

Variation in specific needle area of old-growth Douglas-fir in relation to needle age, within-crown position and epicormic shoot production

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Summary Variation in specific needle area (SNA; cm² projected fresh needle area g⁻¹ oven-dried needle weight) was investigated in relation to needle age, within-crown position and epicormic shoot production in 450-year-old Douglas-fir (*Pseudotsuga menziesii* Mirb. (Franco) var. *menziesii*) trees. Specific needle area decreased with increasing needle age. The magnitude and rate of change in SNA with needle age were greatest for lower-crown branches, and decreased toward the middle- and upper-crown branches. For all branches, there was no difference between regular and epicormic shoots in the relationship between SNA and needle age. Specific needle area decreased with increasing distance from branch base, and this relationship was significant for the majority of needle age classes of the upper- and middle-crown branches. In the lower-crown branches, SNA did not vary with distance from branch base for the majority of needle age classes. For all branches, there was no difference between regular and epicormic shoots in the relationship between SNA and distance from branch base for the majority of needle age classes. These results indicate that renewal of foliage by epicormic shoot production maintains needle quality. Branch SNA increased linearly with decreasing height in the crown at a mean rate of 0.951 ± 0.110 cm² g⁻¹ per vertical meter. Total needle area of branches was estimated from total needle dry weight taking into account within-branch variation in SNA. Analyses of allometric relationships between branch size and foliage amount (needle area and needle dry weight) showed that branch length was a better predictor of foliage amount than branch diameter for old Douglas-fir trees. Total needle dry weight and needle area of the sample trees, estimated from branch length and branch height and taking into account vertical within-crown variation in branch SNA, ranged from 42.4 to 154.2 kg and from 246.2 to 816.0 m² per tree, respectively.

Keywords: foliage area estimation, morphological plasticity, needle morphology, *Pseudotsuga menziesii*, tree aging.

Introduction

Estimation of whole-tree foliage area is an important and critical step in scaling physiological processes measured at the leaf and shoot scale to tree- and stand-scale dynamics, such as growth, carbon budget and water flux. However, foliage area estimation of large, old coniferous trees has presented challenges because of the difficulty of accessing the crown for sampling, and because spatial distribution of foliage and variability in needle morphology are largely unknown. Previous investigations of foliage area in old-growth coniferous forests of the Pacific Northwestern USA have relied on limited sampling and extrapolations from relationships observed in younger stands (Gholz et al. 1976, Grier and Running 1977, Franklin and Waring 1980, reviewed by Thomas and Winner 2000). However, recent studies have suggested that such methods may lead to overestimation of foliage area (Marshall and Waring 1986, Thomas and Winner 2000, Turner et al. 2000).

Sampling strategies for estimating branch- and tree-level foliage area should take into account the spatial distribution of foliage and variation in needle morphology within the crown (Maguire and Bennett 1996, Bond et al. 1999). Foliage distribution and needle morphology of young coniferous trees have been investigated in detail because these factors have important implications for tree growth and yield (e.g., Del Rio and Berg 1979, Smith et al. 1981, Jensen and Long 1983, Borghetti and Vendramin 1986, Webb and Ungs 1993, St. Clair 1994, Kershaw and Maguire 1996, Maguire and Bennett 1996). Young trees show predictable relationships between nondestructive surrogate measures (e.g., branch or stem diameter) and foliage area. These relationships can be used to estimate branch- and tree-level foliage area from measurements of subsamples taken from various parts of the crown (Webb and Ungs 1993, Kershaw and Maguire 1995, Bartelink 1996, Maguire and Bennett 1996). Bond (2000), who defined old age in trees as the developmental stage after maximum tree height is reached, observed that various changes in crown form and needle morphology occur as trees reach old age. Spatial distri-

bution of foliage in the crown of old trees differs from that of young trees, and can be highly variable among individual trees (Massman 1981). Richardson et al. (2000) found less variability in needle morphology for 145-year-old trees of hybrid spruce (*Picea engelmannii* Parry × *Picea glauca* (Moench) Voss × *Picea sitchensis* (Bong.) Carr) compared with younger, 15- and 55-year-old trees, and suggested that needles of old trees may have reduced ability to acclimate morphologically to variable light conditions. In old trees, relationships between branch or stem diameter and foliage area may not be as predictable as in young trees (Ishii et al. 2000). Relatively few studies have investigated the spatial distribution of foliage and variability in needle morphology of large, old coniferous trees, and the implications of these factors on estimates of tree- and branch-level foliage area are largely unknown.

Large old trees of Douglas-fir (*Pseudotsuga menziesii* Mirb. (Franco) var. *menziesii*) characterize old-growth forests of the Pacific Northwestern USA. Tree height reaches 60–80 m, and tree longevity may be over 1000 years (Waring and Franklin 1979). Ishii and Ford (2001) showed that foliage on branches of 450-year-old Douglas-fir trees is maintained by continuous production of epicormic shoots within branches (Figure 1). Several researchers have proposed that epicormic shoot production is an efficient mechanism for maintaining productivity in old trees because it generates new shoots and foliage from existing support tissue (Bryan and Lanner 1981, Ewers 1983, Remphrey and Davidson 1992, Bégin and Filion 1999). However, no studies have investigated whether foliage produced by epicormic shoots of large old trees is morphologically and physiologically similar to foliage produced by terminal buds, thus maintaining foliage quality as well as quantity.



Figure 1. Epicormic shoots (arrow) are produced from suppressed epicormic buds on older parent shoots, and can be distinguished by their internodal position on the parent shoot, vertical angle of attachment, and age difference.

We investigated variation in specific needle area of 450-year-old Douglas-fir trees in relation to needle age and within-crown position. We also compared specific needle area between regular and epicormic shoots to elucidate the effects of epicormic shoot production on foliage renewal in old Douglas-fir trees. Finally, we analyzed relationships between branch size and foliage amount. We discuss the implications of our results for estimation of branch- and tree-level foliage area in large, old Douglas-fir trees.

Study site and methods

The study was conducted in a 450-year-old, old-growth Douglas-fir–western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forest at the Wind River Canopy Crane Research Facility located in the Thornton T. Munger Research Natural Area, Gifford Pinchot National Forest in southwestern Washington State, USA (45°49' N, 121°57' W; altitude 355 m). The stand basal area is dominated by Douglas-fir and western hemlock. Western red cedar (*Thuja plicata* Donn ex D. Don), Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) and Pacific yew (*Taxus brevifolia* Nutt.) are also abundant. Other tree species in the stand include grand fir (*A. grandis* (Dougl. ex D. Don) Lindl.), western white pine (*Pinus monticola* Dougl. ex D. Don) and Pacific dogwood (*Cornus nuttallii* Audubon). Franklin (1972) and Franklin and DeBell (1988) give a detailed description of the area.

Destructive sampling within the Research Natural Area is restricted. Permission was obtained to sample nine branches from three Douglas-fir trees in the stand (Table 1). The Douglas-fir trees in the stand are a cohort that established after a stand-replacing fire in the area (Franklin and DeBell 1988). Tree age at breast height was estimated from increment cores, and was 415 years for Tree 1 and 405 years for Tree 3. Tree 2 could not be successfully aged. Other Douglas-fir trees in the area ranged in age from 385 to 410 years old at breast height.

The three sample trees were climbed in August of 1998 by the single-rope technique (Moffett and Lowman 1995) for measurement of crown characteristics. All primary branches were numbered, and branch height above ground was measured at the branch base with a tape measure that was stretched vertically from the ground along the main stem of each tree. Branch diameter was measured immediately outside the branch collar with a diameter tape for large branches and calipers for small branches. Branch length was measured by extending a 1-inch-wide engineer's tape from the main stem to the farthest foliated section of the branch. The live crown of each tree, from the top of the tree to the lowest foliated branch, was divided into upper-, middle- and lower-crown levels of equal depth. A median-sized branch, in terms of diameter and length, was cut near the middle-height of each crown level. The sample branches were carefully lowered to the ground with ropes to prevent damage and then transported to a nearby building for additional measurements.

The foliated shoots on each harvested branch were divided into “shoot cluster units” (SCU; Ishii and Ford 2001). An SCU

Table 1. Structural attributes of the nine sample branches of 450-year-old Douglas-fir.

Tree and branch position	Height (m)	Diameter (cm)	Length (m)	Needle dry weight (kg)	Needle area (m ²)
<i>Tree 1 (DBH= 135.3 cm, H = 61.6 m)</i>					
Upper crown	56.8	7.6	3.3	0.999 (34.5) ¹	4.24 (38.2)
Middle crown	35.4	20.0	8.1	3.406 (18.3)	19.98 (23.0)
Lower crown	27.1	8.4	3.3	0.711 (15.3)	4.98 (19.9)
<i>Tree 2 (DBH= 153.5 cm, H = 58.7 m)</i>					
Upper crown	50.8	8.6	4.3	1.332 (25.1)	6.98 (27.9)
Middle crown	35.2	11.5	6.1	4.020 (18.6)	25.75 (21.9)
Lower crown	21.2	5.3	2.8	0.827 (23.3)	6.59 (26.6)
<i>Tree 3 (DBH= 93.9 cm, H = 50.8 m)</i>					
Upper crown	45.9	6.0	3.1	0.496 (27.0)	2.31 (31.6)
Middle crown	36.9	10.1	4.9	2.316 (15.3)	13.89 (18.1)
Lower crown	26.8	7.8	2.4	0.584 (17.7)	3.94 (21.6)

¹ Values in parentheses denote percentage of current-year needles.

is a modular unit of shoot organization formed as a result of the symmetrical branching pattern observed in old Douglas-fir trees (Figure 2). The terminal bud usually forms one terminal shoot and two to three lateral shoots each year. As a result, shoots are organized in clusters consisting of a distinguishable main axis, created by the extending terminal bud, and several lateral branchlets. The morphology of the SCU is similar to that of a compound leaf with the main axis analogous to the rachis and lateral branchlets to individual leaflets. The main



Figure 2. The shoot cluster unit (SCU; photograph shows one SCU) is a modular unit of shoot organization in old Douglas-fir trees consisting of a distinguishable main axis, created by the extending main axis terminal bud (MTB), and several lateral branchlets. Regular shoots are produced by continuous growth of the main axis terminal bud, while epicormic shoots (arrows) are produced when epicormic buds along the main axis are released from suppression.

axis terminal bud differentiates *regular shoots* that make up the structure of the SCU. Ishii and Ford (2001) found that SCUs have a mean longevity of 10–15 years, and the main axis terminal bud eventually stops growing. *Epicormic shoots* (Figure 2, arrows) are produced when epicormic buds along the main axis of the SCU are released from suppression. Epicormic shoots can be distinguished from regular shoots because they: (1) originate from internodal positions on older main axis parent shoots; (2) grow out at vertical angles above the plane formed by the regular shoots; and (3) are younger than the annual daughter shoots of the same main axis parent shoot. Epicormic shoots reiterate new SCUs and thereby maintain shoots and foliage on old Douglas-fir branches (Ishii and Ford 2001).

All SCUs on the sample branches were numbered, and radial distance from the branch base to the base of each SCU (hereafter: distance from branch base) was measured before removing it from the branch (Figure 3A). After removal, all foliated shoots on the SCU were aged based on annual bud-scale scars, and separated into regular and epicormic shoots by age class (Figure 3B). For one-half of the SCUs on each branch, 10% of the shoots in each age class for both regular and epicormic shoots were preserved for subsequent needle area measurement (needle-area samples), whereas the remaining shoots were dried for needle weight measurement (dry-weight samples). All needles of the remaining one-half of the SCUs were sorted by age class and shoot type (i.e., regular or epicormic), and oven-dried at 70 °C until constant weight was reached (usually 2–3 days), and weighed to determine needle dry weight.

Projected needle area of the needle-area sample shoots was measured by removing all needles and laying them out on a flatbed scanner (UMAX 1200S, UMAX Corp., Fremont, CA). The needles were flattened with a piece of glass, illuminated from above to obtain the silhouette, and scanned at 300 dpi resolution. The scanned images were processed with the Scion Image (Scion Corp., Frederick, MD) image analysis program

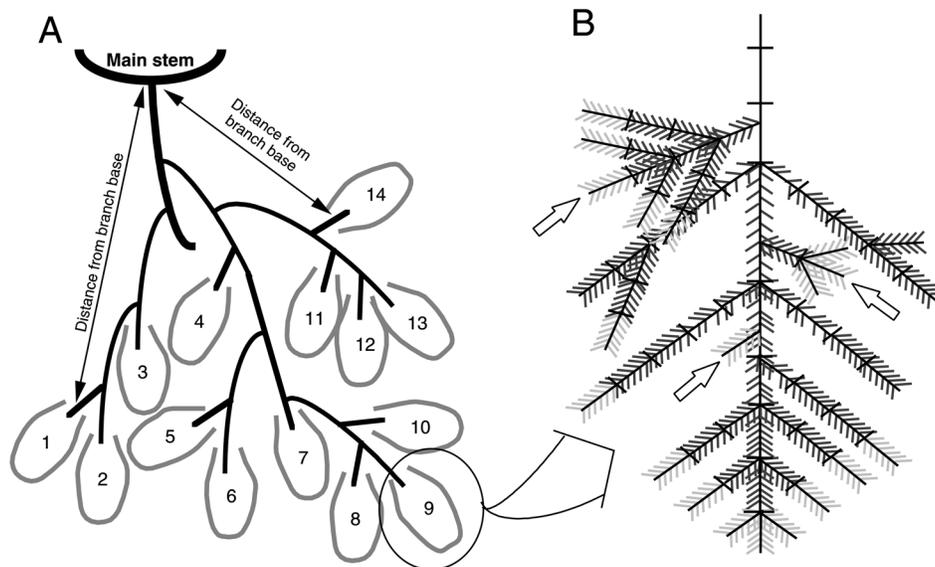


Figure 3. Schematic diagrams of the sample branch (A) comprising 14 shoot cluster units (SCU), and a close-up of one shoot cluster unit (B). The shoot cluster unit consists of both epicormic (arrows) and regular shoots. Foliated shoots of the SCU can be aged based on annual budscale scars (cross bars). Current-year needles are shown in lighter color.

to obtain projected needle area to the nearest 0.1 cm^2 . Relative error for this method was estimated to be less than 2%. The needles were then oven-dried for needle weight measurement. Specific needle area (SNA; cm^2 projected fresh needle area g^{-1} oven-dried needle weight) for each age class and shoot type was determined for each SCU from the needle-area samples. The SNAs were averaged by age class and shoot type for all SCUs on the branch from which needle-area samples were taken to obtain mean SNA for the branch.

To investigate the spatial variation in SNA within branches, linear regressions of the form:

$$\text{SNA} = a\text{DBB} + b, \quad (1)$$

where DBB is distance from branch base, a is the slope estimate, and b is a constant, were fit to the relationship between SNA and distance from branch base of SCUs. This relationship was fit by age class and shoot type for all SCUs from which needle-area samples were taken, and used to estimate SNA from DBB for the remaining one-half of the SCUs on each branch from which needle-area samples were not taken. For age classes where this relationship was not significant, mean SNA of the age class for the branch was used. For each SCU, needle area for each age class and shoot type was calculated by multiplying the respective measured or estimated SNA by the needle dry weight.

Total needle dry weight and needle area of branches was determined by summing needle dry weights and needle areas of all SCUs on the branch. Branch needle area was divided by branch needle dry weight to obtain branch SNA. The relationship between branch height and branch SNA was investigated to infer the pattern of vertical variation in SNA within the crown. Relationships between branch size (diameter, length) and foliage amount (branch needle area and branch needle dry weight) were investigated to assess the use of nondestructive

surrogate measures to estimate foliage amount. Allometric relationships of the form:

$$\ln A = p \ln Z + q, \quad (2)$$

where A is needle area, Z is size, and p and q are the scaling exponent and constant, respectively, have been used to estimate foliage area from measures of tree and branch size (e.g., Gholz et al. 1976, Kershaw and Maguire 1995, Bartelink 1996, Turner et al. 2000). We tested the applicability of this relationship to branches of old Douglas-fir trees. Finally, we estimated total needle dry weight and needle area of the sample trees, taking into account within-crown variation in SNA.

Results

Specific needle area of needles borne on both regular and epicormic shoots increased from upper- to lower-crown branches, and decreased with increasing needle age class (Figure 4). For upper-crown branches, SNA decreased from 53.4 and $54.9 \text{ cm}^2 \text{ g}^{-1}$ for current-year needles of regular and epicormic shoots, respectively, to 41.3 and $42.7 \text{ cm}^2 \text{ g}^{-1}$ for 7-year-old needles. For middle-crown branches, SNA decreased from 73.7 and $73.3 \text{ cm}^2 \text{ g}^{-1}$ for current-year needles of regular and epicormic shoots, respectively, to 49.4 and $50.1 \text{ cm}^2 \text{ g}^{-1}$ for 9-year-old needles. For lower-crown branches, SNA decreased from 89.7 and $86.5 \text{ cm}^2 \text{ g}^{-1}$ for current-year needles of regular and epicormic shoots, respectively, to 59.9 and $54.4 \text{ cm}^2 \text{ g}^{-1}$ for 8-year-old needles. Mean rate of decrease in SNA with increasing needle age was estimated by linear regression as the slope of the linear relationship between SNA and needle age. For upper-crown branches, SNA decreased by 1.50 and $1.24 \text{ cm}^2 \text{ g}^{-1}$ per year for regular and epicormic shoots, respectively ($r^2 = 0.814$, $P < 0.01$ and $r^2 = 0.481$, $P = 0.03$, respectively). For middle-crown branches, SNA decreased by 2.11 and $2.17 \text{ cm}^2 \text{ g}^{-1}$ per year

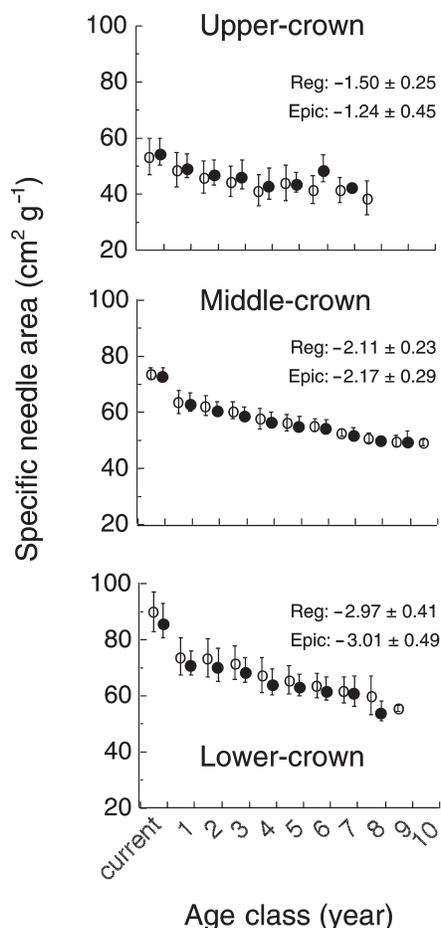


Figure 4. Variation in SNA in relation to needle age for regular (○) and epicormic shoots (●) for upper-, middle- and lower-crown branches. Values are mean SNA for each age class and shoot type for the three sample trees. Bars represent one standard deviation. Figures show linear regression estimates of the slope of the relationship (mean rate of decrease in SNA with increasing needle age, cm² g⁻¹ per year) with standard errors.

for regular and epicormic shoots, respectively ($r^2 = 0.891$, $P < 0.01$ and $r^2 = 0.860$, $P = 0.03$, respectively). For lower-crown branches, SNA decreased by 2.97 and 3.01 cm² g⁻¹ per year for regular and epicormic shoots, respectively ($r^2 = 0.851$, $P < 0.01$ and $r^2 = 0.819$, $P = 0.03$, respectively). Epicormic shoots occurred throughout all parts of the sample branches, and 57–100% of SCUs on each branch contained some epicormic shoots. For all age classes, there was no difference in SNA between regular and epicormic shoots of the same age class (paired t -test, $t = 0.004$ – 3.377 , $P = 0.078$ – 0.998). In addition, the relationship between SNA and needle age did not differ between regular and epicormic shoots (ANCOVA: $F = 1.297$, $P = 0.271$; $F = 0.442$, $P = 0.515$; $F = 2.494$, $P = 0.133$ for upper-, middle-, and lower-crown branches, respectively).

There were significant negative relationships between specific needle area and distance from branch base for both regular and epicormic shoots (Table 2, Figure 5). For upper- and middle-crown branches, slope estimates for Equation 1 were

significantly negative for the majority of age classes for both regular and epicormic shoots. For lower-crown branches, slope estimates were not significant for the majority of age classes, indicating that there was no negative relationship between SNA and distance from branch base. For all branches, there was no difference in the relationship between SNA and distance from branch base between regular and epicormic shoots for the majority of age classes.

Branch SNA increased linearly with decreasing branch height for all three sample trees (Figure 6). No significant differences were found among the sample trees in this relationship (ANCOVA: $F = 0.462$, $P = 0.522$). Regression analysis using all nine sample branches yielded the following relationship between branch height (H ; m) and branch SNA (BSNA; cm² g⁻¹):

$$\text{BSNA} = -0.951H + 95.65 \quad (r^2 = 0.914, P < 0.001). \quad (3)$$

The slope estimate indicated that the mean rate of increase in branch SNA with decreasing height was 0.951 cm² g⁻¹ per vertical meter. Standard error of the regression estimate of the slope was ± 0.110 cm² g⁻¹.

Equation 2 was fit to the relationship between branch size (diameter and length) and foliage amount (needle dry weight and needle area). Foliage amount generally increased with increasing branch size (Figure 7). However, foliage amount of the largest branch (middle-crown branch, Tree 1) was less than that of the second largest branch (middle-crown branch, Tree 2). Branch length was a better predictor of foliage amount than branch diameter for both needle dry weight and needle area. The relationship between branch length (L ; m) and branch needle dry weight (BNW; kg) yielded the best fit of Equation 2:

$$\ln \text{BNW} = -2.26 + 1.80 \ln L \quad (r^2 = 0.860, P < 0.001). \quad (4)$$

Based on the above results, we used Equations 3 and 4 to estimate BSNA and BNW from branch height and branch length, respectively, for all branches of the sample trees. Branch needle area of each branch was calculated as the product of BSNA and BNW. Branch needle dry weights and branch needle areas were summed for each sample tree to obtain tree-level estimates of needle dry weight and needle area (Table 3).

Discussion

Several researchers have found that current-year needles of young coniferous trees have greater SNA than older needles (e.g., Hager and Sterba 1985, Borghetti and Vendramin 1986, Oren et al. 1986, Gilmore et al. 1995, Niinemets 1997a). Smith et al. (1981) found that current-year needles of 25- and 40-year-old Douglas-fir trees in Oregon had less foliage dry weight per area (i.e., greater SNA) than older needles. Del Rio and Berg (1979) found that SNA ranged from 74.8 to 94.5 cm² g⁻¹ for current-year needles, and from 64.7 to 75.8 cm² g⁻¹ for

Table 2. Slope estimates of the relationship between SNA and distance from branch base for regular and epicormic shoots.

Tree and branch position	Shoot type	Needle age (year)									
		Current	1	2	3	4	5	6	7	8	
<i>Tree 1</i>											
Upper crown	Regular	-8.6** ¹	-6.2**	-6.2**	-4.6**	-5.9**	-4.6**	-4.5**	-9.3**	-9.8**	
	Epicormic	-6.0**	-3.9*	-5.8*	-5.0*	-6.0*	-4.7				
Middle crown	Regular	-3.3**	-2.1**	-2.1**	-2.3**	-1.5**	-1.6**	-2.0**	-2.2**	-2.4**	
	Epicormic	-3.1**	-1.4**	-1.9**	-2.5**	-2.7**	-2.1**	-1.6**	-2.3* [†]	-3.6 [†]	
Lower crown	Regular	-11.0**	-8.5**	-4.5*	-2.9*	-0.7	-3.2	-1.9	-1.4	0.0	
	Epicormic	-4.9	-3.9*	-2.6	-0.5	0.5	-0.1	-2.3	-3.6		
<i>Tree 2</i>											
Upper crown	Regular	-1.8	-2.6	-3.0	-3.6**	-4.3**	-2.3	-5.1**	-2.8*	-3.7*	
	Epicormic	-4.7**	-2.3	-3.4	-5.9**	-6.8*	-5.7				
Middle crown	Regular	-3.4**	0.2**	-2.2**	-1.6**	-1.6**	-1.2**	-0.4	-0.9*	-0.7	
	Epicormic	-2.3** ^{†2}	-1.5*	-1.1 ^{††}	-1.4* [†]	-1.0* [†]	-1.3*	-0.9	0.3**	-0.3	
Lower crown	Regular	-1.1	-3.8	-0.9	-2.2	-1.9	-1.1	0.6	-2.1	0.0	
	Epicormic	-0.6 ^{††}	-1.1 ^{††}	1.6 ^{††}	-3.5	-0.1 ^{††}	-8.0	-1.8			
<i>Tree 3</i>											
Upper crown	Regular	-9.5	-5.7	-7.7	-3.9	-5.5	-2.9	-6.8	-1.1	-12.1	
	Epicormic	-10.4*	0.1 [†]	-7.8 [†]	-10.4**	-5.0*	-14.2**	-0.6			
Middle crown	Regular	-3.7**	-2.2**	-1.8**	-2.3**	-2.6**	-2.2**	-2.5**	-2.6**	-2.4**	
	Epicormic	-1.7	-1.3	-1.2	-2.7 [†]	-2.3*	-2.8**	-3.8	-1.6	-0.1	
Lower crown	Regular	1.7	-2.4	-3.6**	-3.4*	-2.3	-3.3*	-2.0	-2.3	-1.5	
	Epicormic	-2.8	-2.3	-1.9 [†]	-3.1* ^{††}	-1.2	-1.7	-1.3	1.2	0.0	

¹ Slope estimates significantly negative (* = $P < 0.05$ and ** = $P < 0.01$).

² Regression estimates significantly different between regular and epicormic shoots (ANCOVA, [†] = $P < 0.05$ and ^{††} = $P < 0.01$).

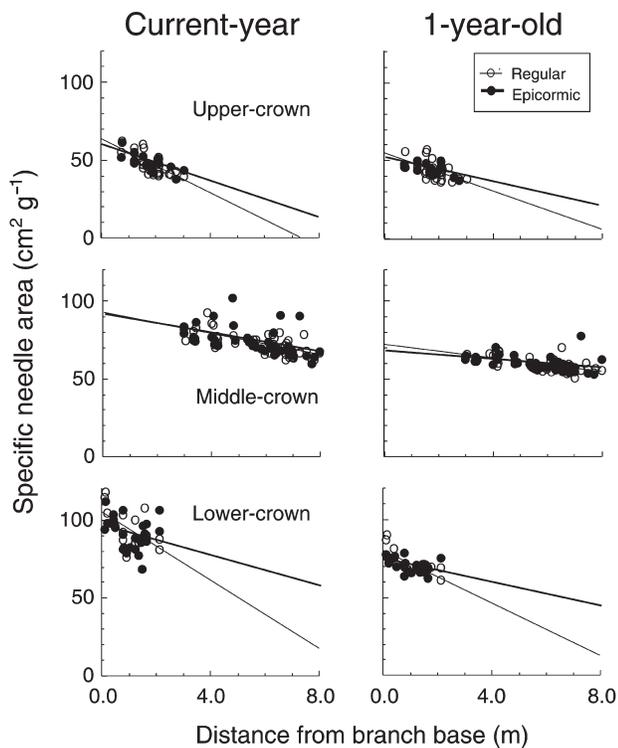


Figure 5. Examples from branches of Tree 1 of the relationship between distance from branch base and SNA for current-year and 1-year-old needles of regular (○, thin line) and epicormic shoots (●, thick line).

older needles of 65-year-old Douglas-fir in Oregon (values converted to projected-area-based SNA from the two-sided original data following Barclay and Goodman 2000). We found a steady decrease in SNA with increasing needle age for old Douglas-fir trees. Lower SNA in older needles than in young needles of young trees has been attributed to changing light conditions as the tree crown develops; i.e., older needles were formed at higher irradiances than younger needles (Niinemets 1997a). However, the Douglas-fir trees in our study have reached maximum crown size (Ishii 2000), and it is unlikely that light conditions within branches have changed markedly over the life span of the needles. Light conditions in

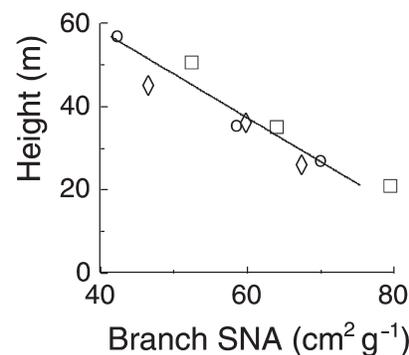


Figure 6. Relationship between branch height and branch SNA for the three sample trees (○ = Tree 1, □ = Tree 2 and ◇ = Tree 3).

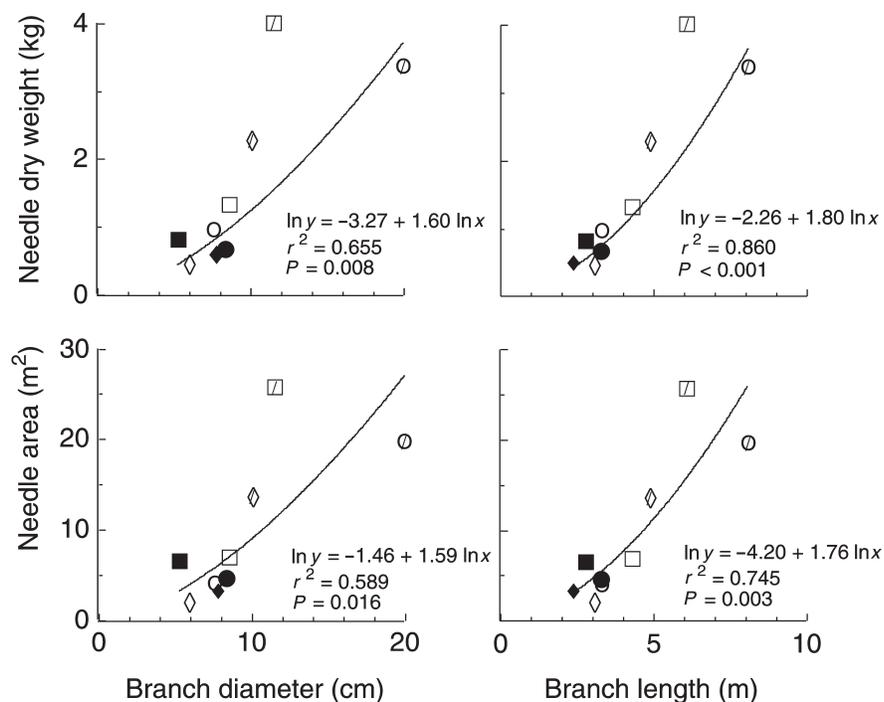


Figure 7. Relationships between branch size and foliage amount for the sample branches. Symbols: \circ = Tree 1, \square = Tree 2 and \diamond = Tree 3. Open, hatched and filled symbols represent upper-, middle- and lower-crown branches, respectively.

the lower crown are most likely to have been relatively constant for the past several years. (Light conditions in old-growth forest canopies are highly spatially variable, but are likely to be temporally stable.) Alternative explanations for the observed decrease in SNA with increasing needle age include accumulation of nonstructural carbohydrates and other secondary substances over time (Niinemets 1997b), and selective retention of needles with lower SNA (Hager and Sterba 1985). Douglas-fir retains most of its needles over the first 3 to 4 years (Mitchell 1974, H. Ishii, unpublished data). Therefore, the initial decline in SNA may be explained by accumulation of secondary substances, whereas selective retention may account for the decrease in SNA in older needles. Selective retention of needles with lower SNA agrees with cost-benefit models of foliage life span that predict leaves with high construction costs should be retained longer to maximize carbon gain (Kikuzawa 1986, Williams et al. 1989). We found a steeper decline in SNA with increasing needle age for lower-crown branches than for upper-crown branches. This suggests that rates of accumulation of secondary substances are greater and needles with greater SNA are shed more rapidly in lower-crown branches than in upper-crown branches. Although this

is a plausible explanation, more detailed investigations of needle anatomy and physiology are needed to explain the observed changes in SNA with needle age.

We found significant negative relationships between SNA and distance from branch base for both regular and epicormic shoots, especially for upper- and middle-crown branches. For upper-crown branches, changes in SNA with increasing distance from branch base may be as much as $-9.5 \text{ cm}^2 \text{ g}^{-1}$ per meter for current-year needles and $-6.2 \text{ cm}^2 \text{ g}^{-1}$ per meter for 1-year-old needles (Table 2). For middle-crown branches, changes in SNA with distance from branch base were smaller. One cause of the marked decrease in SNA with increasing distance from branch base for the upper-crown branches may be an increasing light gradient from inner to outer regions of the branch. Hydraulic limitations may also influence SNA in upper-crown branches. Bauerle et al. (1999) found a steep vertical gradient in daytime water potential with increasing height for 56–65-m-tall Douglas-fir, and showed that there is considerable water stress in the upper crown of these trees. Bond (2000) has proposed that hydraulic limitations may influence needle morphology in large old trees and result in smaller thicker needles in the upper crown. Hydraulic limitation is likely to increase with increasing distance from branch base, especially for upper-crown branches, resulting in greater SNA for needles near the outer region of the branch. For lower-crown branches, the relationship between SNA and distance from branch base was not significant for most age classes. This may reflect the relatively uniform light environment within lower-crown branches and the smaller effect of hydraulic limitation on lower-crown branches compared with upper-crown branches. More detailed studies on the variation in SNA in relation to within-branch light environment and hy-

Table 3. Total needle dry weight and needle area of the sample trees of 450-year-old Douglas-fir.

Tree	Needle dry weight (kg)	Needle area (m ²)
Tree 1	154.24	816.07
Tree 2	144.73	790.12
Tree 3	42.40	246.21

draulic conductance would elucidate possible causes of the directional change in SNA from inner to outer regions of branches.

For all branches, there was no difference in SNA between regular and epicormic shoots of the same age class, and the relationship between SNA and needle age did not differ between regular and epicormic shoots. In addition, only a few age classes showed differences between regular and epicormic shoots in the relationship between SNA and distance from branch base. Remphrey and Davidson (1992) found that epicormic shoot production in branches of green ash (*Fraxinus pennsylvanica* var. *subintegerrima* (Vahl) Fern.) contributed to maintaining productivity by increasing foliage area in older, inner regions of the crown. They point out that, in old trees, the balance between productive and nonproductive organs becomes increasingly important in maintaining overall productivity of the crown. Epicormic shoot production generates productive organs from existing support tissue, resulting in efficient renewal of shoots and foliage. We found that epicormic shoot production functions to maintain foliage not only quantitatively (Ishii and Ford 2001), but also qualitatively in branches of old Douglas-fir trees.

Branch SNA increased linearly with decreasing height for all three sample trees. Branch height explained 91.4% of the vertical variation in branch SNA. Several studies have found increasing trends in SNA with decreasing height in the crown in various coniferous tree species; e.g., Lewandowska and Jarvis (1977) and Ford (1982) for Sitka spruce (*Picea sitchensis* (Bong.) Carr), Hager and Sterba (1985) for Norway spruce (*Picea abies* L. Karst.), and Richardson et al. (2000) for hybrid spruce. Borghetti and Vendramin (1986) found that SNA increased from upper- to lower-crown positions in 25-year-old Douglas-fir, and attributed the increase to decreasing light from upper to lower crown. Bond et al. (1999) proposed that changes in needle morphology correspond to gradients in the light environment within the tree crown. In large old trees, internal physiological factors such as increasing hydraulic limitations with increasing height in the crown (Bond 2000, Ryan et al. 2000) and greater requirement for structural carbon in needles (Niinemets 1997c) may also influence SNA. The light environment within old-growth forest canopies can be highly spatially variable (Parker 1997). It is likely that both decreasing light availability and internal factors that stem from large size and old age affect SNA of old Douglas-fir trees.

Although our sample size was limited to only nine branches, our results indicate that branch length is a better predictor of foliage amount than branch diameter for old Douglas-fir trees. The sample branch with the largest diameter (middle-crown branch, Tree 1) had less needle dry weight and needle area than the second largest branch (middle-crown branch, Tree 2), despite a difference in diameter of 8.5 cm. This suggests that branch foliage amount may reach maximum values while branch diameter continues to increase. As trees grow larger, tree height and amount of foliage culminate, whereas tree diameter continues to increase (Thomas 1996, Ryan and Yoder 1997, Ryan et al. 1997). The same may apply to branches of

old trees that have reached maximum size. Kershaw and Maguire (1995) showed that branch diameter was the overall best predictor of branch needle area for young Douglas-fir. For old trees, however, use of simple allometric relationships to estimate needle area from branch diameter may overestimate needle area for large-diameter branches whose foliage amount has culminated. Ishii et al. (2000) showed that simple allometric relationships do not hold for the most fundamental branch size measures such as the relationship between branch diameter and length in old Douglas-fir trees, because die-back of branches and subsequent regrowth affects the relationship over long time periods. Damage and die-back of branches affects branch length and foliage amount, whereas branch diameter continually increases with time. Because branch diameter represents cumulative branch growth rather than current branch size, branch length is a better predictor of foliage amount in branches of old Douglas-fir trees.

We estimated tree-level needle dry weight and needle area from branch length and branch height, taking into account the vertical variation in branch SNA. Massman (1981) estimated total needle biomass of old-growth Douglas-fir trees ranging in height from 47 to 77 m by dividing the crown into several small axes and deriving allometric relationships between axis diameter and foliage amount. His estimates of tree-level foliage biomass ranged from 115 to 280 kg. Grier and Logan (1977) sampled 19 old-growth Douglas-fir trees for estimation of stand-level biomass. They reported that mean foliage dry weight for these trees was 78.4 kg. Our estimates of tree-level needle dry weight were similar to those obtained in these previous studies of old Douglas-fir trees. However, our estimates of needle area were smaller than those reported by Massman (1981): 1430–3900 m². This discrepancy probably arises because diameter-based estimates of foliage amount are likely to be greater than estimates based on branch length for large, old trees. We also accounted for the vertical variation in SNA within the crown. Because these relationships probably vary depending on site conditions, information on branch size-foliage amount relationships and variation in SNA is critical for the estimation of whole-tree foliage area for large, old Douglas-fir trees.

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