plasticity of N investment to light-harvesting capacity in this shade-tolerant species (Seemann et al. 1987). While A_{max}/mass did not change from 15 m to 5 m in the canopy, R_d/mass decreased (Table 1), indicating a shift in the maximum photosynthesis-to-respiration ratio (from 13:1 to 25:1) toward greater metabolic efficiency in more deeply shaded leaves (Björkman 1981).

Leaves produced in high light at the top of the canopy tend to have higher LMA (Fig. 3) and greater mesophyll cell densities than leaves growing in more deeply shaded portions of the canopy (Jurik 1986). Since A_{max}/mass (Table 1) and mass-based leaf N (Fig. 3) were more or less constant with canopy position in this study while A_{max}/area and N/area varied by two-fold (Table 1, Figs. 3 and 5), we conclude that variation in LMA was primarily responsible for the roughly two-fold vertical variation in these leaf traits. This evidence suggests that the differences in leaf traits along the vertical canopy gradient were largely structural rather than biochemical in nature (with changes in chlorophyll an important exception). Similar structural changes in leaf traits were observed in sugar maple seedlings growing along a light availability gradient among different habitats (Ellsworth and Reich 1992). Tropical shrubs in the genus *Piper* have exhibited varying degrees of structural versus biochemical acclimation across light gradients, however (Chazdon and Field 1987; Walters and Field 1987). Still, alterations in leaf structure/LMA are an important mode of acclimation to shade in many plant species (Björkman 1981).

In this study (Fig. 5) and others (DeJong and Doyle 1985; Ellsworth and Reich 1992; Gulmon and Chu 1981) strong area-based $A_{\max}$-N and $A_{\max}$-LMA relationships were observed for leaves arrayed along gradients in light availability. Within species, $A_{\max}$-N relationships may be stronger on a mass than on an area-basis under circumstances where large variation in mass-based leaf N is observed, such as across leaf aging sequences (Field 1983; Reich et al. 1991). Ecologically, variation in $A_{\max}$-N relationships and their mass- or area-bases can be interpreted as a reflection of the overall proximal resources that limit plant net carbon balance (Field 1991). In forest canopies where light availability is frequently limiting, area-based $A_{\max}$-N relationships may be strongest because of high leaf structural plasticity in response to light and the scaling of leaf N/area with LMA.

Leaf N content is considered a strong correlate of photosynthetic capacity both within and among C_3 species because of the predominance of N-based proteins conferring photosynthetic activity in leaves (Field and Mooney 1986; Evans 1989). It has also been argued that $A_{\max}$-N represents a fundamental relationship among species from predominately N-limited ecosystems (Field and Mooney 1986). For a single species that is one of the most common deciduous forest trees in eastern North America, we have now presented considerable data relating $A_{\max}$ and leaf N (Ellsworth and Reich 1992; Reich et al. 1991, and this study). For fully-expanded leaves, the area-based regression of $A_{\max}$ versus leaf N from the current study had a slope of 5.0 versus a slope of 5.6 from Reich et al. (1991) and 5.9 from Ellsworth and Reich (1992). In these three studies, variation in leaf N/area was primarily due to a number of environmental and endogenous factors: a canopy light gradient, this study; light and microhabitat differences, Ellsworth and Reich (1992); and a leaf aging sequence, Reich et al. (1991). Combining these data sets provides a more generic assessment of leaf $A_{\max}$ versus N which should be valid for sugar maple seedlings, mature trees and forest canopies across seasonal/leaf age or light availability gradients in northern deciduous forests. The similarity in slopes among the three datasets suggests convergence in this relationship toward an $A_{\max}$/area-N/area relationship of some general predictive value with a slope near 6.0 such as was observed for the combined datasets (see Results). Information regarding variance in $A_{\max}$-N for sugar maple across gradients in soil nutrient availability is needed to assess whether the relationships can be more broadly applied to forests on a wide variety of sites.

Field and Mooney (1986) predict that the Y-intercept of the $A_{\max}$-N relationship should be negative since theoretically a minimum investment in leaf N should be necessary for photosynthesis to occur [see also Evans (1989)]. The positive Y-intercept of the $A_{\max}$/area-N/area correlation observed in this paper does not suggest positive net photosynthesis in leaves approaching zero N content since the range of data do not permit such an extrapolation, and the concept of a negative Y-intercept does not consistently extend to area-based $A_{\max}$-N relationships (Reich and Walters 1993). Previous results from sugar maple (Reich et al. 1991) and other tree species (Reich et al. 1993) suggest that proportional differences in scaling between N/mass and LMA with increasing N/area may result in differences between mass-based versus area-based $A_{\max}$-N relationships. Our results support the conclusions of Reich et al. (1993) and Reich and Walters (1993) that mass-based $A_{\max}$-N relationships are more closely related to the metabolic basis of the association between $A_{\max}$ and leaf N/mass, whereas area-based $A_{\max}$-N relationships arise largely from scaling of N/area with LMA (e.g. by definition N/area = LMA*N/mass).

We suggest that variation in LMA within closed forest canopies may be important to ecological scaling relationships at the canopy-level as well as at the leaf-level. A lack of consistent mass-based N differences in the upper versus lower canopy has been observed in several broad-leaved closed forests (Fownes 1985; Hollinger 1989) and does not appear to be exclusive to sugar maple. The strong trends in LMA and N/area with canopy height indicate that examination of the variation in LMA and N through the canopy may provide insight into the functional significance of N distribution with respect to leaf area distribution and photosynthesis in canopies. If leaf-level structural acclimation occurred to the extent of dilution of leaf N concentration, however, this canopy-level pattern would not emerge or would be muted.

The vertical distribution of N/area is strongly related to that of the cumulative LAI overhead, largely through variation in LMA among different canopy positions (Figs. 3 and 4). This pattern supports the previous hypothesis of Field (1983) and Hirose and Werger (1987) that greater leaf N will be allocated to sunny microsites at the top of the canopy versus to more deeply shaded positions, however in broad-leaved closed forests it appears that such N partitioning within the canopy is achieved on an area rather than a mass-basis. Why might this be the case? LMA is highly responsive to shading (Chabot et al. 1979; Jurik 1986), so variation in LMA within a canopy may be an effective means of regulating partitioning of area-based leaf N and $A_{\max}$ according to light availability patterns within the canopy during leaf development. Portions of the canopy which are least-shaded produce leaves with the highest LMA and hence highest N/area and $A_{\max}$/area, with the magnitude of these traits progressively decreasing deeper into the canopy. Other studies have similarly shown that across canopy light gradients, acclimation in leaf N and $A_{\max}$ is primarily achieved by variation in LMA in trees even when fertilized with nitrogen (DeJong and Doyle 1985; DeJong et al. 1989; Jurik 1986). Such a pattern inevitably maximizes canopy photosynthesis, since investment in high leaf mass and N per area yield diminishing long-term photosynthetic returns in more shaded canopy microsites (Field 1983, 1991; Mooney and Gulmon 1979).

In closed canopies a substantial portion (up to 40%) of canopy daily carbon assimilation is contributed by uppermost portions of the canopy where direct shading of leaves is the least (Caldwell et al. 1986). Since the upper 10% of the sugar maple canopy contributes 30–40% of the entire canopy carbon assimilation, it follows that increases in N and mass conferring greater photosynthetic capacity in this uppermost portion of the canopy should yield the largest proportional increases in whole-canopy carbon assimilation. Predicted canopy carbon assimilation is 12–45% higher for a sugar maple forest when LMA and N/area are highest in the upper portions of the canopy rather than in successive canopy levels or when LMA and N/area are constant (Table 2). Other models of canopy A, however, predict no substantial differences in canopy daily A between observed and uniform leaf N distributions (Leuning et al. 1991; Field 1983). The advantages of skewed N and mass distributions toward the top of the canopy may be greatest in canopies where the light gradient from upper to lower canopy levels is the largest, such as for high-LAI, broad-leaved canopies (Hirose and Werger 1987), but not in canopies where leaf size is small or leaf inclination angle is large, permitting deeper penetration of light within the canopy (Leuning et al. 1991). More extensive samples of forest stands varying in species composition and LAI, density and structure are needed to determine whether the significance of canopy patterns in mass and N distribution to whole-canopy carbon assimilation can be generalized to a variety of plant species and ecosystem types.

Conclusions

The results of this study show that LMA, N/area and $A_{\max}$/area are distributed in the forest canopy in a spatially patterned way with respect to height, and are responsive to shading as leaf area index increases with depth in the canopy. It is likely that variation in LMA accounts for most of the vertical variation in N/area and $A_{\max}$/area in sugar maple, and hence has important ramifications for canopy-level scaling relationships and within-canopy patterns of partitioning of nutrient resources and photosynthetic activity. Systematic vertical variation in leaf structural, chemical and photosynthetic characteristics associated with vertical variation in light availability must be incorporated in canopy carbon assimilation models to accurately reflect the disproportionate photosynthetic contributions of different canopy levels to whole-canopy carbon assimilation. Consideration of variation in LMA within closed forest canopies may prove useful in developing scaling relationships appropriate at both the leaf and canopy level.

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