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## Foliage physiology and biochemistry in response to light gradients in conifers with varying shade tolerance

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**Abstract** To examine the predictability of leaf physiology and biochemistry from light gradients within canopies, we measured photosynthetic light-response curves, leaf mass per area (LMA) and concentrations of nitrogen, phosphorus and chlorophyll at 15–20 positions within canopies of three conifer species with increasing shade tolerance, ponderosa pine [*Pinus ponderosa* (Laws.)], Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco], and western hemlock [*Tsuga heterophylla* (Raf.) Sarg.]. Adjacent to each sampling position, we continuously monitored photosynthetically active photon flux density (PPFD) over a 5-week period using quantum sensors. From these measurements we calculated FPAR: integrated PPFD at each sampling point as a fraction of full sun. From the shadiest to the brightest canopy positions, LMA increased by about 50% in ponderosa pine and 100% in western hemlock; Douglas fir was intermediate. Canopy-average LMA increased with decreasing shade tolerance. Most foliage properties showed more variability within and between canopies when expressed on a leaf area basis than on a leaf mass basis, although the reverse was true for chlorophyll. Where foliage biochemistry or physiology was correlated with FPAR, the relationships were non-linear, tending to

reach a plateau at about 50% of full sunlight. Slopes of response functions relating physiology and biochemistry to  $\ln(\text{FPAR})$  were not significantly different among species except for the light compensation point, which did not vary in response to light in ponderosa pine, but did in the other two species. We used the physiological measurements for Douglas fir in a model to simulate canopy photosynthetic potential (daily net carbon gain limited only by PPFD) and tested the hypothesis that allocation of carbon and nitrogen is optimized relative to PPFD gradients. Simulated photosynthetic potential for the whole canopy was slightly higher (< 10%) using the measured allocation of C and N within the canopy compared with no stratification (i.e., all foliage identical). However, there was no evidence that the actual allocation pattern was optimized on the basis of PPFD gradients alone; simulated net carbon assimilation increased still further when even more N and C were allocated to high-light environments at the canopy top.

**Key words** Radiation gradients · Photosynthesis · Conifers Shade tolerance

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### Introduction

The structure, biochemistry, and physiology of leaves within a forest canopy show striking spatial heterogeneity, even in monospecific stands. The mass per unit leaf area (LMA) of topmost leaves, for example, is typically two or three times greater than that of same-age foliage in the lower canopy, and light-saturated photosynthetic capacity ( $A_{\max}$ ) follows a similar trajectory (e.g., Lewandowska and Jarvis 1977; Hollinger 1989; Ellsworth and Reich 1993). Spatial variability in the distribution of foliage characteristics presents a challenge in attempts to understand constraints on carbon uptake and to model physiological processes and growth of whole canopies and stands (Sellers et al. 1992; Baldocchi 1993; Jarvis 1993). Variability of foliage within canopies also complicates the sampling strategies

required to characterize biomass and biochemistry, and physiological performance of whole canopies from measurements of sub-sampled foliage.

A simplifying hypothesis is that the variation in foliage structure and physiology within canopies is a function of gradients in photosynthetically active photon flux density (PPFD; see Appendix for a list of abbreviations and units). Numerous studies have shown that variations in leaf structure, nitrogen content, and  $A_{\max}$  within canopies correspond to variations in light (e.g., Field 1983; DeJong and Doyle 1985; Hirose and Werger 1987; Hollinger 1989, 1996; Ellsworth and Reich 1993; Brooks et al. 1996; Livingston et al. 1998; Schoettle and Smith 1999), and these variations generally mimic the responses that occur when whole plants are grown in controlled experiments at different light levels (Boardman 1977; Björkman 1981). Several investigators (e.g., Gutschick and Wiegand 1988; Takenaka 1989; Field 1991; Jarvis 1993) have proposed that carbon and/or nitrogen are allocated within canopies to optimize use of solar energy.

If foliage properties can be described as functions of light gradients, either empirically or based on optimization theories, it should be possible to predict the characteristics of foliage within whole canopies based on a knowledge of light extinction and the properties of foliage at the top. Such predictions would facilitate sampling procedures, algorithms for canopy process models, and interpretation of remotely sensed information (Sellers et al. 1992). Although many studies document relationships between light extinction and foliage properties, there is little information about the consistency of these trends across species. Since shade-intolerant species are less plastic than tolerant species in response to varying light environments both in their photosynthetic apparatus (Teskey and Shrestha 1985; Kubiske and Pregitzer 1996) and LMA (Chen et al. 1996), one prediction is that the slope of the relationship between local light environment and leaf properties will be steeper in a shade-tolerant compared with an intolerant species.

To better understand the relationships between foliage properties and light gradients within canopies, we studied mature canopies of three conifer species with increasing shade tolerance: ponderosa pine [*Pinus ponderosa* (Laws.)], Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco], and western hemlock [*Tsuga heterophylla* (Raf.) Sarg.]. All three species are common in the Pacific northwest and important commercially. We asked two principal questions.

(1) Are there significant differences among species in foliar responses to light gradients? We tested the hypothesis that the range in foliar properties (especially LMA,  $A_{\max}$  and nitrogen content) within canopies would increase with increasing shade tolerance of the species. If this proved true, we sought to determine whether differences in the range of foliar properties were due to differing plasticity of foliage in response to variation in light or, alternatively, to

differences in the range of light microenvironments due to variations in total leaf area.

(2) Is the allocation of carbon and nitrogen within the canopies "optimized" with respect to light? We defined an "optimized" canopy as one which allocates resources (C and N) to maximize the potential for whole-canopy net carbon assimilation. We simulated light-limited photosynthetic potential over a 24-h period for whole canopies (i.e., the total daily carbon gain expected in ambient light if unaffected by other environmental factors) assuming different allocation patterns of carbon/nitrogen to foliage. Leaf area index and the total amount of carbon and nitrogen within the canopy were held constant, but the distribution varied, to assess the impact of allocation patterns on photosynthetic potential.

Foliage may persist for many years on all of the species we studied, and leaf chemistry, structure and function may change with age, irrespective of illumination. In addition, shoot morphology of many conifer species varies as a function of the light microenvironment (Carter and Smith 1985; Leverenz and Hinckley 1990; Niinemets and Kull 1995; Sprugel et al. 1996) and affects light absorption and photosynthesis for a particular canopy position (Leverenz and Jarvis 1980; Oker-Blom and Kellomäki 1982; Carter and Smith 1985; Leverenz 1996; Stenberg 1996, 1998). In on-going studies, we are investigating interactions between N allocation and stem morphology in multiple age classes of foliage on carbon assimilation. However, to keep the present analysis tractable, here we restrict our consideration to 1-year-old foliage, and we do not analyze the impact of variable stem morphology on light interception. This is consistent with the overall goal of assessing the degree to which leaf physiology and biochemistry can be predicted simply from light gradients.

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## Materials and methods

### Study sites

Our three study sites were located at or near well-studied sites along a west-east transect (OTTER) in Oregon, USA (Matson et al. 1994; Runyon et al. 1994). The Douglas fir site is in the Willamette Valley, near Corvallis, Ore. (44°38'N, 123°17'W); elevation is 317 m, tree height 22.5 m, stand leaf area index (LAI)  $\approx$  6. The western hemlock site is on the west slope of the Cascade Mountains, east of Scio, Ore. (44°40'N, 122°36'W); elevation is 730 m, tree height 18 m, stand LAI  $\approx$  9. The ponderosa pine site, described previously by Yoder et al. (1994), lies on the east slope of the Cascade mountains, near Black Butte, Ore. (44°25'N, 121°40'W). Its elevation is 1032 m, tree height 28 m, and stand LAI  $\approx$  1.5; however, the leaf area/canopy silhouette area was higher, approaching 4.0. Scaffolding with platforms at several levels provided access throughout the canopies of three trees for the western hemlock and Douglas fir sites and one tree at the ponderosa pine site.

At each site, we conducted measurements over a 6- to 8-week period during periods of active photosynthesis. For Douglas fir, western hemlock and ponderosa pine these dates were 28 May–5 July 1995, 11 July–8 August 1995, and 14 June–15 August 1996, respectively.

## Measurements of PPFD

We monitored PPFD continuously during the study periods with an array of 20 quantum sensors (model LI-190-SZ; Li-Cor, Lincoln, Neb.) positioned to be as representative as possible of the range of PPFD gradients within the canopies. Sensors were supported by metal brackets adjacent to a twig that was used in foliage analyses and leveled with a bubble level. One sensor was positioned above the canopy to record unobstructed PPFD. Sensors were attached via 15-m cables to one of two CR10x data loggers (Campbell Scientific, Logan, Utah) and programmed to record PPFD every minute; half-hourly mean values were stored. For each sensor, we calculated FPAR, the total daily PPFD as a fraction of full sun, averaged over clear days.

## Gas exchange and analysis of light-response curves

We measured a photosynthetic light-response curve using 1-year-old foliage adjacent to 19 of the 20 quantum sensors (the topmost sensor was inaccessible with gas exchange equipment). For western hemlock and Douglas fir, we used a portable, steady-state gas exchange system from Data Design Group (PACsys 9900, La Jolla, Calif.). Measurements were conducted in the mornings or on cool, humid days when there was little or no evidence of mid-day stomatal closure for the whole canopy. Cuvette temperature was maintained at 25°C and relative humidity at 40%. Light was provided by two high-intensity projector bulbs (EYF) powered by a 12-V battery. Each light-response curve consisted of seven measurements at decreasing PPFD, with values near 1100, 600, 400, 250, 150, 50, and 5  $\mu\text{mol m}^{-2} \text{s}^{-1}$  achieved by placing neutral screens between the bulbs and the cuvette. After each change in PPFD, we allowed at least 2 min for foliage to acclimate, then waited until the coefficient of variation in net assimilation was not greater than 5%; typically, this took 5–10 min. Projected surface area of foliage in the cuvette was determined using a video image recorder and AgVision software (Decagon Devices, Pullman, Wash.). For ponderosa pine, we used a Li-Cor 6400 gas exchange system with an LED light source. Temperature, humidity, and light were controlled to the same values as for the PACsys 9900 system. Projected area of the pine foliage (two fascicles) in the cuvette was calculated by multiplying the total width of all six needles (measured to the nearest 0.1 mm with precision calipers) by the length of the cuvette.

The non-linear curve-fitting procedure of SigmaPlot (Jandel Scientific Software, Corte Madera, Calif.) was used to fit light-response curves to an equation described by Hanson et al. (1987):

$$A = A_{\max} \times [1 - (1 - R_D/A_{\max})^{(1-PPFD/\Gamma)}] \quad (1)$$

The apparent quantum yield ( $\Phi$ ) can be obtained from the first derivative of this equation, evaluated at  $PPFD = 0$  (Hanson et al. 1987):

$$\Phi = (A_{\max}/\Gamma) \times (1 - R_D/A_{\max}) \ln(1 - R_D/A_{\max}) \quad (2)$$

Equation 1 was also used to estimate the quantum requirement for saturation of photosynthesis for each foliage sample. Because  $A$  approaches  $A_{\max}$  asymptotically, it is not possible to evaluate numerically the PPFD when  $A$  first reaches  $A_{\max}$ . Therefore, for comparative purposes, we determined PPFD when  $A = 0.90 \times A_{\max}(\Theta_{90})$ .

## LMA and foliage biochemistry

Following gas exchange measurements, foliage from cuvettes was harvested, placed in a plastic bag and stored over ice. Within 24 h, sub-samples were analyzed for chlorophyll and chlorophyll a/b as described in Yoder and Waring (1994), and remaining foliage was dried to constant mass at 70°C. LMA was determined from the mass to area ratio of this foliage, which was subsequently subjected to acid digest followed by determination of N and P by Kjeldahl analysis.

## Statistical analyses

Study sites for the three species were unreplicated, so analyses comparing the three sites represent a case study of "species/sites." To compare mean values of foliage properties among the three species/sites we used both the Bonferroni (Dunn) test of multiple comparisons as well as Tukey's test of all possible pairwise comparisons with  $\alpha = 0.05$ . The Bonferroni test provides better control of type I errors, but has a higher probability of type II errors.

We determined whether there were differences in the relationships between foliage properties and local PPFD for the three species/sites by testing for significant differences in slopes and intercepts of linear regressions. The general linear models procedure of SAS (SAS Institute, Cary, NC) was used, with indicator variables for species/sites. The full model was:

$$y = B_{pp} + (B_{df} \times I_{df}) + (B_{wh} \times I_{wh}) + (B_{pp-x} \times x) + B_{df-x} \times x \times I_{df} + (B_{wh-x} \times x \times I_{wh}) + \varepsilon$$

where  $I_{df}$  and  $I_{wh}$  are dummy indicators,  $x$  represents the independent variable [FPAR or  $\ln(\text{FPAR})$ ] and the subscripts represent the three species. Significant differences in regression slopes among species/sites were assessed by determining whether  $B_{df-x}$  and  $B_{wh-x}$  were significant in the model ( $\alpha = 0.05$ ), and differences in intercepts were assessed by evaluating the significance of  $B_{df}$  and  $B_{wh}$ . If there were no significant differences in slopes, intercepts were compared using a reduced model, eliminating  $(B_{df-x} \times x \times I_{df}) + (B_{wh-x} \times x \times I_{wh})$ .

## Testing the hypothesis that allocation of C and N within canopies is optimized with respect to light gradients

To test the optimization hypothesis, we simulated whole-canopy photosynthetic potential over a 24-h period under three scenarios: "no stratification" of C and N (i.e., all foliage assumed identical), "actual stratification" of C and N, and "2 × actual" [doubling the slope of the response to PPFD gradients, resulting in foliage with higher LMA and leaf nitrogen content per unit area ( $N_{\text{area}}$ ) at the canopy top, and lower at the bottom, with the mid-canopy unchanged]. In each case, the total amount of C and N available for the whole canopy was held constant, but the distribution varied. (The simulation was actually performed by varying only LMA because results showed that  $N_{\text{area}}$  was strongly correlated with LMA, and  $N_{\text{area}}$  and LMA were equally good predictors of leaf physiological properties).

Simulated potential net C assimilation for the whole canopy was scaled from leaf-level photosynthetic light-response curves using a four-step process. First, for each of the three allocation scenarios, we estimated  $A_{\max}$ ,  $R_D$ , and  $\Gamma$  for each sampling position from regression relationships with LMA. Then we used these values in Eq. 1, along with hourly field measurements of PPFD from each sampling position averaged over clear days to estimate carbon assimilation for each sampling position on an hourly time step. Because the objective was to compare light-limited potential C assimilation, we did not vary other environmental parameters in the simulation – i.e., we assumed the measurement conditions from light-response curves were constants. In the third step, the hourly estimates were summed over a 24-h period for each sampling position. Finally, the point estimates were integrated spatially by assigning an "LAI class" to each position based on local FPAR. The classes were assigned based on the assumption that light extinction within canopies generally follows Beer's law, with an extinction coefficient of  $-0.5$ , an "average" value for forest canopies (Waring and Running 1998). The Douglas fir canopy had a total LAI of 6, so for this case the classes were as follows: LAI class 1, FPAR 61–100%; class 2, 37–60%; class 3, 22–36%; class 4, 14–21%; class 5, 8–13%; class 6, <8%. The mean value for potential carbon assimilation was calculated for each LAI class, and the values for each canopy layer were summed to derive an estimated whole-canopy potential carbon assimilation over 24 h for a clear summer day. The estimated net carbon assimilation resulting from this

procedure does not represent actual photosynthesis through the canopy because (a) environmental conditions such as temperature and humidity are held constant, (b) all foliage is assumed to have the characteristics of the 1-year-old foliage measured experimentally, and (c) photosynthesis is estimated from PPFD gradients rather than energy absorption. However, the procedure does provide a test of the hypothesis that N and C allocation to 1-year-old foliage is optimized based on light gradients, which addresses our second objective.

## Results

### Variations in foliage properties among species/sites

There were significant differences among species/sites for the mean values of most of the foliage characteristics we investigated (Table 1). In all cases, Bonferroni and Tukey tests provided identical separations of mean values. In general, mean values of foliage properties varied according to the gradient of shade tolerance, with ponderosa pine and western hemlock at opposite ends of the range and Douglas fir in the middle. The difference in mean  $A_{\max\text{-area}}$  among species/sites was particularly large; the light-saturated photosynthesis per unit leaf area of ponderosa pine needles averaged nearly three times that of western hemlock.  $A_{\max}$  and leaf nitrogen and phosphorus showed much greater differences among species/sites when expressed on a leaf area basis than on a mass basis; chlorophyll, however, varied more on a mass basis.

We hypothesized that the range of foliage properties within canopies would increase with increasing shade tolerance. In general, the standard deviation around mean values as well as the absolute range of values was similar for all species/sites, or if anything tending to decrease with increasing shade tolerance (Table 1). However, because mean values for most foliage properties increased as shade tolerance decreased, the varia-

tion as a proportion of mean values did increase with increasing shade tolerance. From lowest- to highest-light environments, LMA increased by 49%, 86%, and 99% for ponderosa pine, Douglas fir, and western hemlock, respectively. The increase in  $A_{\max\text{-area}}$  from bottom to top of the canopy profiles was even greater, at 94%, 187% and 288%, respectively.

### Variations in foliage properties relative to PPFD microenvironment

The relationships between foliage properties and FPAR were non-linear, generally reaching a maximum at about 50% of full sunlight (Fig. 1 shows responses for LMA and  $A_{\max\text{-area}}$ , other response curves were similar). To compare the functions among species/sites, we linearized the relationships by using  $\ln(\text{FPAR})$  (Fig. 2, Table 2).

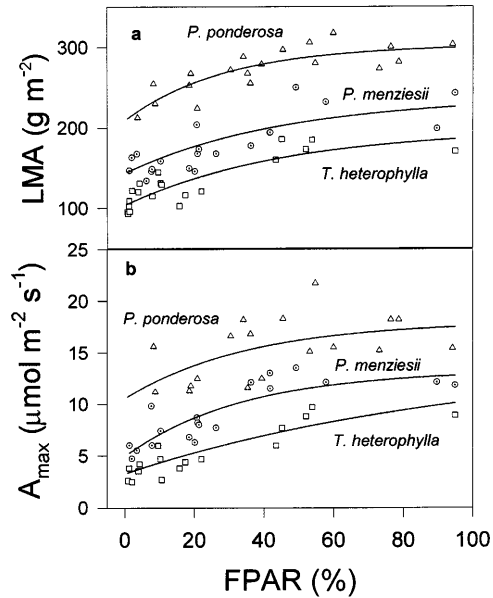
For most of the foliage properties we measured, correlations with  $\ln(\text{FPAR})$  were significant ( $P \leq 0.05$ ; Table 2).  $A_{\max\text{-area}}$ ,  $N_{\text{area}}$  and LMA showed the strongest relationships, with  $\ln(\text{FPAR})$  explaining 85% or more of the variation in these leaf properties for the combined datasets. The slope of  $R_D$  (on either a mass or area basis) versus  $\ln(\text{FPAR})$  was not significantly different from zero for any site ( $P > 0.05$ ); however, for ponderosa pine and Douglas fir,  $R_{D\text{-area}}$  was weakly but significantly correlated with LMA (for ponderosa pine,  $r^2 = 0.23$ ,  $P = 0.048$ ; for Douglas fir,  $r^2 = 0.27$ ,  $P = 0.023$ ) and with  $A_{\max\text{-area}}$  (for ponderosa pine,  $r^2 = 0.27$ ,  $P = 0.026$ ; for Douglas fir,  $r^2 = 0.20$ ,  $P = 0.050$ ).

In all cases but one, there was no significant difference among species/sites in the slopes of their responses to  $\ln(\text{FPAR})$  (Table 2, Fig. 2). The exception was  $\Gamma$ , which for ponderosa pine showed no significant change

**Table 1** Mean ( $\pm$ SE) values and ranges of biochemical and physiological properties of 1-year-old needles from the three sites in this study. Sample size is shown in parentheses. Letters following

mean values for leaf properties indicate significant differences among species/sites ( $P \leq 0.05$ ; see text for details)

	<i>Pinus ponderosa</i>	<i>Pseudotsuga menziesii</i>	<i>Tsuga heterophylla</i>
$A_{\max\text{-area}}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	15.3 $\pm$ 0.7 <sup>a</sup> (18) 11.2 to 21.7	9.0 $\pm$ 0.6 <sup>b</sup> (19) 4.7 to 13.5	5.3 $\pm$ 0.6 <sup>c</sup> (16) 2.5 to 9.7
$A_{\max\text{-mass}}$ ( $\text{mmol g}^{-1} \text{s}^{-1}$ )	0.56 $\pm$ 0.02 <sup>a</sup> (18) 0.43 to 0.77	0.49 $\pm$ 0.02 <sup>a</sup> (19) 0.28 to 0.68	0.37 $\pm$ 0.03 <sup>b</sup> (16) 0.20 to 0.52
$R_{D\text{-area}}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	-0.80 $\pm$ 0.08 <sup>a</sup> (18) -1.57 to -0.25	-0.97 $\pm$ 0.10 <sup>a</sup> (19) -1.80 to -0.31	-0.71 $\pm$ 0.08 <sup>a</sup> (15) -1.15 to -0.27
$R_{D\text{-mass}}$ ( $\text{mmol g}^{-1} \text{s}^{-1}$ )	-0.029 $\pm$ 0.006 <sup>a</sup> (18) -0.056 to -0.009	-0.054 $\pm$ 0.005 <sup>b</sup> (19) -0.124 to -0.021	-0.054 $\pm$ 0.006 <sup>b</sup> (15) -0.101 to -0.021
$\Gamma$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	16.0 $\pm$ 1.5 <sup>b</sup> (18) 4.5 to 27.0	22.9 $\pm$ 2.6 <sup>a</sup> (19) 8.3 to 53.5	19.0 $\pm$ 2.0 <sup>ab</sup> (15) 9.5 to 32.7
$\Phi$	0.052 $\pm$ 0.002 <sup>a</sup> (18) 0.030 to 0.071	0.046 $\pm$ 0.003 <sup>ab</sup> (19) 0.032 to 0.082	0.039 $\pm$ 0.005 <sup>b</sup> (15) 0.018 to 0.089
$\Theta_{90}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	746 $\pm$ 54 <sup>a</sup> (18) 436 to 1255	567 $\pm$ 46 <sup>b</sup> (19) 194 to 876	432 $\pm$ 48 <sup>c</sup> (15) 198 to 778
LMA ( $\text{g m}^{-2}$ )	275 $\pm$ 6 <sup>a</sup> (18) 213 to 317	178 $\pm$ 7 <sup>b</sup> (20) 134 to 249	130 $\pm$ 7 <sup>c</sup> (20) 93 to 185
$N_{\text{area}}$ ( $\text{g m}^{-2}$ )	4.08 $\pm$ 0.12 <sup>a</sup> (18) 2.79 to 4.96	2.25 $\pm$ 0.13 <sup>b</sup> (20) 1.63 to 3.84	2.05 $\pm$ 0.15 <sup>b</sup> (20) 1.20 to 3.60
$N_{\text{mass}}$ ( $\text{mg g}^{-1}$ )	14.8 $\pm$ 1.0 <sup>a</sup> (18) 12.1 to 16.4	12.5 $\pm$ 1.3 <sup>b</sup> (20) 10.1 to 15.4	15.7 $\pm$ 2.4 <sup>a</sup> (20) 12.9 to 2.07
$P_{\text{area}}$ ( $\text{g m}^{-2}$ )	0.41 $\pm$ 0.01 <sup>a</sup> (18) 0.29 to 0.5	0.34 $\pm$ 0.02 <sup>b</sup> (20) 0.26 to 0.69	0.16 $\pm$ 0.01 <sup>c</sup> (20) 0.11 to 0.23
$P_{\text{mass}}$ ( $\text{mg g}^{-1}$ )	1.5 $\pm$ 0.1 <sup>b</sup> (18) 1.3 to 1.8	1.9 $\pm$ 0.4 <sup>a</sup> (20) 1.35 to 2.80	1.3 $\pm$ 0.3 <sup>c</sup> (20) 0.90 to 2.19
$\text{Chl}_{\text{area}}^{\text{a}}$ ( $\text{g m}^{-2}$ )	0.79 $\pm$ 0.02 <sup>a</sup> (18) 0.66 to 0.97	0.67 $\pm$ 0.02 <sup>b</sup> (19) 0.54 to 0.86	0.64 $\pm$ 0.02 <sup>b</sup> (18) 0.45 to 0.78
$\text{Chl}_{\text{mass}}^{\text{a}}$ ( $\text{mg g}^{-1}$ )	2.9 $\pm$ 0.09 <sup>c</sup> (18) 2.28 to 3.81	3.9 $\pm$ 0.1 <sup>b</sup> (19) 3.17 to 4.97	5.2 $\pm$ 0.3 <sup>a</sup> (18) 3.14 to 7.19

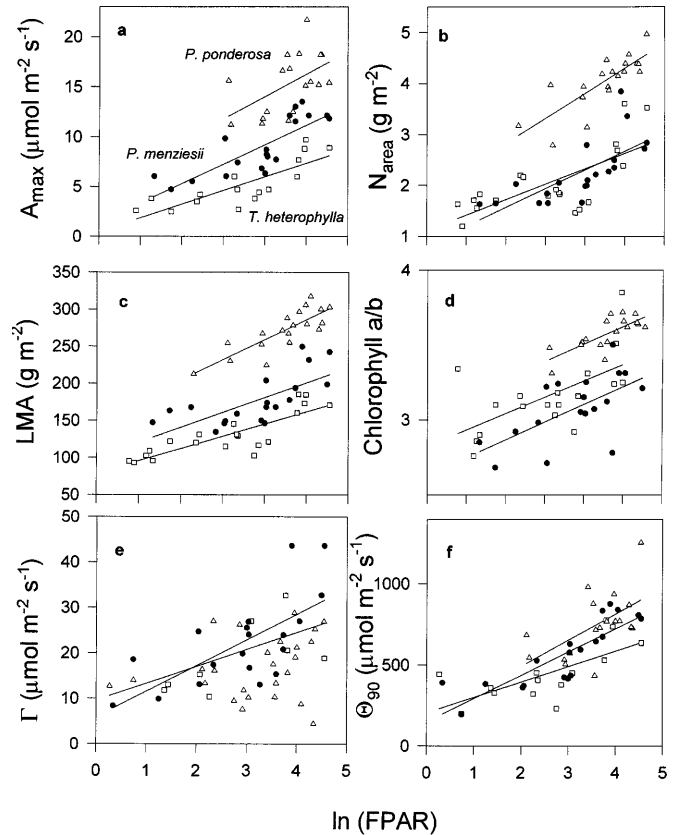


**Fig. 1** Variation in LMA (a) and  $A_{\text{max}}$  (b) as functions of FPAR. Curves were fit to illustrated trends in the data and do not represent specific models (in this and subsequent figures, open triangles *Pinus ponderosa*, closed circles *Pseudotsuga menziesii*, open squares *Tsuga heterophylla*)

with respect to PPFD microenvironment. Intercepts differed significantly among species/sites in all cases. However, the relationship between  $\ln(\text{FPAR})$  and the quantum requirement for 90% saturation of photosynthesis,  $\Theta_{90}$ , was similar across species/sites (Fig. 2f). Although there were significant differences in intercepts, a single regression line explained 59% of the variation in  $\Theta_{90}$  (Fig. 2f), only slightly less than the 65% achieved by using separate intercepts for the three species (Table 2). The average amount of light required for 90% saturation of photosynthesis ranged from just under  $300 \mu\text{mol m}^{-2} \text{s}^{-1}$  to over  $800 \mu\text{mol m}^{-2} \text{s}^{-1}$ . For all species/sites, in canopy positions with  $\text{FPAR} \leq 60\%$ ,  $\Theta_{90}$  averaged  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$  less than the maximum PPFD averaged over any hour on clear days during the measurement period (data not shown).

For all species/sites, correlations between  $A_{\text{max}}$ ,  $N$  or  $P$  and  $\ln(\text{FPAR})$  were much stronger when considered on an area basis than on a mass basis; however,  $\text{Chl}_{\text{mass}}$  was strongly correlated with FPAR, whereas there was no significant relationship between  $\text{Chl}_{\text{area}}$  and  $\ln(\text{FPAR})$ .

On an area basis, the allocation of nitrogen to foliage within the canopies ( $N_{\text{area}}$ ) followed an almost identical pattern to the allocation of carbon (i.e., LMA), and  $N_{\text{area}}$  and LMA were closely correlated ( $r^2 = 0.94$  for the combined dataset, accounting for differences in intercepts). A similar trend occurred with  $P_{\text{area}}$  and LMA ( $r^2 = 0.84$ ). When the data for all species were combined, LMA and  $N_{\text{area}}$  were equally good predictors of  $A_{\text{max}}$  (Fig. 3). Phosphorus also was a good predictor of  $A_{\text{max}}$  ( $r^2 = 0.77$  for combined sites allowing for different slopes and intercepts), although chlorophyll was not.



**Fig. 2a-f** Leaf parameters which showed strong light responses as functions of  $\ln(\text{FPAR})$ . In these figures, independent regression lines are shown for each species to illustrate the similarity of independent slopes except in e, in which case the regression was not significant ( $P > 0.05$ ) for *P. ponderosa*. Table 2 provides results of regression analyses for the data after testing for significant differences among slopes and intercepts

#### Simulated photosynthetic potential with varying allocation of C and N

The overall results of the simulations were similar for the three species/sites so here we focus only on the results for the “intermediate” species, Douglas fir. Because allocation patterns for N were nearly identical to patterns for LMA, and leaf physiological characteristics could be modeled equally well on the basis of either LMA or  $N_{\text{area}}$  (see above), we used LMA as a surrogate for allocation patterns of both N and C. Under the “no stratification” scenario, LMA was held constant at 179, the mean value for Douglas fir. For “actual stratification,” LMA was calculated from measured  $\ln(\text{FPAR})$  at the sampling positions using the appropriate equation for Douglas fir shown in Table 2. For the “ $2\times$  actual stratification” scenario, the slope was doubled and the intercept adjusted to maintain a fixed amount of C for the canopy.  $A_{\text{max}}$ ,  $\Gamma$  and  $R_D$  for each canopy position were evaluated as functions of LMA based on regression relationships for Douglas fir:

$$A_{\text{max-area}} = 0.067 \times \text{LMA} - 3.03 \quad (r^2 = 0.59)$$

**Table 2** Relationships between ln(FPAR) and foliage properties of *P. ponderosa*, *P. menziesii*, and *T. heterophylla* for the linear model  $y = B_0 + B_1 \times \ln(\text{FPAR})$ . Values of  $B_0$  or  $B_1$  were pooled for all species when there were no significant differences in slopes or intercepts ( $P > 0.05$ ; see text for details). Coefficients of determination and  $P$ -values are for full or reduced models as indicated by the coefficients. For leaf properties not shown in this table, correlations with ln(FPAR) were not significant

	Species	$B_0$	$B_1$	$r^2$	$P$
$A_{\text{max-area}}$ $\mu\text{mol (m}^{-2} \text{s}^{-1})$	<i>P. ponderosa</i>	9.18 $\pm$ 1.01	1.72 $\pm$ 0.25	0.85	0.0001
	<i>P. menziesii</i>	4.03 $\pm$ 0.86			
	<i>T. heterophylla</i>	1.022 $\pm$ 0.58			
$A_{\text{max-mass}}$ $\text{mmol (g}^{-1} \text{s}^{-1})$	<i>P. ponderosa</i>	0.374 $\pm$ 0.043	0.051 $\pm$ 0.0106	0.57	0.0001
	<i>P. menziesii</i>	0.346 $\pm$ 0.036			
	<i>T. heterophylla</i>	0.243 $\pm$ 0.034			
$\Gamma$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	<i>P. ponderosa</i>				n.s.
	<i>P. menziesii</i>	4.61 $\pm$ 5.28	6.28 $\pm$ 1.68	0.44	0.0017
	<i>T. heterophylla</i>	9.59 $\pm$ 3.79	3.73 $\pm$ 1.36	0.37	0.017
$\Phi$	<i>P. ponderosa</i>	0.0770 $\pm$ 0.017	-0.00684	0.31	0.0027
	<i>P. menziesii</i>	0.0663 $\pm$ 0.021			
	<i>T. heterophylla</i>	0.0555 $\pm$ 0.015			
$\Theta_{90}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	<i>P. ponderosa</i>	278 $\pm$ 76	131 $\pm$ 19	0.65	
	<i>P. menziesii</i>	187 $\pm$ 64			
	<i>T. heterophylla</i>	120 $\pm$ 60			
LMA ( $\text{g m}^{-2}$ )	<i>P. ponderosa</i>	205 $\pm$ 9	19.3 $\pm$ 2.2	0.91	0.0001
	<i>P. menziesii</i>	123 $\pm$ 8			
	<i>T. heterophylla</i>	90 $\pm$ 6			
$N_{\text{area}}$ ( $\text{g m}^{-2}$ )	<i>P. ponderosa</i>	2.82 $\pm$ 0.18	0.353 $\pm$ 0.046	0.85	0.0001
	<i>P. menziesii</i>	1.26 $\pm$ 0.16			
	<i>T. heterophylla</i>	1.32 $\pm$ 0.13			
$N_{\text{mass}}$ ( $\text{mg g}^{-1}$ )	<i>P. ponderosa</i>	1.36 $\pm$ 0.07	0.036 $\pm$ 0.018	0.45	0.0001
	<i>P. menziesii</i>	1.15 $\pm$ 0.06			
	<i>T. heterophylla</i>	1.49 $\pm$ 0.05			
$P_{\text{area}}$ ( $\text{g m}^{-2}$ )	<i>P. ponderosa</i>	0.332 $\pm$ 0.026	0.0201 $\pm$ 0.0066	0.77	0.0001
	<i>P. menziesii</i>	0.285 $\pm$ 0.023			
	<i>T. heterophylla</i>	0.118 $\pm$ 0.019			
$\text{Chl}_{\text{mass}}$ ( $\text{mg g}^{-1}$ )	<i>P. ponderosa</i>	4.61 $\pm$ 0.29	-0.483 $\pm$ 0.073	0.78	0.0001
	<i>P. menziesii</i>	5.21 $\pm$ 0.24			
	<i>T. heterophylla</i>	6.19 $\pm$ 0.21			
Chl a/b	<i>P. ponderosa</i>	3.17 $\pm$ 0.08	0.113 $\pm$ 0.020	0.73	0.0001
	<i>P. menziesii</i>	2.76 $\pm$ 0.07			
	<i>T. heterophylla</i>	2.92 $\pm$ 0.06			

$$\Gamma = 0.26 \times \text{LMA} - 24.5 \quad (r^2 = 0.60)$$

$$R_{\text{D-area}} = -0.0069 \times \text{LMA} - 0.29 \quad (r^2 = 0.27)$$

Simulated photosynthetic potential for middle canopy layers was unaffected as the allocation patterns changed; this foliage maintained “average-leaf” conditions while carbon and nitrogen were “moved” from lower leaf layers to upper leaf layers (Fig. 4). Potential carbon assimilation of the upper layers increased with additional C and N due to an increase in  $A_{\text{max}}$ , but the gain was partly offset by higher  $R_{\text{D-area}}$  and  $\Gamma$ . The carbon balance of the upper canopy was sensitive to small changes in  $\Gamma$ . In additional simulations (not shown), if the value of  $\Gamma$  was increased by 5  $\text{mmol m}^{-2} \text{s}^{-1}$  while all other parameters were held constant, potential net carbon assimilation at the canopy top decreased by more than 10%.

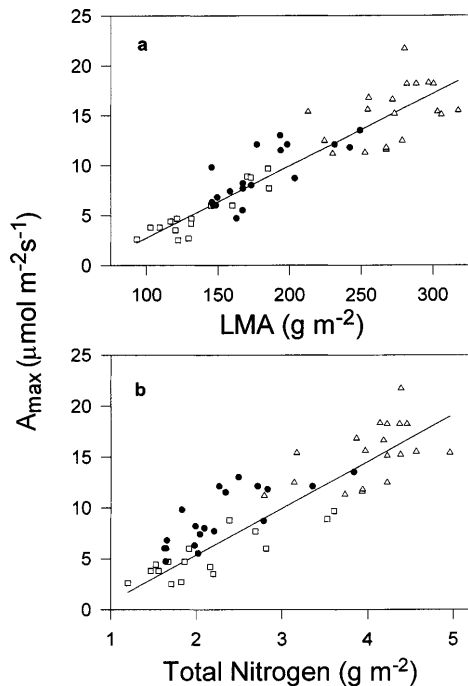
The simulation indicates that the lowest canopy layers had a net loss of carbon over the 24-h period under the “no stratification” and “actual stratification” scenarios. This is partly an artifact of our simplified procedure of holding temperature constant. If a more dynamic temperature regime were used, the carbon economy of lowest foliage would improve because nighttime respiration would be reduced; however, the relative change in whole-canopy net carbon assimilation

for the three scenarios would not be affected. Net carbon assimilation in the lowest canopy layers increased as C and N were preferentially allocated to the upper canopy. Although  $A_{\text{max}}$  was reduced, lower  $R_{\text{D}}$  and  $\Gamma$  allowed heavily shaded foliage to spend more hours of the day in positive carbon balance. However, the lower foliage had relatively little impact on whole-canopy performance irrespective of the allocation scenario.

For the entire Douglas fir canopy, the actual allocation patterns of N and C resulted in a 9.5% gain in potential daily carbon compared with a simulated canopy of the same LAI where all foliage had identical LMA and N (Fig. 4a,b). Potential carbon assimilation increased further (7.9%) when there was even greater preference allocation to high-light environments (Fig. 4c). With simulations using a threefold increase in the slope of the response of LMA to local light, potential carbon assimilation increased still further (data not shown).

## Discussion

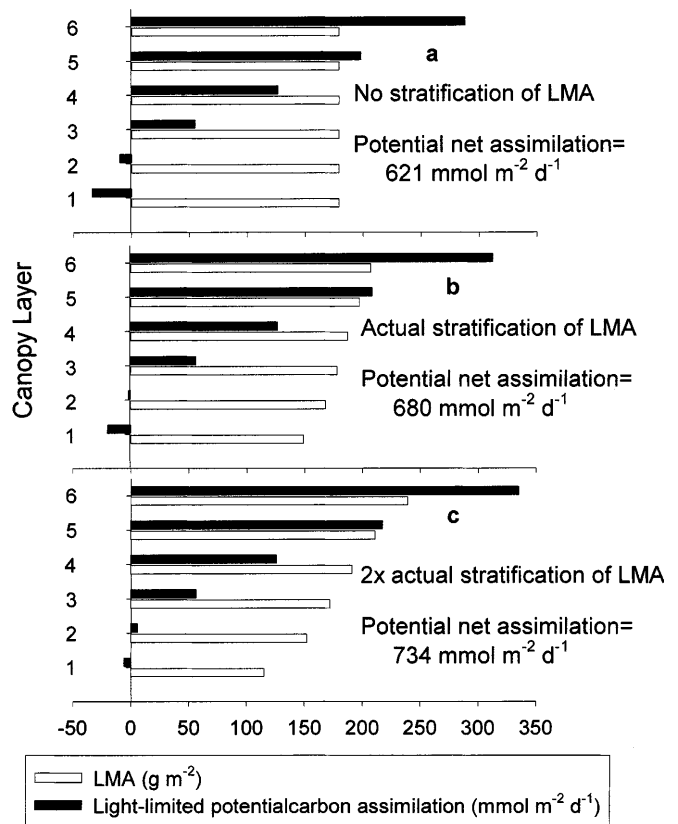
Our results are consistent with many previous reports that the structure, biochemistry, and physiology of foliage within canopies are extremely variable, and much



**Fig. 3**  $A_{\max}$  as a function of LMA (a) and  $N_{\text{area}}$  (b). **a** Linear regression model:  $A_{\max} = -4.07 + 0.071 \times \text{LMA}$ ,  $r^2 = 0.83$ . **b** Linear regression model:  $A_{\max} = -1.50 + 4.07 \times N_{\text{area}}$ ,  $r^2 = 0.77$

variability can be explained by light distribution (e.g., Woodman 1971; Lewandowska et al. 1977; Schulze et al. 1977; Field 1983; DeJong and Doyle 1985; Hirose and Werger 1987; Hollinger 1989; Ellsworth and Reich 1993; Brooks et al. 1996). A notable exception was  $R_D$ , expressed on either a mass or area basis. Typically,  $R_D$  decreases in low-light environments (Boardman 1977; Björkman 1981; Brooks et al. 1996), and J.D. Lewis, R.B. McKane, D.T. Tingey, and P.A. Beedlow (unpublished data) reported significant correlations between  $R_D$  and light environment in two of the species investigated here, *T. heterophylla* and *P. menziesii*. For our measurements of  $R_D$ , variance was high and the values small, so it is possible that we did not detect real relationships.

In our study, as in many other studies of both angiosperms and gymnosperms (Gulmon and Chu 1981; Kull and Koppel 1987; Hollinger 1989; Weinbaum et al. 1989; Ellsworth and Reich 1993; but see also Barker and Booth 1996; Livingston et al. 1998),  $N$  and  $A_{\max}$  expressed on a leaf mass basis were relatively constant within canopies and showed little response to light gradients (slopes were significantly different from but close to 0). Therefore, with increased LMA of foliage in high-light environments,  $N_{\text{area}}$  and  $A_{\max\text{-area}}$  also increased. In fact, one could argue that carbon, rather than nitrogen, was allocated to new foliage relative to the light environment, and nitrogen simply followed carbon in a more or less fixed ratio. A similar trend occurred with phosphorus, although relationships were not as strong as for nitrogen.



**Fig. 4** Light-limited net carbon assimilation for a 24-h period in Douglas fir under different allocation scenarios. LAI and total C available for foliage were held constant, and photosynthesis was modeled using Eq. 1 based on available light with the physiological parameters  $A_{\max}$ ,  $R_D$ , and  $\Gamma$  derived from LMA and  $\Phi$  held constant at 0.066. **a** LMA (and all other leaf properties) are assumed constant through the canopy. **b** LMA increases from bottom to top of the canopy based on the measured response with  $\ln(\text{FPAR})$ . **c** Slope of the response of LMA to  $\ln(\text{FPAR})$  is twice the measured response

Are there significant differences among species in foliar responses to light gradients?

The species we investigated span a wide range in shade tolerance. Western hemlock grows in moist environments, forming dense canopies with a LAI often exceeding 10; thus, foliage deep in the canopy survives with less than 1% of full sunlight. It can regenerate and persist in the canopy understory, and it is a climax species in many Pacific northwest forests (Franklin and Dyrness 1988). Ponderosa pine, on the other hand, rarely forms canopies with LAI > 4; foliage is likely to shed when average irradiance falls to about 10% of full sun. Douglas fir is intermediate.

We predicted that slopes of regression relations between leaf properties and  $\ln(\text{FPAR})$  would increase with increasing shade tolerance. We found, however, that the leaf properties that were most sensitive to PPFD, including LMA,  $A_{\max}$ ,  $N_{\text{area}}$ ,  $P_{\text{area}}$  and  $\text{Chl}_{\text{mass}}$ , responded to light gradients within canopies in a similar fashion in the three species we investigated. Expressed in terms of percent change from lowest to highest values, the range

for most foliage characteristics increased with increasing shade tolerance, but the slopes of response functions did not vary among species and the absolute ranges tended to increase with shade tolerance. For reasons yet to be explained, it appears that the shade-intolerant pine simply does not grow new leaves in low-light environments, but new foliage is similarly responsive to light gradients. The only significant difference among species in foliar responses to light was in  $\Gamma$ , which was not correlated with  $\ln(\text{FPAR})$  in the pine canopy but was in western hemlock and Douglas fir.

Our study, like nearly all other studies of variation through profiles of large canopies, was limited by having a single tower for canopy access at each of three locations, each with a different species. This necessarily limits the inference that may be drawn from our analyses. However, if future investigations confirm our findings for other species, sites, and age classes of foliage, it could provide a simplified way to “scale up” measurements and models from individual leaves to whole canopies. The implication is that foliage biomass, N content, P content and many physiological characteristics should be predictable from measurements of topmost foliage in addition to a knowledge of light extinction within the canopy. To employ such a strategy, one would need to adjust intercepts of the regression equations so that measurements from tops of canopies would correspond with  $\ln(\text{FPAR}) = 4.6$  (i.e., 100% full sun). It is unlikely that all tree species will show the same response functions as the western conifers we studied. For example, Barker and Booth (1996) reported higher N values in the upper-middle canopy of a tropical rainforest species than in topmost foliage. But if the approach could be applied even among distinct species groups, it could simplify models and measurement required to scale from leaf to canopy.

This study was limited to 1-year-old needles, and as the light environment changes in canopies with multiple age classes of foliage, nitrogen may be remobilized from older needles (Field 1983). In ongoing studies, we are investigating the impact of current light environment compared with the light environment during leaf development on LMA and N content of multiple age classes of needles. Brooks et al. (1996) found that thick needles tended to have more nitrogen than thin needles irrespective of their current light environment or needle age, indicating that the close relationship between carbon and nitrogen is maintained to some degree from initial allocation through the life span of the foliage. However, Schoettle and Smith (1999) reported a poor relationship between  $A_{\max}$  or  $N_{\text{area}}$  and light gradients when multiple age classes of *Pinus contorta* foliage were pooled – age classes had to be analyzed separately to obtain close relationships.

Is allocation of carbon and nitrogen “optimized” with respect to light gradients?

An alternative to using empirically derived equations to predict foliage properties from light gradients is to

derive theoretical relationships based on optimization theories. Several optimization theories have been proposed (Field 1983, 1991; Gutschick and Wiegand 1988; Takenaka 1989; Jarvis 1993), most commonly in terms of nitrogen allocation. Because there is strong evidence for a positive linear relationship between foliage N content (on a leaf area basis) and  $A_{\max}$  (e.g., Field and Mooney 1986), and because N is typically limiting to plant growth, Field (1983) proposed that N should be preferentially allocated to foliage in high-light environments, and optimal allocation of N should occur when  $dA/dN$  is constant.

There is also strong evidence for a positive linear relationship between LMA and  $A_{\max}$ , (Nygren and Kellomäki 1983; Oren et al. 1986), and an argument for optimization of C allocation can be developed that is similar to that for N allocation. Gutschick and Wiegand (1988) determined that LMA profiles within canopies of crop plants are similar to what would be expected if carbon were allocated within a canopy of fixed leaf area to maximize whole-canopy carbon assimilation.

Simple radiative transport analysis predicts that if  $dA/dN$  and  $dA/dLMA$  are constant through a canopy profile, then N and C should be allocated in direct proportion to FPAR (Sellers et al. 1992; Anten et al. 1995; also discussed in Hollinger 1996). Instead, we found, as Hollinger (1996) reported previously, that both N and LMA varied non-linearly with FPAR, reaching a plateau at about 50% of full sunlight. The non-linearity is consistent with other studies showing that LMA and N decrease linearly with canopy height (Hollinger 1989; Livingston et al. 1998) or cumulative LAI (Ellsworth and Reich 1993). Our simulations of light-limited canopy potential under different allocation scenarios lead to a similar conclusion. If photosynthesis within the canopy were limited only by leaf photosynthetic capacity and light gradients, much more C and N would need to be allocated to canopy tops to maximize photosynthesis.

In some canopies, gradients in temperature, water vapor or  $\text{CO}_2$  may also be important in determining photosynthesis and defining optimum allocation patterns of N and C. However, the structural heterogeneity through canopy profiles is probably much more important. For many species, the distribution and arrangement of foliage on shade shoots can greatly increase light interception, and therefore photosynthesis, in the lower canopy relative to local FPAR (Leverenz and Jarvis 1980; Oker-Blom and Kellomäki 1982; Carter and Smith 1985; Leverenz 1996; Stenberg 1996, 1998). Needle clustering and penumbral effects of small leaf size also affect light penetration, interception, and photosynthesis (Stenberg 1998). A more realistic optimization model for C and N allocation must consider canopy structure, and  $dA/dN$  or  $dA/dLMA$  must be analyzed relative to light interception by individual needles rather than gradients in FPAR. However, such models can become extremely complex, and for predictive purposes the empirical models will probably be more useful if they prove robust.

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## Appendix: symbols and units

$A$	Net CO <sub>2</sub> assimilation rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
$A_{\text{max-area}}$	Net CO <sub>2</sub> assimilation at light saturation, leaf area basis ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
$A_{\text{max-mass}}$	Net CO <sub>2</sub> assimilation at light saturation, leaf mass basis ( $\text{mmol g}^{-1} \text{s}^{-1}$ )
$\text{Chl}_{\text{area}}$	Leaf chlorophyll content per unit area ( $\text{g m}^{-2}$ )
$\text{Chl}_{\text{mass}}$	Leaf chlorophyll content per unit mass ( $\text{mg g}^{-1}$ )
FPAR	Time-integrated PPFd at a particular point within a canopy relative to full sunlight above the canopy (%)
LAI	Leaf area index (dimensionless)
LMA	Leaf mass per area ( $\text{g m}^{-2}$ )
$N_{\text{area}}$	Leaf nitrogen content per unit area ( $\text{g m}^{-2}$ )
$N_{\text{mass}}$	Leaf nitrogen content per unit mass ( $\text{mg g}^{-1}$ )
$P_{\text{area}}$	Leaf phosphorus content per unit area ( $\text{g m}^{-2}$ )
$P_{\text{mass}}$	Leaf phosphorus content per unit mass ( $\text{mg g}^{-1}$ )
PPFD	Photosynthetically active photon flux density ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
$R_{\text{D-area}}$	Daytime dark respiration rate, leaf area basis ( $\mu\text{mol m}^{-2} \text{s}^{-1} \text{CO}_2$ )
$R_{\text{D-mass}}$	Daytime dark respiration rate, leaf mass basis ( $\text{mmol g}^{-1} \text{s}^{-1} \text{CO}_2$ )
$\Phi$	Apparent quantum yield of photosynthesis (dimensionless)
$\Theta_{90}$	PPFD when $A = 90\%$ of $A_{\text{max}}$ , an index of the quantum requirement for light saturation of photosynthesis
$\Gamma$	Light compensation point ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetically active radiation)

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