NOTE

Foliage height influences specific leaf area of three conifer species

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Abstract: Specific leaf area (SLA), the ratio of projected leaf area to leaf dry mass, is a critical parameter in many forest process models. SLA describes the efficiency with which the leaf captures light relative to the biomass invested in the leaf. It increases from top to bottom of a canopy, but it is unclear why. We sampled stands with low and elevated canopies (young and old stands) to determine whether SLA is related to water potential, as inferred from branch height and length, or shade, as inferred from branch position relative to the rest of the canopy, or both. We studied western white pine (*Pinus monticola* Dougl. ex D. Don), ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.), and interior Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca*) in northern Idaho. SLA decreased with branch height ($P < 0.0001$) at rates that varied among species ($P < 0.0001$). Branch length had no influence on SLA ($P = 0.85$). We detected no differences with canopy elevation ($P = 0.90$), but the slopes of lines relating SLA to branch height may have differed between the canopy elevation classes ($P = 0.039$). The results are consistent with predictions based on the hypothesis that SLA decreases as the gravitational component of water potential falls. The lack of a strong shading effect simplifies the estimation of canopy SLA for process models, requiring only species and branch heights.

Résumé : La surface foliaire spécifique (SFS), c'est-à-dire le rapport de la projection de la surface foliaire sur le poids sec du feuillage, est un paramètre indispensable dans plusieurs modèles forestiers basés sur les processus. La SLS représente l'efficacité avec laquelle le feuillage intercepte la lumière relativement à la biomasse consentie au feuillage. Elle augmente du sommet vers la base du couvert mais la raison n'est pas claire. Nous avons échantillonné des peuplements avec un couvert bas ou élevé (jeunes ou vieux peuplements) pour déterminer si la SLS est reliée au potentiel hydrique comme le laissent supposer la hauteur et la longueur des branches ou à l'ombrage comme le laisse supposer la position des branches par rapport au reste du couvert ou aux deux. Nous avons étudié le pin blanc de l'Ouest (*Pinus monticola* Dougl. ex D. Don), le pin ponderosa (*Pinus ponderosa* Dougl. ex P. & C. Laws.) et le douglas de Menzies bleu (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca*) dans le Nord de l'Idaho. La SLS diminue avec la hauteur des branches ($P < 0{,}0001$) à un taux qui varie selon l'espèce ($P < 0{,}0001$). La longueur des branches n'a pas d'influence sur la SLS ($P = 0{,}85$). Nous n'avons observé aucune différence reliée à la hauteur du couvert ($P = 0{,}90$) mais la pente des droites reliant la SLS à la hauteur des branches pourrait être différente selon la classe de hauteur du couvert ($P = 0{,}039$). Les résultats concordent avec les prédictions basées sur l'hypothèse que la SLS diminue à mesure que la composante gravitationnelle du potentiel hydrique diminue. L'absence d'un effet d'ombre significatif simplifie l'estimation de la SLS du couvert pour les modèles basés sur les processus car il suffit de connaître l'espèce et la hauteur des branches.

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Introduction

The ratio of leaf surface area to leaf mass is a key variable in our understanding of forest ecosystem function (Ellsworth and Reich 1993; Pierce et al. 1994; Landsberg and Waring 1997). Leaf surface area predicts the rate at which the canopy absorbs photosynthetically active radiation, which is used in photosynthesis. Leaf mass measures the metabolic cost of leaf construction. The ratio of leaf area to mass, commonly designated specific leaf area (SLA), thus describes benefit relative to cost. The area to mass ratio is inversely correlated with maximum photosynthetic rate (Jurik 1986; Oren et al. 1986; Ellsworth and Reich 1993), respiration rate (Ellsworth and Reich 1993), and photosynthetic water-use efficiency (Hultine and Marshall 2000). SLA is positively correlated with light compensation point, the light intensity at which instantaneous photosynthetic carbon gain exactly balances respiratory losses (Salisbury and Ross 1992, p. 255). More broadly, the ratio of leaf area to mass can be viewed as the tradeoff between ecosystem mass bal-

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ance and ecosystem energy balance. Such exchange ratios (Bloom et al. 1985) require accurate parameterization if process models are to make accurate predictions of forest growth processes (Körner 1991; Pierce et al. 1994; Running 1994; Landsberg and Waring 1997).

Leaves produced in the lower canopy generally have higher SLA than leaves from near the top (Chabot et al. 1979; Hollinger 1989; Ellsworth and Reich 1993; Bond et al. 1999). Shading experiments have demonstrated that high SLA can be induced by low light intensity in many tree species (e.g., *Salix aquatica*, Waring et al. 1985; *Abies amabilis*, Brooks et al. 1994). However, other variables may also influence SLA. For example, SLA was correlated with tree height in *Picea abies* (Niinemets and Kull 1995). This study distinguished between height and light effects, attributing the height-induced decrease in SLA to increased density of needle tissue (Niinemets and Kull 1995).

Recent research has focused new attention on the consequences of canopy height on water relations (Yoder et al. 1994; Bond and Ryan 2000 and references therein). The static consequence of tree height is a reduction in xylem pressure potential by 0.010 MPa for every metre of height (Scholander et al. 1965). A further reduction in water potential may result from the reduction in stem conductance as the stem grows taller. Such a reduction is a necessary consequence of longer path length, all else being equal. The reduction in conductance would cause more negative xylem pressure potentials in the leaves at any given transpiration rate (Whitehead et al. 1984; Hubbard et al. 1999). Because turgor pressure, which drives cell expansion, would likewise be reduced, the increase in leaf density described above might be induced by low water potential. One might also expect that such water stress might be associated with the development of xeromorphic features including thick cuticles and lignified cell walls, both of which would tend to reduce specific leaf area.

Our objective was to analyze vertical variation in SLA within crowns. Specifically, we analyzed variation with respect to branch height, branch length, and canopy elevation class for each of three conifer species. We measured young, short trees from recent clearcuts as well as old trees in mature stands. By sampling branches of similar height in both types of stand, we proposed to reduce the confounding of branch height and canopy elevation class that necessarily results when sampling within a single stand.

Materials and methods

The study was conducted on the Priest River Experimental Forest in northern Idaho, U.S.A. (48°21′N, 116°45′W), on the west side of the Rocky Mountain crest. The climate is intermediate between maritime climates west of the Cascades and the continental climates east of the Rockies (Finklin 1983). Sampled stands were between 800 and 950 m above sea level, and all were within 3 km of one another. The species under investigation were western white pine (*Pinus monticola* Dougl. ex D. Don), ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.), and inland Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca*). All sample trees were naturally occurring (not planted) in mixed-species stands or in recent clearcuts.

Field measurements for the broader study have been described in detail in Monserud and Marshall (1999), which also includes a description of the eight sampled stands. All stands were mixed species, but not every species occurred in every stand. Basal areas ranged from 9.5 to 43.5 $m^2 \cdot ha^{-1}$, and tree density ranged from 328 to 1876 trees/ha. Two to 14 trees were sampled per stand. The data were collected from 66 trees felled and destructively sampled in 1994. The first trees were harvested immediately after needle elongation was complete and the last were harvested just before the commencement of autumn needle drop. Douglas-fir were harvested from June 21 to September 20; ponderosa pine from July 6 to September 8, and western white pine from July 20 to September 14. The trees were chosen to represent the full range of heights and diameters on the forest. Therefore, young trees were sampled from recent clearcuts, as were trees from all canopy strata from mature stands. Tree height ranged from 3.6 to 44.7 m (Table 1). We sampled tree sizes and ages randomly across the growing season to avoid confounding differences in SLA with uncontrolled sources of variation such as starch concentration.

After felling, tree height and crown length were measured. The crown was divided into quarters of equal length. Two branches with minimal damage were randomly chosen from within each quarter. Branches were generally symmetrical around the crowns of the sampled trees. The two branches per crown quarter were antithetical variates, which is to say that they were sampled the same random number of whorls from opposite ends of the crown quarter (Monserud and Marshall 1999). The number of whorls per quarter was counted, and branch height was estimated by assuming all main-stem internodes within a crown quarter were of equal length. Branch lengths were measured by running a tape from the bole to the bud on the longest axis of the branch. We assumed whole branches were held at equal heights, because these conifer species generally hold their branches horizontally. A sample of 10–25 current-year needles was collected near the end of each sample branch, placed in a plastic bag, and frozen until it could be analyzed. The projected areas of the needle samples were determined by the Mocha image analysis software (Jandel Scientific). The areas were calibrated against needles measured with a micrometer and dissecting scope. The samples were then dried at 70°C and weighed.

Sources of variation in specific leaf area were analyzed by mixed-models analysis of variance (Littell et al. 1996). Variables identified as fixed effects included branch height, branch height × species interaction, branch length, branch length × species interaction, canopy elevation class, and species. We used canopy elevation class as a categorical variable to determine if young, fully exposed branches from within the clearcuts differed from shaded branches of similar height at the base of the canopy in mature stands. The canopy elevations were “high” or “low”. The distinction between branch height and canopy elevation class is critical to this analysis, where branch height describes the height above ground of a single branch and canopy elevation class describes the whole canopy of which that branch is a part.

Two random effects were estimated: stand within canopy elevation class and tree within stand and canopy elevation class. All analyses were conducted using the PROC MIXED

Table 1. Size characteristics of sample trees by species.

Variable	Species	Mean	Minimum	Maximum	SD
Diameter (cm)	DF	35.4	5.3	87.9	21.2
	PP	36.6	4.8	70.6	19.5
	WP	34.1	4.7	73.7	22.2
Height (m)	DF	20.4	3.5	39.6	12.1
	PP	25.3	3.5	40.9	11.1
	WP	27.7	3.7	44.7	13.6
Crown length (m)	DF	13.0	2.5	32.3	6.8
	PP	13.3	3.0	25.8	7.3
	WP	16.2	3.0	32.4	8.4
Crown ratio	DF	0.60	0.12	0.96	0.24
	PP	0.54	0.21	0.84	0.19
	WP	0.61	0.40	0.95	0.18

Note: The number of destructively sampled trees is 22 for Douglas-fir (DF), 21 for ponderosa pine (PP), and 21 for western white pine (WP). Stand density measures and species composition are given in Table 7 of Monserud and Marshall (1999).

Table 2. Summary of results from simultaneously testing the four hypotheses with PROC MIXED in SAS (Littell et al. 1996).

Source of variation	Numerator df	Denominator df	*F*	*P* >*F*
Branch height (H)	1	439	47	<0.0001
Species (S)	2	439	43	<0.0001
H × S	2	439	8.1	0.0004
Branch length (L)	1	439	0.06	0.81
L × S	2	439	0.50	0.60
Canopy elevation class (C)	1	9	0.02	0.90
H × C	1	439	4.28	0.039
L × C	1	439	0.05	0.83

Note: The four hypotheses are described in the Results. The dependent variable is specific leaf area (SLA). Independent variables are species, branch height above ground, branch length from stem to tip, and canopy elevation class (a categorical variable that distinguishes between mature trees growing in older even-aged stands versus young saplings growing in recent clearcuts).

procedure in SAS version 8.1 (Littell et al. 1996). We assumed compound symmetry of the variance–covariance matrix and treated stands as subjects in the analysis. Percentages of variation explained by the various models were compared using PROC GLM to estimate sums of squares. A simplified model was constructed by sequentially eliminating all nonsignificant sources of variation.

Results

Mixed-models analysis simultaneously tested a set of four related hypotheses on the combined species. To simplify the presentation, the results are presented sequentially, in order of increasing complexity.

Hypothesis 1

We tested for differences in SLA among the three species. The species clearly differed ($P < 0.0001$). Mean SLA, corrected for other sources of variation, was 34.3 ± 1.0 $\mathrm{cm}^2\cdot\mathrm{g}^{-1}$ (mean ± SE) for Douglas-fir, 41.4 ± 1.0 $\mathrm{cm}^2\cdot\mathrm{g}^{-1}$ for western white pine, and 25.8 ± 1.0 $\mathrm{cm}^2\cdot\mathrm{g}^{-1}$ for ponderosa pine. Note that this analysis of species effects accounts for the unequal distribution of species among stands and for any variation in branch length or height.

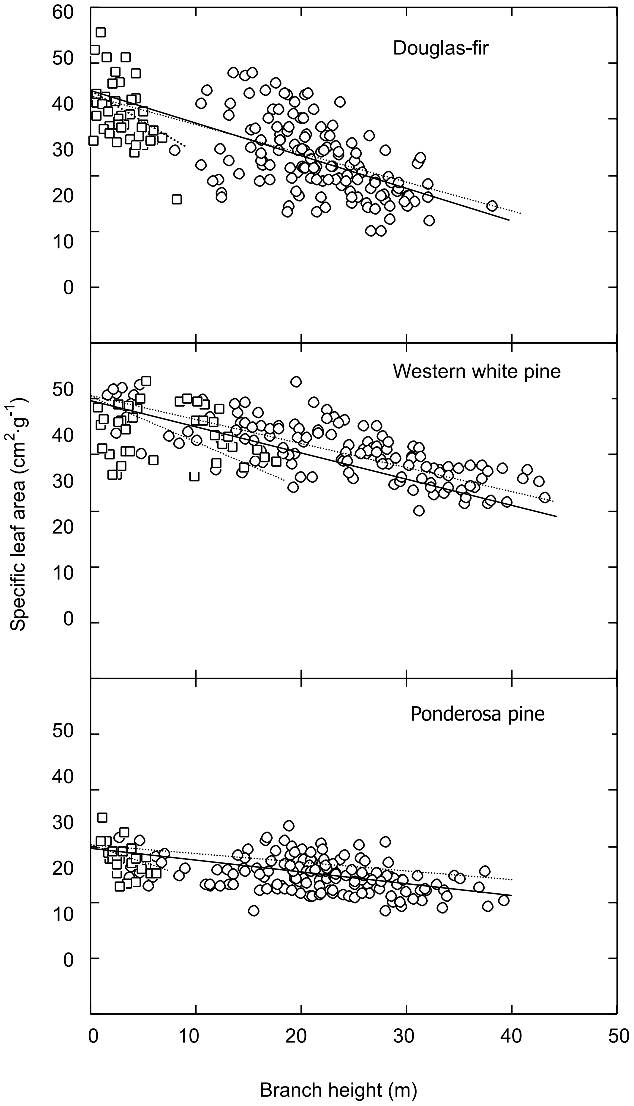
Hypothesis 2

We examined the effect of branch height above ground, which accounts for the hydraulic resistance of the stem and the gravitational component of water potential. Branch height strongly influenced SLA ($P < 0.0001$), and the slope varied among the three species ($P < 0.0001$). The slopes were consistently negative, meaning that specific leaf area (SLA) decreased strongly and linearly as branch height increased in all three species (Fig. 1, Table 2). Douglas-fir had the steepest slope (–0.59 ± 0.06 $\mathrm{cm}^2\cdot\mathrm{g}^{-1}\cdot\mathrm{m}^{-1}$), white pine was intermediate (–0.45 ± 0.04 $\mathrm{cm}^2\cdot\mathrm{g}^{-1}\cdot\mathrm{m}^{-1}$), and ponderosa pine was the least responsive (–0.22 ± 0.06 $\mathrm{cm}^2\cdot\mathrm{g}^{-1}\cdot\mathrm{m}^{-1}$). The steep decline in Douglas-fir resulted in SLA values similar to those of ponderosa pine in branches approaching 43 m above the ground, which approximates the heights of the tallest trees observed in these stands.

Hypothesis 3

We extended our hydraulic path hypothesis to consider branch length as well as branch height. Branch length might

Fig. 1. Specific leaf area versus branch height for Douglas-fir, western white pine, and ponderosa pine. Squares designate foliage from stands with low canopies, and circles are from stands with elevated (high) canopies. The regression equations shown by the solid lines are presented in the Results (eqs. 1–3). The broken lines represent the regression equations accounting for the small improvement in predictive power that results when the canopy elevation class × branch height interaction is accounted for.



impose additional hydraulic resistance on a branch of a given height. We compared young trees with short branches to mature trees with long branches at a similar height. This design increased the probability of detecting a branch length effect, if one existed. We also considered the possibility that results might vary by species. The branch length effect was not significant (P = 0.81), and there were no species differences (P = 0.60).

Hypothesis 4

We also tested for any influence of canopy elevation class. Recall that canopy elevation class is a categorical variable in this analysis, differentiating stands that bear their canopies near the ground from those with elevated canopies. Because the analysis accounted separately for variation in length and height of a particular branch, canopy elevation class accounted primarily for differences in light intensity resulting from the shading by the canopy above the subject branch. Thus, the canopy elevation class effect compared branches of similar height and length growing with or without a canopy above them. The canopy elevation class effect was not significant (P = 0.90).

We found a weak interaction between canopy elevation class and branch height (P = 0.039), however. A significant interaction indicates that the slopes relating branch height and SLA differ between the low and the high canopies (young vs. old stands). Our evidence on the importance of this interaction is quite weak and is not conclusive. The equations that would result from this interaction are plotted as broken lines in Fig. 1.

We deleted nonsignificant variables from our analysis and re-estimated the parameters. We eliminated the branch height × canopy elevation class interaction, because it explained so little of the variation in SLA (76.2% of the variation with the interaction vs. 75.7% of the variation excluding the interaction) and because the evidence in its favor was so weak (P = 0.039). This simplification changed parameter values and predictive power only slightly (cf. the solid and broken regression lines in Fig. 1). The simplified equations are as follows:

[1] $\text{SLA (cm}^2\cdot\text{g}^{-1}) = 45.3 - 0.59 \times \text{branch height (m)}$

for Douglas-fir

[2] $\text{SLA} = 49.7 - 0.45 \times \text{branch height}$

for western white pine and

[3] $\text{SLA} = 29.9 - 0.22 \times \text{branch height}$

for ponderosa pine. The Douglas-fir equation explained 41% of the variation, the white pine equation explained 44% of the variation, and the ponderosa pine equation explained 22% of the observed variation in SLA.

Discussion

A simultaneous test of multiple hypotheses relating specific leaf area to path length and canopy height led to a clear result for all three species. SLA declined with branch height in all three species, but rates of decline varied significantly among species. The amount of leaf area displayed for a given amount of leaf biomass was nearly halved at the top of a 40-m Douglas-fir tree compared with that in a 1-m sapling (Fig. 1). We detected no effect of branch length on SLA. Canopy elevation class was insignificant as a main effect and weakly significant as an interaction with branch height. The lack of a canopy elevation class effect means that we could ascribe limited variation to the presence or absence of a canopy above a given branch, after other sources of variation had been accounted for.

The influence of tree height on SLA was earlier noted by Niinemets and Kull (1995). An important distinction between their study and ours is that they used total tree height as a covariate whereas we use the actual height of the foliage in question. If the change in SLA were related to water relations, then one should account for smaller hydrostatic gradient and shorter path length of the foliage on the lower branches of a tall tree, rather than assuming that the whole tree experiences the water potential of the uppermost foliage.

The three species studied here vary in shade tolerance, a classification used to predict survival and growth under an overtopping canopy. Intolerant species generally show low plasticity in SLA as a function of light intensity (Chen et al. 1996). Ponderosa pine is shade intolerant (Burns and Honkala 1990). Therefore, one would not expect SLA to increase with depth in the canopy if it were controlled only by light intensity. Consistent with this expectation, Chen (1997) was unable to detect changes in SLA with light regime in ponderosa pine in stands of constant age and similar height. Pataki et al. (1998) found no change in SLA in even-aged, 5 m tall *Pinus taeda* stands. Similarly, Nagel and O'Hara (2001) were unable to detect a height effect on SLA in even-aged ponderosa pine stands but did detect one in multiaged stands. On the other hand, if SLA were to decrease primarily because of low water potentials rather than shade, then one might find a height effect even in a species as intolerant as ponderosa pine (Monserud and Marshall 1999; Nagel and O'Hara 2001), as we did in this study.

Interior Douglas-fir and western white pine are considered intermediate in tolerance, although white pine tends to survive better than Douglas-fir under dense canopies (Burns and Honkala 1990). Unlike ponderosa pine, interior Douglas-fir was reported to increase in SLA at low light intensity, even in the absence of height differences, at a site in British Columbia (Chen 1997). The same effect was observed in a study of naturally regenerated Douglas-fir saplings, which were less than 1.3 m in height (Chen et al. 1996). These earlier results are inconsistent with the results of the present study.

What was the cause of these significant trends in SLA with respect to branch height? Our correlation analysis cannot answer this question, but we can consider possible explanations.

Based on a simple physical analysis of water flow, one might expect greater water stress as trees grow taller (Whitehead et al. 1984; Margolis et al. 1988; Yoder et al. 1994; Bond and Ryan 2000; but see Pothier et al. 1989). Elevation of the canopy as trees gain height would both lengthen the path of water flow and decrease the gravitational component of water potential at the top of the stem. Because of lower water potential, stomata would partially close (Zhang et al. 1994; Schafer et al. 2000) and turgor pressure would decline (Waring and Schlesinger 1985). A decrease in turgor pressure might result in a decrease in SLA.

The influence of turgor on SLA can be understood as a consequence of volume increase and the carbon budget of the leaf (Tardieu et al. 1999). The rate of cell expansion can be modeled as follows:

$$r = \frac{\mathrm{d}V}{V\,\mathrm{d}t} = \phi\,(\psi_{\mathrm{p}} - Y)$$

where r is the rate of volume increase, V is volume, ϕ is a yield coefficient (a measure of the ease with which the cell wall expands), ψ_{p} is the turgor pressure within the cell, and Y is a threshold water potential necessary for cell expansion to commence (Cosgrove 1986). A decline in ψ_{p} would result in slower cell expansion. In fact, studies vary in what they identify as the controls over volume expansion. Some report turgor pressure as a key control (Tardieu et al. 1999); others report that turgor pressure is maintained homeostatically and that cell expansion is determined by variation in ϕ (Roden et al. 1990; McDonald et al. 1992), which in turn may be controlled by temperature (McDonald et al. 1992; Tardieu et al. 1999). If a given amount of mass were expanded over a smaller amount of volume, the effect, when summed over a leaf, would be a decrease in SLA (Tardieu et al. 1999). Drought experiments, provided they are not too severe, commonly report decreased SLA in the drought treatments (Phillips and Riha 1993; Ibrahim et al. 1998; Myers et al. 1998).

Similarly, if hydraulic conductivity controlled SLA to some extent, then branch length might significantly affect SLA as path length increases. This hypothesis is supported by the argument that branch length may significantly influence gas exchange (Waring and Silvester 1994) and hydraulic conductivity (Panek 1996). Because of the regular pattern of conifer crowns, the longest branches are generally found at the bottom of the crown (e.g., Monserud and Marshall 1999, Table 4). In the current study, we were unable to detect a significant branch length effect on SLA, despite a large sample size (see Table 2) and considerable variation in branch length.

We have previously presented evidence of hydraulic limitations in these same trees and stands (Marshall and Monserud 1996; Monserud and Marshall 2001). These studies analyzed water-use efficiency inferred from stable carbon isotope composition of tree ring cellulose. Water-use efficiency generally increases as water potential falls (Yoder et al. 1994; Zhang et al. 1994). Trees were analyzed two ways: with height held constant by measuring different trees over time (Marshall and Monserud 1996) and with height increasing throughout the lives of individual trees (Monserud and Marshall 2001). Water-use efficiency increased as trees grew taller (Monserud and Marshall 2001), but no such increase was observed in trees compared at a constant height (Marshall and Monserud 1996). SLA behaved similarly in this study, decreasing as trees grew taller and constant at a given height.

The lack of a strong canopy elevation class effect should not be interpreted as evidence that no such effect exists. As noted above, the difference in the slopes of the curves between old and young stands may be interpretable as a light-intensity effect. Beyond that, statistical analyses are designed for conservative decisions with respect to the detection of an effect (Parkhurst 2001). It may instead mean that the experiment was not powerful enough to detect canopy elevation class as a main effect. Given the low P value (P = 0.90), we think this unlikely, but the possibility cannot be eliminated with the present data. Careful measurements of light intensity throughout the canopy would have provided more power for this test. Consequently, we cannot (and do not) argue that light has no effect on SLA in these species. Instead, we focus on the negative correlations between branch height and SLA and note that they are consistent with theoretical expectations (Fig. 1).

The monotonic decreases in SLA with branch height present a simple means of modeling canopy SLA as trees grow in height. Given a description of the vertical distribution of leaves through the canopy, mean SLA could be estimated for each species for each vertical layer. The SLA distribution could be updated as the canopy grows. As noted earlier, the accurate description of SLA may be an important part of making accurate growth predictions, given the central importance of this variable in forest process models (e.g., Aber and Federer 1992; Landsberg and Waring 1997).

If light were the sole environmental control over SLA, then the shaded lower branches in tall canopies would be expected to have higher SLAs than the sunlit upper branches in short canopies, when the branches were deployed at similar height. Instead, we found that SLA was similar at a given height regardless of canopy type, in all three species. Furthermore, we found that SLA decreased significantly as branch height increased, for all three species. Limitations of our correlative study on SLA cannot conclusively resolve competing explanations, such as light intensity versus water potential. Based on our results, we offer a hypothesis that water potential at the point of leaf display modifies specific leaf area. Controlled experiments are needed to test this hypothesis. Such experiments would be most informative if conducted under water potentials observed in normal forest grown trees.

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