The Ratio of Live Crown Length to Sapwood Area as a Measure of Crown Sparseness

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ABSTRACT. Leaf area density is a biologically appealing index of forest tree health because it can provide an assessment of foliage loss or retention; however, it is difficult to measure directly. In contrast, the ratio of crown length to sapwood area (CL:SA) is quite amenable to objective field measurement, and could be interpreted as an index of crown sparseness. CL:SA was computed for Douglas-fir trees from 70 plots covering a range in average size, stand density, site quality, and crown condition in the Oregon Coast Range. When expressed as $cm:cm^2$, the index ranged from 2 to 100 for individual trees and from 2 to 11 for plot averages based on the 200 largest trees per ha. In general, individual trees with a high CL:SA had a lower relative height within the stand. The index also increased with increasing severity of needle loss on sites where Swiss needle cast (SNC) is causing premature loss of foliage. After correcting for stand density and stand age, plot basal area growth increased significantly with a decrease in plot average CL:SA across a gradient in Swiss needle cast severity. CL:SA has strong potential for discriminating effectively among stands with varying degrees of foliage loss and growth reduction due to other disturbances as well, such as air pollution and defoliating insects. FOR. SCI. 48(1):93–100.

Key Words: Sapwood area, crown length, leaf area, leaf area density, defoliation.

THE PROPORTIONAL RELATIONSHIP between foliage area and sapwood cross-sectional area (Büsgen and Münch 1929, Grier and Waring 1974) has been exploited extensively in analyses of forest growth (Waring et al. 1981); assessments of growth efficiency (Smith and Long 1989, O'Hara 1988, 1996); detection of disease impacts (Waring et al. 1980, Oren et al. 1985); and estimation of susceptibility to insect attack (Waring and Pitman 1985). Likewise, gross crown dimensions, such as crown length or crown volume, have served as effective predictors of individual tree growth in forest growth and yield models (Mitchell 1975, Ritchie and Hann 1985, Hann and Ritchie 1988, Wykoff 1990). The efficacy of gross crown size in predicting tree growth can presumably be attributed to its correlation with total leaf area and tree photosynthetic capacity (Maguire and Bennett 1996, Gilmore et al. 1996). Likewise, the popularity of crown ratio in forest stand examinations and silvicultural research no doubt persists because this type of gross dimension is generally more convenient to measure in the field. However, variation in the density of foliage per unit crown length or per unit crown volume may render its application less reliable across stands and sites. This variation may be imposed by inherent site differences or by agents causing direct foliage loss. In the case of fungal diseases that cause premature needle drop (for example, Swiss needle cast in Dou-

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glas-fir; Hansen et al. 2000) or insect attack resulting in partial or complete consumption of foliage (for example, spruce budworm defoliation of balsam fir; Ostaff and MacLean 1995), gross crown dimensions alone would not accurately reflect the total foliage area or mass.

In contrast, if a close dynamic equilibrium does exist between foliage area and the cross-sectional sapwood area that services the foliage (for example, Margolis et al. 1988), then sapwood area should have the advantage of being able to track short-term variations in total tree leaf area. However, if both sapwood area and gross crown dimensions are considered simultaneously, it becomes evident that a ratio of the two (for example, sapwood area to crown volume) has potential as an indicator of leaf area density or crown bulk density. The ratio of live crown length to sapwood area has the special appeal of being amenable to easy and objective measurement in the field, since crown length is frequently measured in operational inventories and sapwood area can be estimated from increment cores for most conifers. Various types of visual estimates of crown density have been proposed and implemented in forestry, particularly in recent systems for monitoring forest health (Innes and Boswell 1990). However, these visual estimates present challenges in regard to repeatability within and among observers (Innes 1988, Innes and Boswell 1990).

The overall objective of this study was to assess the potential of CL:SA as an index of tree condition, including crown density and growth vigor. The utility of CL:SA would depend in part on the degree of variability in the index, and in part on how well it was correlated with other more operationally challenging indices and with indicators of tree condition such as growth rate. Therefore, the specific objectives were: (1) to quantify the variation in CL:SA within and among stands of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) in coastal Oregon; (2) to test the hypothesis that CL:SA is correlated with direct and independent estimates of foliage loss in Douglas-fir stands experiencing varying intensities of Swiss needle cast (SNC), a defoliation disease caused by the fungus *Phaeocryptopus gaeumannii*; and (3) to test the hypothesis that CL:SA is related to tree vigor, one measure of which is basal area growth.

Methods

The target population for this study was defined by species composition, stand age, and geographic region. A list of stands meeting the following criteria was constructed: (1) ≥90% Douglas-fir by basal area; (2) total stand age between 10 and 30 yr; and (3) geographical location between the Pacific coast and 32 km inland (between approximately 123˚46′ and 123˚59′ W long.) and between Newport, Oregon, in the south and Astoria, Oregon, in the north (between approximately 44˚34′ and 46˚06′ N lat.). The listed population included 4,504 stands covering 75,929 ha (187,545 ac). A sample of 70 plantations with total area of 2,783 ha (6,873 ac) was drawn from this list, with probability of selection set proportional to stand area. Douglas-fir plantations in the Coast Range typically contain a large mix of other conifer and hardwood species that regenerate naturally, even where management of competing vegetation has been aggressive; hence, most of the sample stands contained a significant component of western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) and other conifers that are not affected by SNC (Table 1).

Fieldwork

A randomly located, 75 m transect was established in each of the 70 sample plantations in March and April 1997. Each transect contained five sample points separated by 15 m, and at each sample point, two dominant or codominant Douglas-fir were identified on opposite sides of the transect. Several types of SNC disease ratings were recorded for each tree, including average foliage retention (yr). A 0.02 ha circular plot was subsequently centered on the third sample point of each transect. Species and dbh (nearest 0.1 cm) were recorded for all trees taller than 1.37 m. In addition, total height (nearest 0.01 m) and height to lowest live branch (nearest 0.01 m) were recorded for up to 40 Douglas-fir per plot. Eight Douglas-fir trees were then felled on each plot for intensive growth and foliage analysis. These eight trees included the

Table 1. Mean, range, standard deviation, and coefficient of variation for sample plot attributes (n = 70).

Attribute	Mean	Standard deviation	Coefficient of variation	Range
Breast height age (yr)	12.2	4.9	40	3.3–28.3
Douglas-fir basal area growth (m^2/ha/yr)	1.72	0.81	47	0.49–3.95
Total basal area (m^2/ha)	20.2	11.9	59	2.8–55.3
Douglas-fir basal area (m^2/ha)	15.8	9.0	57	2.0–37.2
Other conifer basal area (m^2/ha)	0.4	1.1	291	0.0–5.8
Hardwood basal area (m^2/ha)	2.1	4.1	199	0.0–24.9
Douglas-fir quad. mean dbh (cm)	17.8	6.6	37	5.5–33.6
Douglas-fir trees per ha	688	347	50	148–1927
Site index (m at 50 yr)[a]	41.0	5.1	12	24.4–52.1
Plot top height (m)	14.3	4.7	33	5.9–31.1
Curtis relative density, conifers[b]	4.5	2.5	55	1.0–15.5
Stand density index, conifers[c]	427	235	55	91–1430
Pseudothecia count	35	17	48	0–80
Foliage retention (yr)	2.2	0.5	24	1.1–3.7
$CL{:}SA_{TOP}$ (cm/cm^2)	5.4	1.6	29	2.4–10.7
$CL{:}SA$ (cm/cm^2)	8.5	4.0	47	3.4–24.0

[a] Bruce (1981).
[b] Curtis (1982); $m^2ha^{-1}cm^{-1/2}$.
[c] Reineke (1933); equivalent number of 25.4 cm tree/ha.

four largest Douglas-fir by dbh, the two smallest Douglas-fir by dbh, and the two Douglas-fir nearest to the midrange of the diameter distribution. One stem disk was removed at breast height from each felled tree, and another just below the lowest live whorl. Because the south side of tree crowns tended to express SNC symptoms most strongly, sample branches were selected from this side with the objective of finding the most sensitive indicators of SNC severity. A whorl branch in the fifth whorl from the tip of the tree and on the south side of the crown was cut from the fourth largest Douglas-fir, and approximately 50 needles of each age class were removed, stored in a cooler, and transported to the lab. The rest of the sample branch was placed in a paper bag and transported to the lab for immediate drying. An increment core was removed from each standing Douglas-fir tree to estimate annual radial growth trends and sapwood area. The side of the tree from which this core was extracted was defined by an imaginary line from plot center to the center of the tree at breast height.

Lab Analysis

Breast height stem disks were brought to the lab and measured for annual radial growth (nearest 0.5 mm) on the two radii forming the long axis of the disk and on the two radii forming the axis perpendicular to the longest. On the crown base disks, four sapwood radii (nearest 0.5 mm) were delineated by color on the same two axes, and sapwood cross-sectional area (cm^2) was computed assuming that the total cross-sections and heartwood cross-sections were elliptical in shape. Annual radial growth and sapwood radii were also measured on the increment cores from standing trees, and sapwood area at crown base was estimated from the computed breast height measurement and a sapwood taper equation (Maguire and Batista 1996).

Before drying, each sample branch was clipped and sorted by age class. The material was then oven-dried at 70˚C, the foliage was separated from the wood and bark, and foliage was weighed by age class.

Projected leaf area (cm^2) was determined by image analysis for the 50-needle subsample of 2-yr-old foliage collected from each sample branch. This subsample also served as the basis for assessing the abundance of fungal hyphae. Hyphae of the SNC causal fungus, *Phaeocryptopus gaeumannii*, grow in intercellular spaces within the needles (Hansen et al. 2000). Fruiting structures, or pseudothecia, emerge from stomates during the late spring and sporulate through June; therefore, the disease has often been quantified by counting the number of stomates occluded by pseudothecia (Hansen et al. 2000). Following this protocol, pseudothecia were counted on 10 of the 2-yr-old needles analyzed for projected leaf area on each sample branch. A contiguous set of 100 stomata were examined in the middle of the second row to the right of the needle midrib, with the petiole pointing downward. Pseudothecia counts therefore represent the number or percentage of these 100 stomates blocked by pseudothecia. After counting pseudothecia, all of the original 50 needles were oven-dried for 24 hr at 70˚C and weighed. Specific leaf area was computed as the ratio of projected leaf area to oven-dry weight (cm^2/g).

Data Analysis

The variation in CL:SA among individual trees was summarized by computing means, standard deviations, coefficients of variation, and ranges among plots. CL:SA was also plotted on height and relative height for individual stands to depict the trend in CL:SA among crown classes.

The relationship between SNC severity and CL:SA was then tested by regressing CL:SA for the fourth largest Douglas-fir tree (that is, the tree from which a branch was sampled) on combinations of six variables capable of indicating SNC severity: (1) years of foliage retention; (2) pseudothecia counts for 2-yr-old needles; (3) sample branch foliage mass in 1-yr-old needles; (4) percent of sample branch foliage mass in 2-yr-old needles; (5) ratio of sample branch foliage mass to branch basal area; and (6) specific leaf area of 2-yr-old needles on the sample branch (cm^2/g).

The efficacy by which mean CL:SA distinguishes among stands with varying levels of foliage loss would depend in part on the degree of variation in average CL:SA among plots; hence, descriptive statistics were also computed for the plot-level means. Plot CL:SA ($CL:SA_{TOP}$) was based on the four largest trees per plot (200 largest per ha) to avoid the influence of differences in stand structure (for example, differences in the number of trees in lower crown classes, since CL:SA was expected to vary by crown class).

Finally, the relationship between stand growth and $CL:SA_{TOP}$ was isolated by introducing $CL:SA_{TOP}$ into a simple model of plot basal area growth:

$$\ln(\Delta BA) = b_0 + b_1 \cdot \ln(BA_{TOTAL}) + b_2 \cdot \ln(BA_{DF}) + b_3 \cdot AGE_{BH} + b_4 \cdot SI + b_5 \cdot CL{:}SA_{TOP} \quad (1)$$

where

$\ln(\bullet)$ = natural logarithm

BA = Douglas-fir basal area growth in 1996 (m^2/ha/yr)

BA_{TOTAL} = total plot basal area at beginning of 1996 (m^2/ha)

BA_{DF} = total Douglas-fir basal area at beginning of 1996 (m^2/ha)

AGE_{BH} = average breast-height age of Douglas-fir (yr)

SI = site index (Bruce 1981)

$CL{:}SA_{TOP}$ = plot-level CL:SA (cm/cm^2) based on the largest four Douglas-fir trees on each plot

Results

Individual tree CL:SA ranged from 1.3 to 100.6 cm/cm^2 for the 785 trees that were measured for sapwood area on either crown base stem disks or breast height increment cores (Table 2). The range for CL:SA on sectioned trees was less (1.3 to 72.7), presumably because measurement error was less for trees on which sapwood was estimated directly from disks cut at crown base; in contrast, sapwood area at crown base for standing trees was estimated from a single increment core at breast height, followed by adjustment for taper.

Table 2. Mean, range, standard deviation, and coefficient of variation for all attributes of Douglas-fir trees measured for sapwood area by stem disk (n = 502) or increment core (n = 283).

Attribute	Mean	Standard deviation	Coefficient of variation	Range
All Douglas-fir sample trees (n = 785)				
Dbh (cm)	15.7	7.7	48.9	1.2–40.8
Height (m)	11.28	4.83	42.85	2.09–31.08
Crown length (m)	8.58	3.62	42.23	0.16–20.34
Sapwood area at crown base (cm^2)	136.9	107.3	78.4	0.4–836.4
Crown length:sapwood area (cm/cm^2)	10.2	9.7	94.8	1.3–100.6
Relative height in stand	0.79	0.16	20.79	0.26–1.00
All stem-sectioned Douglas-fir sample trees (n = 502)				
Dbh (cm)	17.7	7.9	44.5	2.3–40.8
Height (m)	12.21	4.90	40.15	3.11–31.08
Crown length (m)	9.80	3.48	35.51	2.02–20.34
Sapwood area at crown base (cm^2)	171.6	114.2	66.5	2.8–836.4
Crown length:sapwood area (cm/cm^2)	8.7	8.4	96.5	1.3–72.7
Relative height in stand	0.82	0.16	19.38	0.26–1.00

As might be expected, the wide range in CL:SA for all sample trees is partly attributable to the wide range in relative tree height (individual tree height as a proportion of the tallest tree on the plot) that was observed in the sample (0.26 to 1.0; Table 2). Within plots, the ratio of crown length to sapwood area (CL:SA) typically declined as the competitive position of the tree improved (Figure 1a). The general level of CL:SA varied from stand to stand, particularly in the lower crown classes. However, the rate of increase in CL:SA from trees in the upper canopy to trees in the lower canopy seemed to vary as well with respect to absolute height (Figure 1a). When the heights of individual trees were computed on a relative basis, that is, as a proportion of the tallest tree in the plot, the differences among plots were moderated somewhat (Figure 1b).

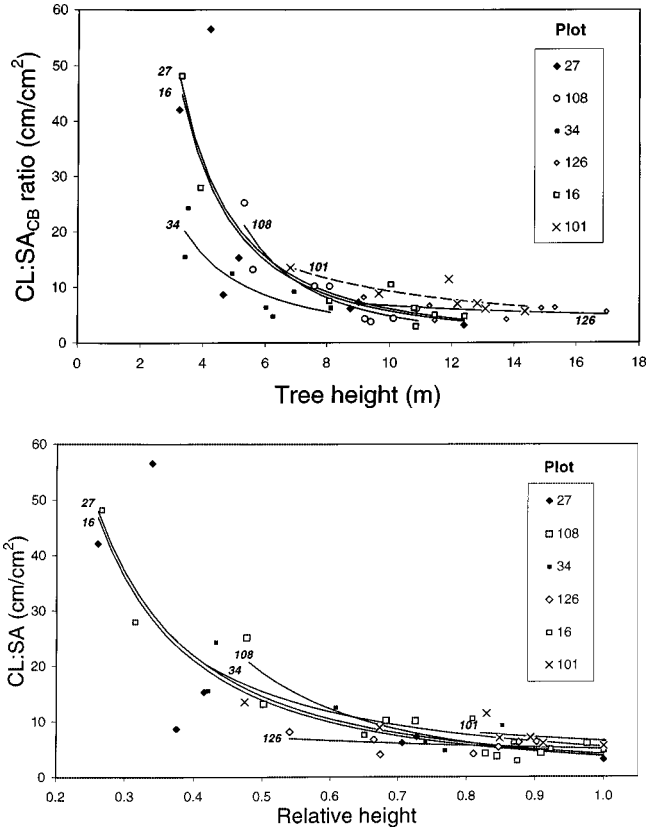

Figure 1. Relationship between: (a) individual tree CL:SA and height; and (b) individual tree CL:SA and relative height (tree height as proportion of tallest tree on plot). Data are from six representative plots, and lines are plot-level trends fitted as $CL{:}SA = g_1 X^{g2}$ where X = height or relative height.

The CL:SA values for the foliage sample trees (fourth largest Douglas-fir on each plot) varied from 2.7 to 12.6, indicating considerable variability in this index within the target population, independent of crown class (Table 3). Of the individual needle cast variables tested, the strongest correlation was found between sample tree CL:SA and foliage mass in 2-yr-old needles (r = –0.29, r^2 = 0.09; P = 0.0095). Mass of 2-yr-old needles is an effective index of SNC by itself, because this mass declines rapidly as the disease intensifies and more 2 yr foliage is lost. Combinations of SNC variables were able to explain even more of the variability in CL:SA over single variables; for example, the percentage of branch foliage mass contributed by 2-yr-old needles and the total mass of 1-yr-old needles together accounted for the largest proportion (15%) of the variation in mean CL:SA of any two SNC indices (parameter estimate standard deviations shown in parentheses):

$$\ln(CL{:}SA) = 2.166 - 0.001642 \bullet FM1 - 0.007538 \bullet PFM2 \quad (2)$$
$$(0.127)\ (0.000645)\qquad (0.003705)$$

where

$FM1$ = total mass of 1-yr-old needles on the sample branch (g)

$PFM2$ = 2-yr-old needle mass as percentage of total sample branch mass

Crown sparseness, or CL:SA, increased as the total foliage mass in 1-yr-old needles declined and as the percentage of total branch biomass in 2-yr-old needles declined (Figure 2).

Plot-level estimates of CL:SA exhibited much smaller ranges and coefficients of variation than the individual trees (Table 1 vs. Table 2). Likewise, when the index was based on only the top height component of the stand (200 largest trees per ha by dbh), the plot-level means were not quite as variable (CL:SA vs. $CL{:}SA_{TOP}$ in Table 1).

Table 3. Mean, range, standard deviation, and coefficient of variation for attributes of foliage sample trees and sample branches (southmost branch in fifth whorl from tip of fourth largest Douglas-fir on each plot; *n* = 66).

Attribute	Mean	Standard deviation	Coefficient of variation	Range
Tree attribute				
Crown length:sapwood area (cm/cm^2)	6.3	1.92	30.6	2.7–12.6
Foliage retention (yr)	2.2	0.55	24.6	1.1–3.8
Branch attribute				
Mass of 1 yr old foliage (g)	92.1	53.61	58.2	7.7–255.7
Mass of 2 yr old foliage (g)	50.1	31.73	63.3	0.5–143.2
Mass of 3 yr old foliage (g)	20.6	19.88	96.7	0.0–90.4
Mass of 4 yr old foliage (g)	1.6	3.56	227.6	0.0–16.5
Total foliage mass (g)	164.3	92.80	56.5	25.4–439.2
% mass of 1 yr old foliage	58.6	16.43	28.0	17.5–98.9
% mass of 2 yr old foliage	29.1	9.33	32.0	0.8–45.5
% mass of 3 yr old foliage	11.1	8.81	79.4	0.0–38.4
% mass of 4 yr old foliage	1.1	3.13	273.4	0.0–18.5
Pseudothecia count, 2 yr needles	36.0	15.45	43.0	7.8–70.1
Specific needle area, 2 yr needles (cm^2/g)	61.2	9.99	16.3	46.5–94.0
Needle mass:branch basal area (g/cm^2)	42.1	17.11	40.7	10.6–108.7

As would be expected under the assumption that CL:SA served as an index of crown sparseness or relative foliage loss, plot basal area growth declined significantly as $CL{:}SA_{TOP}$ increased (parameter estimate standard deviations shown in parentheses):

$$\begin{aligned}\ln(\Delta BA) = {} & 0.40809 - 0.09712 \bullet AGE_{BH} \\ & (0.1963) \qquad (0.01047) \\ & +1.0018 \bullet \ln(BA_{DF}) - 0.3907 \bullet \ln(BA_{TOTAL}) \\ & (0.0957) \qquad (0.1011) \\ & - 0.04754 \bullet CL{:}SA_{TOP} \\ & (0.02088)\end{aligned} \tag{3}$$

Site index (Bruce 1981) was dropped from the final model since its was not statistically significant ($\alpha = 0.05$), regardless of the presence or absence of any other predictors. The final equation accounted for 72% of the variation in plot basal area growth for Douglas-fir trees, with CL:SA accounting for 2% of the total variation beyond that proportion already accounted for by other variables in the final model. Douglas-fir basal area growth increased with increasing level of growing stock (initial Douglas-fir basal area), decreasing total stand density or competition from other species (total basal area), and decreasing crown sparseness (CL:SA for the top component of the stand) (Figure 3). The potential importance of CL:SA is underscored by the fact that Equation (3) implies a basal area growth in stands with a sparseness index of 10 that averaged 28% less than in stands with a sparseness index of 3.

Discussion

The degree of variation in both tree-level and stand-level CL:SA was sufficiently large to render the ratio a potential index for discriminating among trees of varying crown condition. A large portion of the natural variation in individual-tree CL:SA was associated with crown class or relative height in the stand. Patterns in light extinction would lead to the expectation that trees situated lower in the canopy would

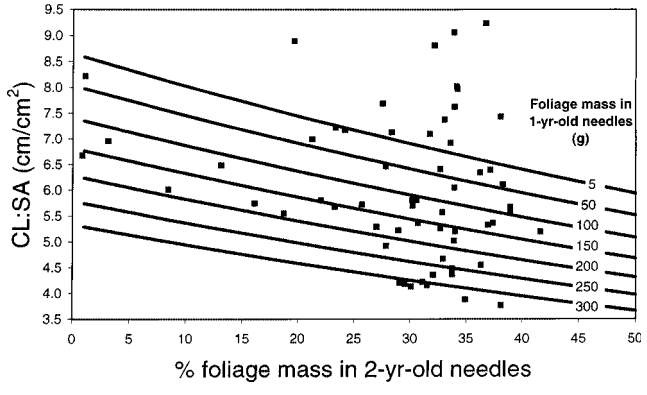

Figure 2. Smoothed trends in CL:SA over two sample branch attributes: foliage mass in 1-yr-old needles; and percentage of foliage mass in 2-yr-old needles. Trends are the results from fitting Equation (2) to data from the fourth largest Douglas-fir on each plot. Sample branch on this tree was the southmost branch in the fifth whorl from the tree tip.

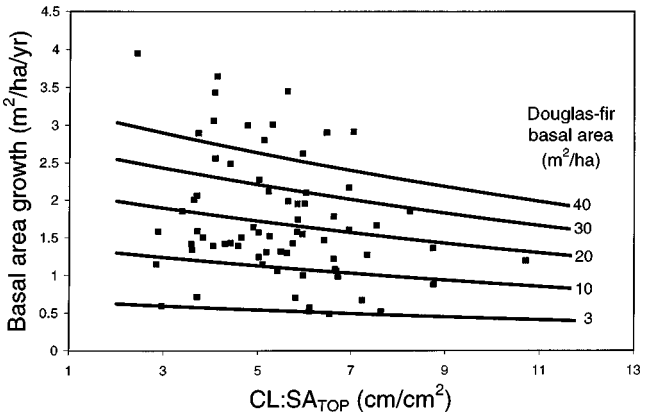

Figure 3. Response of basal area growth to initial Douglas-fir basal area and $CL{:}SA_{TOP}$ [surface described by Equation (3)] . Total basal area (BA_{TOTAL}) was set equal to Douglas-fir basal area (BA_{DF}), and breast height age (AGE_{BH}) was set to the sample mean, 12 yr.

have foliage less densely distributed along the bole; hence, CL:SA would be greater. However, the inference that a high CL:SA of shorter trees implies a lower leaf area density must be tempered with two additional observations: (1) suppressed trees can also have more leaf area per unit sapwood area (Dean and Long 1986); and (2) crown profile has been observed to shorten and widen under severe suppression (Raulier et al. 1996). In these Douglas-fir stands, the decline in sapwood area per unit live crown length and the increase in CL:SA were continuous, suggesting a net reduction in leaf area density with decreasing relative height. The apparent increase in leaf area density with greater relative height was consistent with the trends in leaf area per unit live crown length implied in foliage distribution models for healthy Douglas-fir plantations (Maguire and Bennett 1996); that is, trees of greater relative height generally would have greater diameter, greater crown length and greater quantity of foliage per unit crown length. For example, an average codominant in plot 108 (dbh =15.0, height = 9.5, crown length = 8.4) is expected to have 21 m^2 of foliage per m crown length and an intermediate tree (dbh = 12, height = 8.8, crown length = 7.9) is expected to have only 14 m^2 of foliage per m crown length.

The range, standard deviation, and coefficient of variation for tree-level CL:SA were substantially larger than for the plot-level CL:SA ratios. Although the large differences in CL:SA among crown classes within a stand imposed much of this variation, some extreme values for individual trees likely had at least two additional causes: (1) asymmetry in the live crown (Rouvinen and Kuuluvainen 1997), leading to a relatively low crown base (lowest live branch) for a given cumulative leaf area; and (2) measurement error in estimating sapwood area, particularly from a single core on standing trees (Maguire et al., in review). A larger CL:SA for one-sided crowns would be consistent with the rationale behind this ratio as an index of crown sparseness; that is, the live crown would have to be approximately twice as long on a tree with a one-sided crown to produce the same cumulative leaf area and corresponding sapwood area at crown base, compared to a perfectly symmetrical crown. However, because sapwood area has been shown to expand below the lowest live branch even without additional accumulation of foliage (Waring et al. 1982, Maguire and Hann 1987, Maguire and Batista 1996), additional sapwood area probably also accrues within the live crown of one-sided trees beyond the increase expected simply from the increase in cumulative foliage. On the other hand, crown asymmetry was relatively uncommon in this study due to the young age and intensity of stocking control typical of these managed stands.

Regardless, mean CL:SA values for plots tended to dampen the effect of unusually large or small individual tree values and, given the probable sources of error, should be more reliable indicators of average defoliation status for a plot or stand. Likewise, basing CL:SA on only a dominant or codominant portion of the stand reduces the variation in plot-level CL:SA attributable to variation in stand structure and to possible variation in sample tree distribution across crown classes. For stands managed at relatively low densities, smaller Douglas-fir stems are generally removed during precommercial or commercial thinning. Hence, for a range in stand densities or management intensities, CL:SA computed from all trees or a sample of all trees would vary according to the number of trees present in lower strata of the stand. These stand structural effects can be avoided by determining CL:SA for some upper tier of the stand, which should be relatively unaffected by the number of trees in lower tiers. In this study, the subset comprising the four largest Douglas-fir trees per plot, approximately equivalent to the largest 200 trees/ha, minimized the variability in CL:SA arising from differences in stand structure.

The CL:SA ratio integrates the numerous complex responses of crowns to light availability and defoliation, as indicated by the close relationship between CL:SA and the combination of percent of branch foliage mass in 2-yr-old needles and total branch foliage mass in 1-yr-old needles. Individual indices of SNC generally portray only one type of response to foliage disease. Foliage retention, for example, indicates the average number of years that needles remain on a sample branch, but does not necessarily provide the relative distribution of foliage by age class or the total amount of foliage. Reduced foliage retention in the upper and middle portion of the crown could conceivably promote longer retention in the bottom of the crown, since more foliage would be illuminated above the light compensation point. Similarly, improved light conditions in the bottom parts of the crown could stimulate additional production of current-year foliage. Even within a single sample branch, the relative distribution of foliage area or mass is more accurately reflected in variables such as percent foliage mass in 2-yr-old needles, but as indicated by Equation (2), some measure of absolute foliage amount contributes significantly as well. Pseudothecia count on 2 yr foliage may indicate the extent to which surviving foliage is incapacitated physiologically, but does not necessary provide a measure of total foliage loss, which most likely is the major source of growth impact. Even more problematic is the fact that variables associated with foliage mass distribution and pseudothecia counts are not practical as operational stand assessment tools. CL:SA, on the other hand, offers the advantage of being relatively easy to measure in the field and able to integrate a number of complex crown responses to infection intensification.

As mentioned initially, the efficacy of CL:SA as an index of crown sparseness, or of SA:CL as an index of crown density, relies on a relatively close dynamic equilibrium between total foliage area and sapwood area. The validity of the index will depend on the dynamics of foliage loss (Horntvedt 1993); that is, relatively rapid loss may be more difficult to track due to lag time between foliage loss and subsequent re-adjustment of sapwood area. Although some pruning experiments indicate that the sapwood adjustment is rapid (Margolis et al. 1988), other experiments suggest a lag time of at least four years (Långström and Hellqvist 1991). Two of several factors expected to influence the lag time would be rate of foliage loss and age distribution of both lost and retained foliage. In the case of SNC, foliage loss appears to proceed gradually over many years, whereas, in pruning experiments,

foliage is removed quite suddenly and to varying degrees, depending on the intensity of pruning. Also, since older foliage is less physiologically active, loss of a given amount of older age classes as is typical of SNC may have a less pronounced effect than loss of younger foliage, which is more typical of insect defoliators.

In addition to the ability of CL:SA to depict degree of defoliation, the index has relevance to tree vigor as well; for example, CL:SA proved to be a significant predictor of plot basal area growth when combined with other traditional variables such as stand age and initial stand basal area. Although it initially seemed reasonable to expect that CL:SA could be negatively correlated with site quality, site index was an ineffective predictor when added to the model describing plot basal area growth, regardless of whether CL:SA was already in the model. The conclusion reached from this analysis, therefore, was that CL:SA functioned largely as an index of crown sparseness and could not be regarded as a surrogate for site quality. It was clear from the analyses relating CL:SA to other SNC indices that the crown sparseness index increased commensurately with intensified foliage loss. Likewise, analyses relating CL:SA to growth suggested that CL:SA integrated the effects of various crown responses on tree growth; as mentioned above, basal area growth rate was 28% lower in stands with a sparseness index of 10 relative to those with a sparseness index of 3. This result also suggests that CL:SA could be a useful predictor variable in forest growth modeling, both in models that explicitly incorporate stand leaf area as a predictor and in models for which various combinations of basal area, stand age, and site index serve as surrogates for stand leaf area.

Smith and Long (1989) investigated the relationship between lodgepole pine canopy architecture and stem volume growth on the stand level. Foliar density (m^2m^{-3}) in their study was estimated as the ratio of stand leaf area per unit stand canopy volume. Algebraically, this foliar density was equivalent to the ratio of stand leaf area index to canopy depth; hence, their foliar density was similar to the inverse of CL:SA, but represented a different level of resolution. At the stand level, foliar density is largely a function of stand density and crown geometry; that is, all else being equal, two closed stands of a differing number of trees per unit area should have approximately the same total leaf area, but a higher density of individual stems forces that leaf area into a vertically thinner layer. The primary issue addressed by Smith and Long (1989) was the question of whether longer vertical distribution of a given amount of leaf area led to greater and more efficient growth (greater stem volume growth per unit leaf area). Their statistical model illustrated greater growth with more restricted vertical distribution of a fixed leaf area, but also implied greater growth with greater leaf area at a fixed canopy depth; however, the latter result was not addressed explicitly (Smith and Long 1989). The effect of differences in stand structure, particularly as they influence the amount of between-crown canopy volume vs. within-crown canopy volume is difficult to assess. Regardless, the results for lodgepole pine stands exhibited some similarities to the results for Douglas-fir trees presented here. Explicit representation of stand density by basal area and age in this study and assessment of the marginal effects of crown length and crown base sapwood area (leaf area) allow better separation of the stand density effect on potential crown length from the crown density effect at a given crown length. For Douglas-fir trees at a given stand density and potential crown length, sparser crowns under the influence of a pathogen are associated with poorer growth regardless of whether the crowns retain the same leaf area along a greater length or hold less foliage within the expected crown length.

In summary, consideration of both total amount of leaf area and the volume or length over which it is distributed can provide an objective measure of tree condition during silvicultural stand examination, operational forest inventory, or forest health monitoring. Rather than being mutually exclusive measures of crown size, gross crown dimensions and sapwood area can be complementary in forest assessments (Maguire and Hann 1989). Gross dimensions contain important information on crown geometry, including spatial occupancy and competition for aerial growing space, while sapwood area is a more reliable indicator of total foliage amount. The combination exemplified by the index of crown sparseness, CL:SA, has been effective for quantifying relative defoliation in Douglas-fir plantations experiencing Swiss needle cast. Insights into other important ecophysiological and stand developmental processes will likewise require both types of information on crown structure.

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