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NOTE / NOTE

Sapwood area – leaf area relationships for coast redwood

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Abstract: Coast redwood (*Sequoia sempervirens* (D. Don) Endl.) trees in different canopy strata and crown positions were sampled to develop relationships between sapwood cross-sectional area and projected leaf area. Sampling occurred during the summers of 2000 and 2001 and covered tree heights ranging from 7.7 to 45.2 m and diameters at breast height ranging from 9.4 to 92.7 cm. Foliage morphology varied greatly and was stratified into five types based on needle type (sun or shade) and twig color. A strong linear relationship existed between projected leaf area and sapwood area at breast height or sapwood at the base of the live crown despite the variability in foliage morphology. Ratios of leaf area to sapwood were 0.40 m^2/cm^2 at breast height and 0.57 m^2/cm^2 at crown base. Measurements of sapwood at the base of the live crown improved leaf area predictions because of sapwood taper below the crown base. A sapwood taper model was also developed.

Résumé : Des séquoias côtiers (*Sequoia sempervirens* (D. Don) Endl.) appartenant à différentes strates de couvert et classes sociales ont été échantillonnés pour établir des relations entre la superficie d'aubier et la superficie foliaire projetée. Au cours des étés 2000 et 2001, des arbres de 7,7 à 45,2 m de hauteur et de 9,4 à 92,7 cm de diamètre à hauteur de poitrine ont été échantillonnés. La morphologie foliaire variait grandement et a été stratifiée en cinq groupes se distinguant par le type de feuille (lumière ou ombre) et la couleur des ramilles. La superficie foliaire projetée était linéairement et fortement reliée à la superficie d'aubier à hauteur de poitrine ou à la base de la cime vivante malgré la variabilité de la morphologie foliaire. Les rapports de la superficie foliaire sur la superficie d'aubier étaient de 0,40 m^2/cm^2 à hauteur de poitrine et de 0,57 m^2/cm^2 à la base de la cime vivante. Les mesures de superficie d'aubier à la base de la cime vivante ont amélioré les prédictions de superficie foliaire en raison du défilement de l'aubier sous la base de la cime. Un modèle de défilement de l'aubier a aussi été mis au point.

[Traduit par la Rédaction]

Introduction

Leaf area estimates for trees and forest stands provide useful information for research and management of forest productivity and forest ecosystem analyses. The pipe model theory imparts biological justification for the use of cross-sectional sapwood area (A_S) as a surrogate for leaf area (A_L) (Shinozaki et al. 1964). A_L:A_S prediction equations have been developed for many conifer species (Waring et al. 1982; Vose et al. 1994; Margolis et al. 1995; DeLucia et al. 2000). Although these equations have been widely applicable for a given species, variations exist as a result of management history (e.g., thinning, pruning; Brix and Mitchell 1983), sapwood permeability (Whitehead et al. 1984), ring width (Albrektson 1984), and other factors. Lower A_L:A_S with increasing water vapor pressure deficits have been reported for pines, but not for other conifers (DeLucia et al. 2000). Species with greater shade tolerance or from more mesic environments may also have greater A_L:A_S (Waring et al. 1982; Margolis et al. 1995) confounding comparisons across genera.

Coast redwood (*Sequoia sempervirens* (D. Don) Endl.) is the dominant species in one of the world's most productive forest ecosystems. No published A_L:A_S relationships exist for coast redwood. Given the relatively high shade tolerance of redwood and its occurrence along California's humid coast, a high A_L:A_S would be expected. Waring et al. (1982) sampled a single redwood but did not publish a coefficient. An unpublished Ph.D. dissertation included coefficients of 0.25 and 0.38 for breast height and crown base A_L:A_S for redwood on the north coast of California (Cavallaro 1989). Leaf area estimation in redwood is complicated by variations in foliage morphology (Koch et al. 2004): "shade" foliage generally consists of flat sprays of two-ranked needles and "sun" foliage consists of shorter, appressed scaled needles that are arranged in several ranks on stems or twigs. Needles are elliptical in cross-section, whereas stems are cylindrical.

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The present study examined sapwood area, leaf area, and foliage morphology of redwood growing in a variety of crown positions in stands located in the middle of the redwood range in California. The objectives were to
(*i*) develop a A_L:A_S relationship for projected leaf area;
(*ii*) develop a model for estimating sapwood area at crown base (A_{SBLC}) from sapwood area at breast height (A_{SBH}); and
(*iii*) categorize and examine distribution of foliage types and projected leaf area.

Study area

The study area was located within the Jackson Demonstration State Forest (39°22′22′′N, 123°39′20′′W), a 20 000-ha coast redwood forest on the California coast in Mendocino County. The climate is Mediterranean, characterized by a pattern of high rainfall in winter and cool, dry summers with coastal fog. Precipitation in nearby Caspar Creek watershed averages approximately 130 cm/year.

Materials and methods

Twelve trees of different size, and from various canopy strata and crown positions (from suppressed to dominant) were sampled in four different second-growth stands during the summers of 2000 and 2001. Trees were classified by crown class and strata following Oliver and Larson (1996). Trees varied in age from approximately 28 to 80 years. Trees of smaller size sampled in the study included suppressed trees in older stands and trees occupying dominant and codominant crown positions in younger stands. Each tree was carefully felled to avoid contact with other crowns and prevent branch loss or mixing of foliage. However, estimates for large trees include some uncertainty about origins of a few branches and foliage on the ground, as some crown damage and (or) mixing occurred during felling. After the tree was felled, total height and crown length were measured to the nearest centimetre. The location of the lowest living vigorous branch defined the base of the live crown. Summary data for sampled trees are presented in Table 1.

Crowns were stratified into three sections of equal length. Branches were removed from each section and stratified in two to four different categories based on branch length. Categories were weighed separately for fresh mass using a spring scale (±150 g) or an electronic scale (±0.1 g) depending on size. Because some branches were damaged during tree felling, a random branch from each category would not have been representative in most situations. For categories with minor or no damage, branches were selected at random. Where crown damage was more common, a random sample was selected out of the intact branches. The total fresh mass of each of these sample branches was measured and recorded. The photosynthetic tissue was then separated from these sample branches and stratified into one of five morphological types:
(1) Old shade needles on brown stems older than 2 years, needles easy to detach;
(2) Young shade needles with photosynthetic twigs. Twigs up to 2 years old. Foliage and twigs green colored. Twig thin and soft with needles difficult to detach without damaging twig;

Table 1. General data for the 12 trees sampled in the study.

Statistics	DBH (cm)	Total height (m)	Crown ratio (%)	A_{SBLC} (cm^2)	A_{SBH} (cm^2)
Mean	31.1	21.1	67	237.97	333.29
SD	25.1	13.4	15	315.66	443.13
Min.	9.4	7.7	43	44.74	53.83
Max.	92.7	45.2	90	1158.03	1601.75

Note: DBH, diameter at breast height; A_{SBLC}, sapwood area at crown base; A_{SBH}, sapwood area at breast height; SD, standard deviation.

(3) Sun needles with photosynthetic twigs. Possible to separate needles from twig. Twig diameter generally less than 5 mm;
(4) Sun needles with photosynthetic stems. Needles possible to separate from stem. Twig diameter generally greater than 5 mm;
(5) Sun needles with photosynthetic twigs. Very small needles impossible to separate from twig.

After stratification, each morphological type was weighed for total fresh mass using an electronic scale (±0.1 g), and a smaller random sample (0.4–8.0 g) was selected for leaf area analysis. To avoid carbon loss through respiration, this foliage was placed on ice in the field and later was stored in a refrigerator. In the lab, every sample was scanned for projected leaf area using the Regent Instruments WinSeedle software (transparency unit active, 300 dpi resolution, automatic threshold for object detection). For leaf types 1, 2, 3, and 4, needles were detached from twigs or stems before scanning. Needles and twigs or stems were scanned separately for sections 2, 3, and 4 to avoid overlap. For leaf type 5, entire twigs (with needles attached) were scanned. Finally, projected leaf area was proportionally expanded from the scanned sample to morphological type, branch level, branch category level within a crown section, entire crown section, and tree level.

To determine A_S, a stem disk was cut at the base of the tree at breast height (1.37 m) and at the base of the live crown. Bark was removed in the field, and disks were sealed in plastic bags and brought to the lab for analysis. The boundary between sapwood and heartwood was delineated based on coloration changes across the disk. Disks were sanded, scanned, and images were enhanced using Adobe® Photoshop®. Images were analyzed for sapwood area using Regent Instruments WinSeedle software (transparency unit active, 300 dpi resolution, automatic threshold for object detection).

A taper model was developed to predict sapwood area at the base of the live crown (A_{SBLC}) as a function of sapwood area at breast height (A_{SBH}) and height to the crown base (H_{BLC}). A_L was regressed against A_{SBH} and A_{SBLC}. Linear and quadratic models were fitted and compared. Given the small number of sampled trees, it was difficult to assess if they came from a normally distributed population. Therefore, a bootstrap resampling method with 10 000 replications was implemented for all three models to develop more realistic confidence intervals for our estimates. This method calculates the confidence intervals on 10 000 data sets (replications) obtained through resampling with replacement of the original data set (i.e., different combinations of values from the original data set are used in each replication) (Crawley 2002). Furthermore, for the A_L:A_S relationships, to assess the influence on the slope of the regression line of the big trees and any other individual tree in our sample, a jackknife procedure was used. This procedure uses different combinations of values from the original data set in each replication to assess the effect of individual values on the resulting model (Crawley 2002).

Leaf area measurements were discarded from analysis for tree 1 because of measurement errors. However, stem disks coming from tree 1 were still used to develop the sapwood taper model. Trees 2 and 3 were sampled before the distinction between leaf morphological types 1 and 2 was recognized, and separate totals for these two foliage types are not available. Tree 12 had a stem injury at the base that appeared to have affected sapwood formation in the lower stem. Although sapwood at breast height appeared normal, we considered the base section too close to the injured part of the stem for leaf area and sapwood taper analysis. As the crown base was further up on the stem, the corresponding A_L and A_S data for this tree were included in the A_L:A_{SBLC} regression. Therefore, sample size (*n*) was 11 for A_L:A_{SBLC} relationships, 11 for the taper equation, and 10 for the A_L:A_{SBH} relationships. S-Plus 6.0 statistical software was used for data analysis.

Results

Specific leaf area (SLA), or the ratio of leaf surface area to leaf mass, decreased more than four times from shade shoots with needles (type 2) to sun stems with needles (type 4) (Table 2). SLA also decreased with increasing height, although heights of samples were only documented by crown third and are not shown. The trees sampled were highly variable in terms of their distribution of morphological types (Table 3). Trees in lower strata and canopy classes generally had lower percentages or none of the sun leaf morphological types. Type 2 was the most common foliage type in every tree except tree 8. Trees 2 and 3 consisted entirely of leaf morphological types 1 and 2.

Strong relationships were apparent between projected leaf area and sapwood area at breast height and base of the live crown. The second-degree term of the quadratic models was not statistically significant. Therefore, linear models were considered most appropriate. Linear regression through the origin was performed because linear models proved in both cases (SA_{BLC} and SA_{BH}) to have statistically nonsignificant intercepts ($P > |t|$ was 0.2419 and 0.6317, respectively). As expected for both models, bias-corrected and adjusted (Bca) 95% confidence intervals (after bootstrap) were wider than empirical 95% confidence intervals developed from linear regression (Table 5). Final regression models are presented in Figs. 1 and 2.

Although sample size in this study was small, tree size ranged considerably (Table 1). As Figs. 1 and 2 show, two trees were much larger than all others sampled. For both A_L:A_S regressions, the value of the mean slope obtained with the jackknife procedure was very similar to the observed one (for A_L:A_{SBLC}, 0.5640 and 0.5672, respectively; for A_L:A_{SBH}, 0.3963 and 0.4005, respectively). Also, the bias and the standard error had relatively small values (for A_L:A_{SBLC}, –0.03184 and 0.04474, respectively; for A_L:A_{SBH}, –0.03745 and 0.05629, respectively). Therefore, the final models were based on samples that included the largest trees.

Table 2. Average specific leaf areas (SLA) for five leaf morphology types.

Morphological type	SLA (cm^2/g)	SD (cm^2/g)	*n*
1	51.60	12.98	23
2	56.46	15.20	23
3	29.50	3.58	3
4	14.11	2.90	3
5	17.00	4.19	6

Note: Types 2–5 included green twig tissues. Sample sizes were the number of samples taken that included up to three samples per tree. SD, standard deviation.

Multiple regression was used to develop the sapwood taper model. Because having a positive intercept would lead to overestimates of sapwood area for very small trees, regression through origin was performed, and the final model became $A_{SBLC} = 0.7460A_{SBH} - 3.8293(H_{BLC} - 1.37)$ (H_{BLC}: height to base of the live crown, in metres; breast height = 1.37 m). Both sapwood at breast height and height to the crown base proved to be statistically significant in the equation (Table 4). In this case, the resulting bias-corrected and adjusted 95% confidence intervals were rather large compared with the empirical 95% confidence intervals (Table 5).

Discussion

Large differences were observed between foliage morphological types in coast redwood. SLA decreased fourfold from the most shade foliage (type 1) to the most sun foliage type (type 4) (Table 2). Koch et al. (2004) also reported a fourfold increase in SLA with height of sample on larger old forest redwood trees but expressed their measure as specific leaf mass (grams per square metre). Koch et al. (2004) attributed variations in SLA primarily to height of sample or position within the crown. Our results indicate foliage type was related to light environment and the effects of stand structure, where height of the sample was only a contributing factor. For example, tree 4 was 7.8 m tall and had all types of foliage, whereas tree 12 was 10.2 m tall and had no sun foliage (Table 3).

The similarity in our SLA values for morphological types 1 and 2, and 4 and 5 suggested that a simpler classification may have been sufficient for development of A_L:A_S relationships. Additionally, type 5 was found on only two trees and represented less than 1% of each in terms of foliage mass. However, variation in SLA within individual trees was large (Tables 2 and 3), but was not apparent in the averages for all trees. Other fundamental differences were that morphological type 1 included only needles, whereas type 2 included green twigs and needles. Also, types 3 and 4 included both twigs or stems and needles, whereas type 5 approached the form of a cylinder, as needles were small and appressed, and were not detached.

Despite the morphological differences in redwood foliage, the strong A_L:A_S relationship indicates a general model could

Table 3. Foliage distribution by leaf morphological type and canopy position.

Tree No.	Crown strata – crown class	Total foliage mass (kg)	% of total foliage mass for each leaf morphology type: 1	2	3	4	5
2*	D–S	3.45	—	—	0	0	0
3*	C–D	14.99	—	—	0	0	0
4	C–C	20.45	14.5	84.7	0	0	0.7
5	C–I	24.78	13.9	86.1	0	0	0
6	D–S	10.10	23.6	76.4	0	0	0
7	B–C	133.58	20.0	52.7	27.0	4.6	0.3
8	A–D	386.85	8.7	31.1	60.1	7.5	0
9	B–I	37.16	31.6	68.4	0	0	0
10	B–I	49.15	35.5	64.5	0	0	0
11	B–C	51.95	36.8	57.6	5.6	1.4	0
12	D–S	5.29	41.8	58.2	0	0	0

Note: Canopy strata were (A) emergent with subsequent letters denoting lower strata (Oliver and Larson 1996). Crown classes: D, dominant; C, codominant; I, intermediate; S, suppressed.
*Trees 2 and 3 included only foliage types 1 and 2, but these foliage types were not separated for these two trees.

Fig. 1. Projected leaf area (A_L) as a function of sapwood area at the base of the live crown (A_{SBLC}): $A_L = 0.5672A_{SBLC}$ (adjusted $R^2 = 0.9833$; SE = 0.0221; t ratio = 25.6362; $P > |t| = 0.0000$; root mean square error = 29.40.

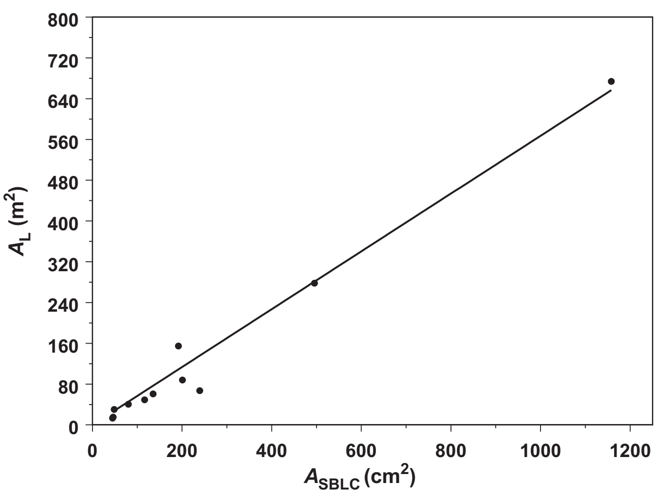
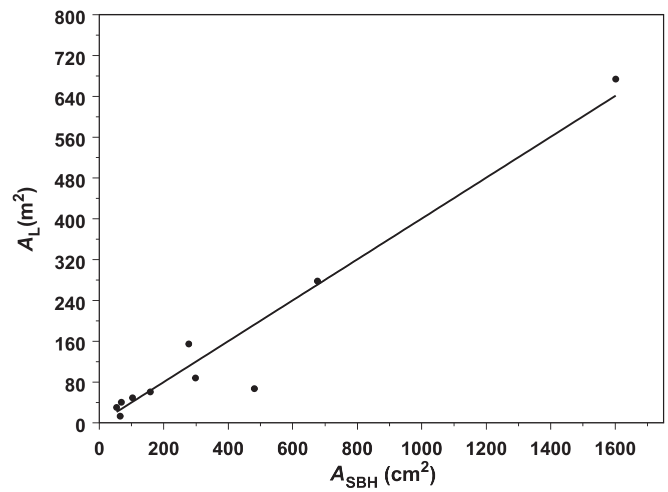


Fig. 2. Projected leaf area (A_L) as a function of sapwood area (A_{SBH}): $A_L = 0.4005A_{SBH}$ (adjusted $R^2 = 0.9605$; SE = 0.0255; t ratio = 15.7338; $P > |t| = 0.0000$; root mean square error = 47.40.



be applied across trees from a variety of strata and crown positions. Variations in leaf morphology and SLA have been documented for other species. For example, the decrease in SLA with height has been documented in temperate broadleaf trees (Ellsworth and Reich 1993), temperate conifers (Hager and Sterba 1985), and tropical mangroves (Farnsworth and Ellison 1996). However, this is the first study to document a constant A_L:A_S relationship when such disparate leaf morphology is present. Further studies should examine whether there is a corresponding increase in sapwood requirements of different foliage types with increasing light environments that result in constant A_L:A_S when leaf morphology is highly variable. Regardless of the mechanisms involved, this work indicates that sapwood is a useful predictor of A_L for coast redwood trees growing in a variety of canopy positions.

The proposed models for leaf area estimation are similar to work done previously with redwoods. Cavallaro's (1989)

Table 4. Parameter estimates and fit statistics (before bootstrapping) for the sapwood taper model: $A_{SBLC} = 0.7460A_{SBH} - 3.8293(H_{BLC} - 1.37)$.

Term	Estimate	SE	t ratio	$P > \|t\|$
A_{SBH}	0.7460	0.0220	33.89	0.0000
(H_{BLC} – 1.37)	–3.8293	1.5400	–2.49	0.0346

Note: The model has a root mean square error = 31.15 and an adjusted $R^2 = 0.9939$. A_{SBLC}, sapwood area at base of the live crown (cm²); A_{SBH}, sapwood area at breast height (cm²); H_{BLC}, height to the base of the live crown (m); SE, standard error.

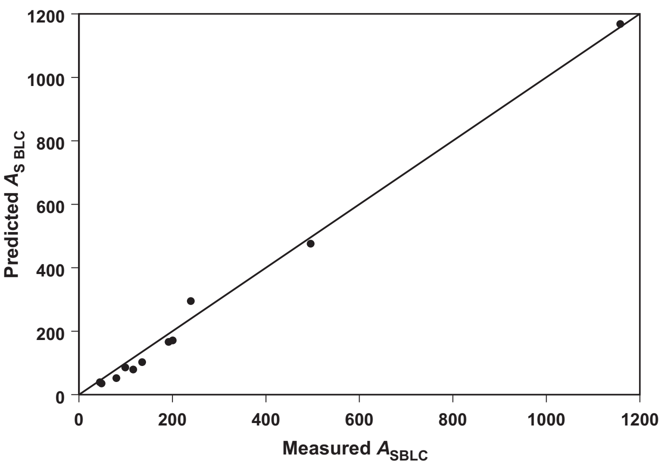
coefficients of 0.38 m²/cm² for A_{SBLC} and 0.25 m²/cm² for A_{SBH} were smaller than those of the present study, but the regressions included an intercept, and sampling methods were different. Waring et al. (1982) used similar methods as our study to obtain a ratio of 0.51 m²/cm² for sapwood at breast height based on a single tree (R.H. Waring, personal

Table 5. Coefficients, bias-corrected and adjusted (BCa) confidence interval (after bootstrap), and empirical confidence interval for leaf area – sapwood area and taper models run through origin.

Model	Term	Coefficient	Empirical 95% CI	Bca 95% CI
1	A_{SBLC}	0.5672	(0.5179; 0.6165)	(0.4642; 0.6360)
2	A_{SBH}	0.4005	(0.3429; 0.4581)	(0.2641; 0.4616)
3	A_{SBH}	0.7460	(0.6962; 0.7958)	(0.3687; 0.8534)
3	$(H_{BLC} - 1.37)$	3.8293	(–7.3130; –0.3456)	(–11.2280; 0.3437)

Note: 10000 replications were used for the bootstrap resampling method. A_L, leaf area (m^2); A_{SBLC}, sapwood area at base of the live crown (cm^2); A_{SBH}, sapwood area at breast height (cm^2); H_{BLC}, height to the base of the live crown (m); CI, confidence interval.

Fig. 3. Measured versus predicted sapwood area at base of the live crown (A_{SBLC}). The diagonal line represents a 1:1 ratio between measured and predicted A_{SBLC}.



communication, 2003). The value of the slope coefficient for the breast height regression equation proposed in this work (0.40) is within the range of those reported previously.

The relatively large A_L:A_{SBLC} ratio for coast redwood (0.57 m^2/cm^2) is consistent with larger coefficients corresponding with more shade-tolerant species and species from more mesic environments (Waring et al. 1982; Margolis et al. 1995). However, differences between genera in terms of sapwood conductivity, foliage longevity, or water use efficiency likely outweigh differences attributed to shade tolerance. For example, DeLucia et al. (2000) found a strong relationship between the A_L:A_S ratio and average maximum summer water vapor deficit among seven *Pinus* species. There was no relationship among a group of 10 other conifers, suggesting differences between genera do not coincide with A_L:A_S ratios. An A_L:A_S ratio for coast redwood is also potentially confounded by foliar uptake of moisture during heavy coastal fog (Burgess and Dawson 2004). This may contribute to higher A_L:A_S ratios in redwood, and particularly in large redwoods or trees with greater exposure to heavy fog. Since sampling was targeted at second-growth redwoods, the resulting models may not apply to old forest trees.

Projected leaf area in this paper was used for all five morphological types. If we had considered the all-sided area for photosynthetic parts that were not flat (sun leaves with photosynthetic twigs from type 5; twigs and stems from types 3 and 4) a greater amount of A_L would be predicted per unit area of sapwood. Conversions from projected to all-sided leaf area for redwood would be more complex than for most species, because of the variation in morphology. Morphological type 1 would have a conversion factor close to 2.0, because of the relatively flat needles on nonphotosynthetic twigs. Types 2–5 include both needles of various shapes and photosynthetic twigs. Conversions would therefore fluctuate between approximately 2.0 for flat foliage to 3.14 (π) for twigs depending on the relative amounts of each kind of tissue.

In the sapwood taper model, A_S at breast height explained most of the variation in A_S at the base of the live crown. Adding distance from breast height to crown base to the regression provided only a small increase in adjusted R^2; however, the term was statistically significant. Using distance between the two sections (breast height and base of the live crown) is considered realistic because of taper between the base of the tree to the base of the crown (Waring et al. 1982; Maguire and Hann 1987). The large values for the bias-corrected and adjusted 95% confidence intervals reflect not only the small sample size but also a greater scatter in the data compared with the A_L:A_S models. However, the actual taper model can be used, since the empirical and predicted values were similar (Fig. 3). Sampling more trees with more diverse crown ratios and also taking more cross-sections between breast height and crown base along the stem of a tree would help improve the model.

Because of the time-consuming sampling and measurement procedures for leaf area, the sample size for developing A_L:A_S relationships in this study was small. Therefore, the potential to develop more complex models was limited. However, the bootstrap resampling procedure provided more realistic confidence intervals for our model parameters compared with the empirical ones. Additionally, the results of the jackknife method proved that all trees had similar effects on the slope of the leaf area – sapwood area linear regression model. Nevertheless, further development of leaf area prediction models for redwood should include a larger sample and more detailed examination of the effect of foliage morphology on leaf area.

Conclusions

Foliage morphology is highly variable in coast redwood trees. Upper canopy or crown classes have higher proportions of sun foliage with lower SLA. Despite differences in foliage, A_S is a useful estimator for A_L in coast redwood. A_S

at base of the live crown is a better predictor of A_L than A_S at breast height, as it is not affected by sapwood taper. When crown base exceeds breast height, A_L predictions should be based on predictions of A_S at crown base.

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