Influence of Swiss needle cast on foliage age-class structure and vertical foliage distribution in Douglas-fir plantations in north coastal Oregon

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Abstract: Swiss needle cast (SNC) causes premature loss of foliage and subsequent growth decline in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Although the mechanisms leading to this growth decline include loss of photosynthetic surface area and physiological disruption of surviving foliage, estimating the relative contribution of these two primary sources requires precise quantification of SNC effects on total foliage mass, foliage age-class structure, and vertical foliage distribution. The effect of SNC severity on these crown structural attributes was tested across a range of stand densities and site qualities in 10- to 60-year-old plantations in north coastal Oregon. Foliage mass in each age-class was sampled at the branch level, and the resulting equations were applied to all live branches on intensively measured sample trees. Vertical distribution of each foliage age-class was described by a beta distribution fitted to each sample tree, and sources of variation in vertical distribution were tested by regressing beta parameter estimates on SNC intensity and other covariates representing tree, stand, and site attributes. Distribution of foliage mass by age-class and by relative height in the crown was significantly affected by SNC severity, in addition to other covariates such as crown size and tree social position. SNC caused a reduction in the amount of foliage in each age-class and greater relative representation of younger needles. SNC also shifted the mode of relative vertical distribution toward the top of the tree for the three youngest foliage age-classes, but toward the base of the crown for 4- and 5-year-old foliage. Quantification of foliage age-class structure and vertical distribution across a range of SNC severity has helped to establish diagnostic criteria for assessing changes in crown structure that precede declines in growth and vigor. The induced changes in crown structure will also help to identify the relative contribution of several mechanisms causing growth losses in diseased trees.

Résumé : La rouille suisse cause la chute prématurée du feuillage et une diminution subséquente de croissance chez le douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco). Bien que les mécanismes responsables de cette diminution de croissance incluent la perte de surface photosynthétique et la perturbation physiologique du feuillage survivant, il faut quantifier avec précision les effets de la maladie sur la masse totale de feuillage, la structure des classes d'âge du feuillage et la distribution verticale du feuillage pour estimer la contribution de ces deux sources principales. L'effet de la sévérité de la maladie sur les attributs structuraux de la cime a été testé parmi une gamme de densités de peuplement et de qualités de station dans des plantations âgées de 10 à 60 ans situées dans la zone côtière septentrionale de l'Oregon. La masse foliaire de chaque classe d'âge a été échantillonnée à l'échelle de la branche, ce qui a permis de produire des équations de prédiction qui ont été appliquées à toutes les branches vivantes sur les arbres-échantillons qui ont fait l'objet d'un mesurage intensif. La distribution verticale de chaque classe d'âge de feuillage a été décrite par une distribution bêta ajustée à chaque arbre-échantillon et les sources de variation dans la distribution verticale ont été testées en faisant une régression entre les paramètres bêta estimés et l'intensité de la maladie ainsi que d'autres covariables représentant les attributs des arbres, du peuplement et de la station. La distribution de la masse du feuillage par classe d'âge et hauteur relative dans la cime a été significativement affectée par la sévérité de la maladie en plus d'autres covariables comme la dimension de la cime et la position sociale de l'arbre. La maladie a entraîné une réduction de la quantité de feuillage dans chaque classe d'âge et une plus forte représentation relative des aiguilles plus jeunes. La maladie a également modifié le mode de distribution verticale relative vers le sommet de l'arbre pour les trois plus jeunes classes d'âge, mais vers la base de la cime pour le feuillage âgé de 4 et 5 ans. La quantification de la structure des classes d'âge du feuillage et la distribution parmi une gamme de sévérités de la maladie ont permis d'établir des critères diagnostiques pour évaluer les changements dans la structure de la cime qui précèdent la diminution de croissance et la perte de vigueur. Les changements induits dans la structure de la cime vont aussi aider à identifier la contribution relative de plusieurs mécanismes responsables des pertes de croissance chez les arbres malades.

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Introduction

Growth impacts of forest insect and disease outbreaks are best estimated through an understanding of biological mechanisms inducing the impacts. For example, growth losses from defoliating insects have been successfully predicted from degree of defoliation in various foliage age-classes (Baskerville and Kleinschmidt 1981; Williams et al. 2003) or from total defoliation across age-classes (Wickman 1979; MacLean 1985). Protocols for most standard forest health assessments, however, call for only coarse measures of foliage condition and crown density within a stand (Innes 1993). The resulting indices of tree and stand condition have to be linked to more detailed tree and stand attributes to understand the implications for tree physiology and stand growth.

The condition of young conifer plantations in Europe is often rated by foliage retention, alternatively defined as needle longevity or the average number of needle cohorts held by the trees (Innes 1993). Foliage retention is currently the primary index of Swiss needle cast (SNC) severity in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; Hansen et al. 2000). Other foliage attributes such as crown color and crown density have been explored as indices of SNC severity, but foliage retention is less subjective and performs better than or as well as other alternatives for predicting tree and stand growth (Maguire et al. 2002). SNC is caused by an endemic fungal pathogen, *Phaeocryptopus gauemannii*, whose hyphae grow into needles through stomates and interrupt gas exchange by occluding stomates with fruiting bodies, or pseudothecia (Hansen et al. 2000). The fungus causes premature loss of older foliage, reducing mean foliage retention to as little as 1 year and volume growth by as much as 50% (Maguire et al. 2002). The disease eventually changes several crown structural and morphological attributes such as live crown length, branch size, and specific leaf area (Weiskittel 2003). Currently, over 72 000 ha in the Oregon Coast Range are showing symptoms detectable by aerial survey, reflecting the dramatic increase in this disease since 1990 (Kanaskie et al. 2004).

Foliage retention is highly correlated with the proportion of stomates occluded by fungal pseduothecia; however, foliage retention does not necessarily translate directly into the relative or absolute amount of foliage held in each age-class. The latter is also determined by the total shoot length in each age-class, needle density per unit shoot length, and the average size of needles. Furthermore, trees may compensate for premature loss of foliage in ways that leave total foliage mass or young foliage mass relatively unchanged. These compensatory responses may also change over time with variation in the carbon status of the tree.

Needle retention has been shown to decline with increasing site quality (Reich et al. 1995) and after fertilization treatments that lead to significant gains in growth (Balster and Marshall 2000). Despite a decline in foliage retention induced by fertilization, total foliage mass concurrently increased in Douglas-fir (Brix 1983). The fact that foliage retention is not necessarily correlated with total foliage mass is also illustrated by the relative performance of alternative surrogates for foliage amount. In a study of genetic differences in SNC tolerance, crown density and crown color were found to be more strongly correlated with growth than with needle retention (Johnson 2002). The distribution of foliage mass on 5-year-old primary branches shifted toward higher relative amounts of younger age-classes in stands with lower foliage retention (Maguire et al. 2002); however, this response may vary with height in the crown. Likewise, an index of crown sparseness (ratio of crown length to sapwood area; CLSA) was highly correlated with the mass of 1-year-old foliage and the proportion of 2-year-old foliage on the same 5-year-old primary branches (Maguire and Kanaskie 2002). As a result, crown sparseness was also a strong predictor of stand growth loss to SNC (Maguire and Kanaskie 2002). The relationship of any of these SNC indices to the specific crown structural attributes that drive tree growth is poorly defined. Foremost among these crown attributes are foliage age-class structure, vertical foliage distribution, and total foliage mass and area.

Prediction of canopy photosynthesis, transpiration, and biomass accumulation in evergreen coniferous forests requires accurate knowledge of the amount and spatial location of needles in different age-classes (Cermák et al. 1998; Bernier et al. 2001; Ogée et al. 2003). Several mechanistic models for Douglas-fir have been built on strong assumptions about foliage age-class structure (e.g., Mitchell 1975; Mohren 1987; Manter et al. 2003*a*). These assumptions, however, are based on limited data and have not been rigorously tested. Although vertical distribution of foliage has been studied intensively in some species (Xu and Harrington 1998), its response to environmental conditions, silvicultural intervention, and other disturbances is not well understood. Even less is known about the vertical distribution of specific needle age-classes (see Kellomäki et al. 1980 for one exception). Because most studies on vertical foliage distribution have been limited to younger plantations (e.g., Maguire and Bennett 1996), any shifts attributable to stand age and canopy height are largely unknown.

The goal of this study was to test and quantify the relationship between indices of SNC severity and the total amount, age-class structure, and vertical distribution of foliage on 10- to 60-year-old coast Douglas-fir. To isolate the effects of SNC severity on these crown attributes, the influence of tree age, crown aspect, and other factors were assessed as covariates. If total amount, age-class structure, and vertical distribution of foliage can be reliably estimated by one or several alternative indices of SNC severity, then growth losses can be estimated from basic principles of tree physiology.

Materials and methods

Study area

The 21 plots included in this study were located in the Oregon Coast Range, within 32 km of the Pacific Ocean. All plots were north of Newport (44°40′N, 124°04′W) and south of Astoria (46°7′N, 123°45′W). The climate is humid oceanic, with a distinct dry summer and a cool, wet winter. Rainfall varies from approximately 180 to 300 cm·year^{-1}, and January mean minimum and July mean maximum temperatures range from –2 to 2 °C and from 20 to 28 °C, respectively (Franklin and Dyrness 1973). Variation in precipitation and temperature is strongly related to elevation

Table 1. Attributes of the 21 plots sampled in fall of 2002 (young plantations) and winter of 2003 (older plantations).

Attribute	Mean	SD	Min.	Max.
Young plantations (n = 12)				
Douglas-fir basal area (m^2/ha)	23.3	7.8	9.9	36.6
Douglas-fir trees per ha	707.0	327.8	259.4	1222.6
Douglas-fir quadratic mean diameter (cm)	22.4	8.1	11.4	36.5
Total basal area (m^2/ha)	30.9	14.9	10.4	69.6
Average breast-height age (year)	18.7	4.9	11.0	27.8
Average foliage retention (year)	2.6	0.8	1.2	4.3
Site index (Bruce 1981; height at 50 year, in m)	39.5	3.2	34.8	43.9
Average crown sparseness index (cm/cm^2)	5.8	1.4	3.6	7.9
Older plantations (n = 9)				
Douglas-fir basal area (m^2/ha)	43.1	13.7	26.7	72.6
Douglas-fir trees per ha	346.7	139.1	150.0	580.0
Douglas-fir quadratic mean diameter (cm)	41.2	7.1	32.9	53.5
Total basal area (m^2/ha)	47.9	12.8	30.3	76.8
Average breast-height age (year)	46.5	11.4	33.7	62.4
Average foliage retention (year)	2.4	1.1	1.3	4.4
Site index (Bruce 1981; height at 50 year, in m)	37.9	5.3	26.6	45.1
Average crown sparseness index (cm/cm^2)	5.5	1.1	4.3	8.1

Note: SD, standard deviation.

and proximity to the coast. Elevation ranged from 45 to 550 m and all aspects were represented by the study sites.

The plantations in which plots were established ranged from 10 to 60 years old at breast height and contained ≥75% Douglas-fir by basal area, with varying amounts of naturally regenerated western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and hardwood species (Table 1).

Plot monitoring

Two data sets were combined to cover the desired range in stand age. The first was constructed from 36 trees sampled in the fall of 2002 from 12 relatively young (10- to 30-year-old) Douglas-fir plantations (Weiskittel 2003). These plantations were part of a large network established to monitor SNC severity and growth impacts in the Oregon Coast Range (Maguire et al. 2002). The selected plots were similar in structure and composition, but varied in SNC intensity as measured by average stand foliage retention. The second data set was constructed from 36 trees sampled in the winter of 2003 from nine older (30- to 60-year-old) Douglas-fir plantations. These older plantations were part of a study to test the influence of commercial thinning on tree growth and SNC severity (Mainwaring et al. 2005). Plots were chosen to fill a sampling matrix based on three levels of SNC severity (severe, moderate, light) and two levels of Douglas-fir stand density (relative density 3–5 and 5–7 $m^2 \cdot ha^{-1} \cdot cm^{-0.5}$; Curtis 1982). One plot was selected from each of these six combinations, and one additional plot was selected from high SNC – low density, low SNC – high density, and median SNC – median density, yielding nine plots. The high-density stands were unthinned control plots, and the low-density stands had been commercially thinned 3–5 years prior to sampling.

In the younger plantations, all trees were tagged on square 0.08 ha permanent plots established in 1998. In addition to measuring standard tree dimensions every 2 years, the Oregon Department of Forestry scored 10 trees annually on each plot for SNC severity. On each tree, crown length was divided into thirds and the average number of annual needle cohorts was estimated visually with the use of binoculars (nearest 0.1 years). Trees were also rated for two additional attributes, crown density (1–10, with 10 being the most healthy or with high foliage density) and crown color (1–4, with 4 being the most healthy or with the least discolored foliage). Plot ratings were computed as the mean of all 10 trees.

In the older plantations, all trees were tagged on two 0.2 ha permanent plots (control plus thinned) established in 2001. Five trees on each plot have been scored annually for SNC severity since 2001. Because of the crown heights and associated visibility problems in these older, larger trees, a single average rating was recorded for the whole crown. Two breast-height cores were taken perpendicular to slope from each tree and used to compute sapwood area. The sapwood area at crown base was estimated using a previously constructed sapwood taper equation for Douglas-fir (Maguire and Batista 1996). Crown sparseness (CLSA) was computed as the ratio of crown length (CL; cm) to sapwood area at crown base (SA; cm^2). Plot ratings were computed as the average of all five trees.

Felled-tree sampling

Three or four sample trees were selected from each stand. All sample trees were outside but adjacent to the permanent monitoring plots and similar to plot trees with regard to diameter at breast height (DBH, 1.3 m), foliage retention, and spacing distance from adjacent Douglas-fir trees. All sample trees were located away from gaps or landings and were free of any damage or obvious defect (e.g., double tops, excessive sweep, crooks). Before felling, DBH (to the nearest 0.1 cm) and crown width (CW; to the nearest 0.1 m) were measured, and crown color and crown density were esti-

Table 2. Attributes of the 73 Douglas-fir trees sampled in 2002 (young plantations) and 2003 (older plantations).

Attribute	Mean	SD	Min.	Max.
Young plantations (*n* = 36)				
DBH (cm)	23.9	5.2	12.5	35.1
Height (m)	18.8	4.9	11.9	33.5
Height to live crown (m)	6.6	2.9	0.5	11.9
Relative stand height (tree height/stand top height)	1.00	0.11	0.73	1.37
Crown ratio	0.66	0.11	0.44	0.96
Crown length / sapwood area ratio (cm/cm^2)	7.4	5.7	2.2	34.9
Older plantations (*n* = 37)				
DBH (cm)	42.4	9.1	31.0	66.6
Height (m)	33.5	5.7	22.8	45.8
Height to live crown (m)	16.7	4.7	8.1	28.3
Relative stand height (tree height/stand top height)	0.86	0.07	0.69	0.97
Crown ratio	0.50	0.09	0.23	0.69
Crown length / sapwood area ratio (cm/cm^2)	6.7	2.5	3.3	16.3

Note: SD, standard deviation.

Table 3. Attributes of the 882 sample branches collected in 2002 (young plantations) and 2003 (older plantations).

Attribute	Mean	SD	Min.	Max.
Young plantations (*n* = 350)				
Diameter (mm)	16.8	9.2	1.1	41.6
Length (m)	1.7	0.9	0.1	4.6
Foliated length (m)	1.5	0.9	0.1	4.3
Depth in crown (m)	5.6	3.4	0.3	14.8
Older plantations (*n* = 532)				
Diameter (mm)	23.0	13.6	1.7	63.9
Length (m)	2.1	1.3	0.1	6.1
Foliated length (m)	1.7	1.1	0.1	4.8
Depth in crown (m)	7.4	4.7	0.3	27.3

Note: SD, standard deviation.

mated. Each sample tree was then felled, and total height (HT; nearest 0.01 m) from the base of the stump to the tip of the tree and height to crown base (HCB; nearest 0.01 m; lowest live branch) were measured by stretching a fiberglass tape along the bole. Basal diameter (BD; nearest 0.1 mm) and depth into the crown (DINC; nearest 0.01 cm) were recorded for each live branch. Branch aspect (north vs. south side of the tree) was also determined for trees sampled from the older plantations. Sample trees ranged in DBH from 12 to 67 cm (Table 2). A total of nine whorl branches (three from each third of the crown) and six interwhorl branches (two from each third of the crown) were selected at random for laboratory analysis. Sample branches were cut at the base and measured for total length along the main branch axis. Sample branches ranged in basal diameter from 1 to 64 mm (Table 3). Each sample branch was clipped into segments and placed in a plastic bag. After branch sampling, thin disks were removed from the tree at breast height and crown base.

Laboratory work

The sample branches were clipped and bagged by age-class, then dried in an oven at 85 °C for 3 days. The needles were separated from woody material and weighed to the nearest 0.01 g. The two stem disks from each tree were measured for sapwood width on the two radii forming the long axis of the disk and on the two radii perpendicular to the longest axis. Sapwood was computed assuming that both the total cross section and heartwood cross section were elliptical.

Data analysis

Various linear and nonlinear regression models were fitted to the data to develop branch- and tree-level equations for estimating foliage mass by age-class and for testing the effect of SNC and other tree and stand variables on foliage age-class structure and vertical foliage distribution. Final models were chosen on the basis of residual analysis, Furnival's index (FI; Furnival 1961), Akaike's information criterion (AIC), and biological interpretability. A system of equations approach, iterative seemingly unrelated regression, was applied to fit regression models to the data for the set of age-classes simultaneously, thereby addressing cross-equation correlation (Kmenta 1997). Additivity of individual age-classes to total foliage mass was also forced in the system of equations (Parresol 2001). All analyses were done in SAS v8.2 (SAS Institute Inc., Cary, North Carolina) and S-PLUS v6.2 (Mathsoft, Seattle, Washington).

Branch-level foliage age-class equations

Total branch-level foliage mass was estimated for each age-class as the product of estimated total foliage mass and predicted proportion of total mass contributed by each age-class (Kleinschmidt et al. 1980). Total foliage mass (all age-classes) was estimated by plot-specific equations following the model form presented by Kershaw and Maguire (1995):

$$[1] \qquad \ln(\mathrm{BFDM}_k) = \beta_{10\mathrm{k}} + b_{11k}\ln(\mathrm{BD}) + \beta_{12k}\ln(\mathrm{DINC}) + \beta_{13k}\ln(\mathrm{RHACB}) + \beta_{14\mathrm{k}}I_{\mathrm{w}} + \varepsilon_1$$

where BFDM is the estimated foliage mass (g) for branches on plot *k*; BD is branch basal diameter (mm); DINC is depth into crown (m); RHACB is relative height above crown base

Table 4. List of variables used in modeling foliage amount, age-class structure, and vertical distribution.

Symbol	Definition	Source
a_i	Estimated alpha parameter of the beta distribution for foliage age-class *i*	—
AGE	Mean stand breast height age (years)	—
b_i	Estimated beta parameter of the beta distribution for foliage age-class i	—
BD	Branch diameter (mm)	—
BFDM	Branch foliage dry mass (g)	—
CW	Crown width (m)	—
DBH	Diameter at breast height (cm)	—
DINC	Depth into crown (m)	—
CC	Crown color (1–4 scale)	—
CD	Crown density (1–10 scale)	—
CF_i	Cumulative proportion of foliage in age-class i	—
CL	Crown length (m)	—
CLSA	Tree crown sparseness index (crown length/sapwood area at crown base; $\mathrm{cm}^2/\mathrm{cm}$)	Maguire and Kanaskie 2002
$\mathrm{CLSA}_{\mathrm{PLOT}}$	Plot mean crown sparseness index (mean of 10 dominant and codominant trees; $\mathrm{cm}^2/\mathrm{cm}$)	Maguire and Kanaskie 2002
CR	Crown ratio	—
F_i	Foliage dry mass in foliage age-class i (kg)	—
FOLRET	Stand mean foliage retention (years)	—
HCB	Height to crown base (m)	—
HCM	Height to crown midpoint (m)	—
HT	Tree height (m)	—
$\mathrm{I_W}$	Indicator for branch type (1 if whorl branch, 0 if interwhorl branch)	
RD	Stand relative density ($\mathrm{m}^2\ \mathrm{ha}^{-1}/\sqrt{\mathrm{cm}}$)	Curtis 1982
RHT	Relative height in stand (HT/stand top height)	—
RHACB	Relative height above crown base	—
SI	Site index (base age of 50 years; m)	Bruce 1981
TFDM	Tree foliage dry mass (kg)	—

(1 – DINC/CL); CL is crown length (m); I_{W} is an indicator variable for type of branch (1 if whorl, 0 if interwhorl); the β_{ik}'s are parameters to be estimated from the data for plot *k*; and $\varepsilon_1 \sim \mathrm{N}(0, \sigma^2{}_1)$, where ε_1 is independently identically distributed (Table 4). Preliminary analysis suggested that branch aspect was inconsequential, so it was dropped as a potential covariate.

Proportions of foliage in each age-class on a branch were modeled by a system of reverse sigmoidal functions fitted to the successive cumulative foliage mass data (Weiskittel 2003):

$$\begin{aligned} &\mathrm{CF}_1 = \exp(\gamma_{21}\mathrm{DINC}^{\gamma_{22}}) + \varepsilon_{21} \\ &\mathrm{CF}_2 = \exp(\gamma_{23}\mathrm{DINC}^{\gamma_{24}}) + \varepsilon_{22} \\ [2]\quad &\mathrm{CF}_3 = \exp(\gamma_{25}\mathrm{DINC}^{\gamma_{26}}) + \varepsilon_{23} \\ &\mathrm{CF}_4 = \exp(\gamma_{27}\mathrm{DINC}^{\gamma_{28}}) + \varepsilon_{24} \\ &\mathrm{CF}_5 = 1 - \mathrm{CF}_4 + \varepsilon_{25} \end{aligned}$$

where CF_i is cumulative proportion of foliage in age-class *i* and younger (*i* = 1, 2, 3, 4, 5 for 1-, 2-, 3-, 4-, and ≥5-year age-classes, respectively); DINC is defined previously; the γ_i's are parameters to be estimated from the data for each plot; and $\varepsilon_k \sim \mathrm{MVN}(\mathbf{0}, \mathbf{\Sigma})$, where $\varepsilon_k' = [\varepsilon_{21}, \varepsilon_{22}, \varepsilon_{23}, \varepsilon_{24}, \varepsilon_{25}]$ and $\mathbf{\Sigma}$ is a $k \times k$ variance–covariance matrix. Restrictions were also placed on the γ parameters to ensure correct additive behavior of the various age-classes (i.e., $\gamma_{27} > \gamma_{25} > \gamma_{23} > \gamma_{21}$ and $\gamma_{28} > \gamma_{26} > \gamma_{24} > \gamma_{22}$).

Estimates of absolute foliage mass in each age-class were obtained as the product of estimated total foliage mass of the branch (eq. 1) and predicted foliage proportion in each age-class (eq. 2). Preliminary results had indicated that this approach achieved less bias than was introduced by allometric equations estimating absolute foliage mass in each age-class directly (e.g., Xiao and Ceulemans 2004).

Tree-level foliage age-class equations

Total foliage mass of all 73 intensively measured sample trees was estimated by applying eqs. 1 and 2 to each live branch and summing these branch-level estimates for the entire tree by age-class (1, 2, 3, 4, and ≥5 years old). The relationship between SNC severity and tree-level foliage mass was tested by regressing the latter on a set of variables that included foliage retention. Alternative models specific to each age-class were identified by all-subsets regression, and final models were selected on the basis of biological expectation and statistical performance. Final parameters for the system of five equations (one for each age-class) were estimated with seemingly unrelated regression (Kmenta 1997) in SAS PROC MODEL. Preliminary analysis had indicated that tree-level equations for absolute foliage mass in each age-class achieved less bias than was introduced by the product of estimated total foliage mass and estimated proportion in each age-class.

Vertical foliage distribution

Observed vertical foliage distribution was characterized on the sample trees by dividing crown length into 10 equal segments and summing the foliage mass estimated for all

Table 5. Model form, R^2, and root mean square error (RMSE) for equations predicting the total amount of foliage in each age-class at the individual tree-level.

Equation	Model form	R^2	RMSE
1-year foliage mass (kg)	$\ln(F_1) = -1.5367 + 0.0451 \times \mathrm{CL} + 1.3622 \times \dfrac{\mathrm{DBT}}{\mathrm{HT}} + 0.0349 \times \mathrm{HT} - 0.0405 \times \mathrm{CLSA}$	0.72	0.34
2-year foliage mass (kg)	$\ln(F_2) = -0.6274 + 0.02857 \times \mathrm{CL} + 0.2029 \times \mathrm{RHT} + 0.9479 \times \dfrac{\mathrm{DBT}}{\mathrm{HT}} + 0.0296 \times \mathrm{HT} - 0.00725 \times \mathrm{CLSA}$	0.72	0.34
3-year foliage mass (kg)	$\ln(F_3) = -0.0188 + 0.6156 \times \dfrac{\mathrm{DBT}}{\mathrm{HT}} + 0.0274 \times \mathrm{HT} - 0.1024 \times \mathrm{CLSA} + 0.2977 \times \ln(\mathrm{FOLRET})$	0.58	0.49
4-year foliage mass (kg)	$\ln(F_4) = 0.0357 + 0.0379 \times \mathrm{HT} - 0.2141 \times \mathrm{CLSA} + 0.2560 \times \mathrm{FOLRET}$	0.51	1.06
≥5-year foliage mass (kg)	$\ln(F_5) = 4.2747 - 5.7569 \times \mathrm{RHT} - 0.2505 \times \mathrm{CLSA} + 2.3594 \times \ln(\mathrm{FOLRET})$	0.47	1.62

Note: All parameter estimates are significant at $\alpha = 0.05$.

branches within that segment. The proportion of tree foliage in each of the foliage age-classes in each of the 10 segments was then computed. A standard two-parameter beta distribution (Johnson and Kotz 1970) was fitted to the empirical distribution for each tree. The beta distribution has the desirable properties of being extremely flexible and logically defined on an interval with fixed endpoints:

$$f(x;a,b) = \frac{1}{B(a,b)} x^{a-1}(1-x)^{b-1}, \quad 0 \le x \le 1$$

where

$$B(a,b) = \frac{\Gamma(a)\Gamma(b)}{\Gamma(a+b)}$$

$$\Gamma(a) = \int_0^\infty e^{-z} z^{a-1}\, dz \text{ for all } a > 0$$

where $f(x)$ is a probability density, a and b are shape parameters ($0 < a$, $b < \infty$), and x is a beta random variable (in this case equal to relative depth in crown with 0 being tree tip and 1 being HCB). Estimates of the parameters a and b were determined by maximum likelihood estimation for each of the 73 sample trees.

To test the effects of SNC on vertical foliage distribution, beta distribution parameters for individual trees were modeled as a linear function of SNC severity (FOLRET, CLSA, CC, or CD) as well as standard tree covariates (DBH, HT, and CL). Parameters for the final models were estimated by seemingly unrelated regression to account for cross-equation correlation. The models for predicting beta distribution parameters were of the following form:

$$[3] \qquad a_i = \beta_{301} + \beta_{302}\mathrm{HCM} + \beta_{303}\ln(\mathrm{HT}) + \beta_{304}\ln(\mathrm{FOLRET}) + \beta_{305}\mathrm{FOLRET} + \varepsilon_{ai}$$

$$b_i = \beta_{306} + \beta_{307}\mathrm{CL} + \beta_{308}\mathrm{HCM} + \beta_{309}\mathrm{CR} + \beta_{310}\mathrm{CLSA}_{\mathrm{PLOT}} + \varepsilon_{bi}$$

where a_i is the alpha parameter for foliage age-class i (i = 1, 2, 3, 4, or 5); b_i is the beta parameter for foliage age-class i; $\mathrm{CLSA}_{\mathrm{PLOT}}$ is plot mean crown length to sapwood area ratio; CR is crown ratio; the β_i's are parameters to be estimated from the data; $\varepsilon_{ab} \sim \mathrm{MVN}(\mathbf{0}, \Sigma)$, where $\varepsilon_{ab'} = [\varepsilon_{a1}, \varepsilon_{b1}, \ldots, \varepsilon_{a5}, \varepsilon_{b5}]$ and Σ is a 10 × 10 variance–covariance matrix. Logarithmic transformations on several independent variables were made to linearize nonlinear relationships.

Vertical foliage distributions implied by the fitted equations were then plotted for the average tree at two ages (20 and 45) and at two foliage-retention levels (1.5 and 3.5 years) to provide a graphical assessment of SNC and age effects.

Results

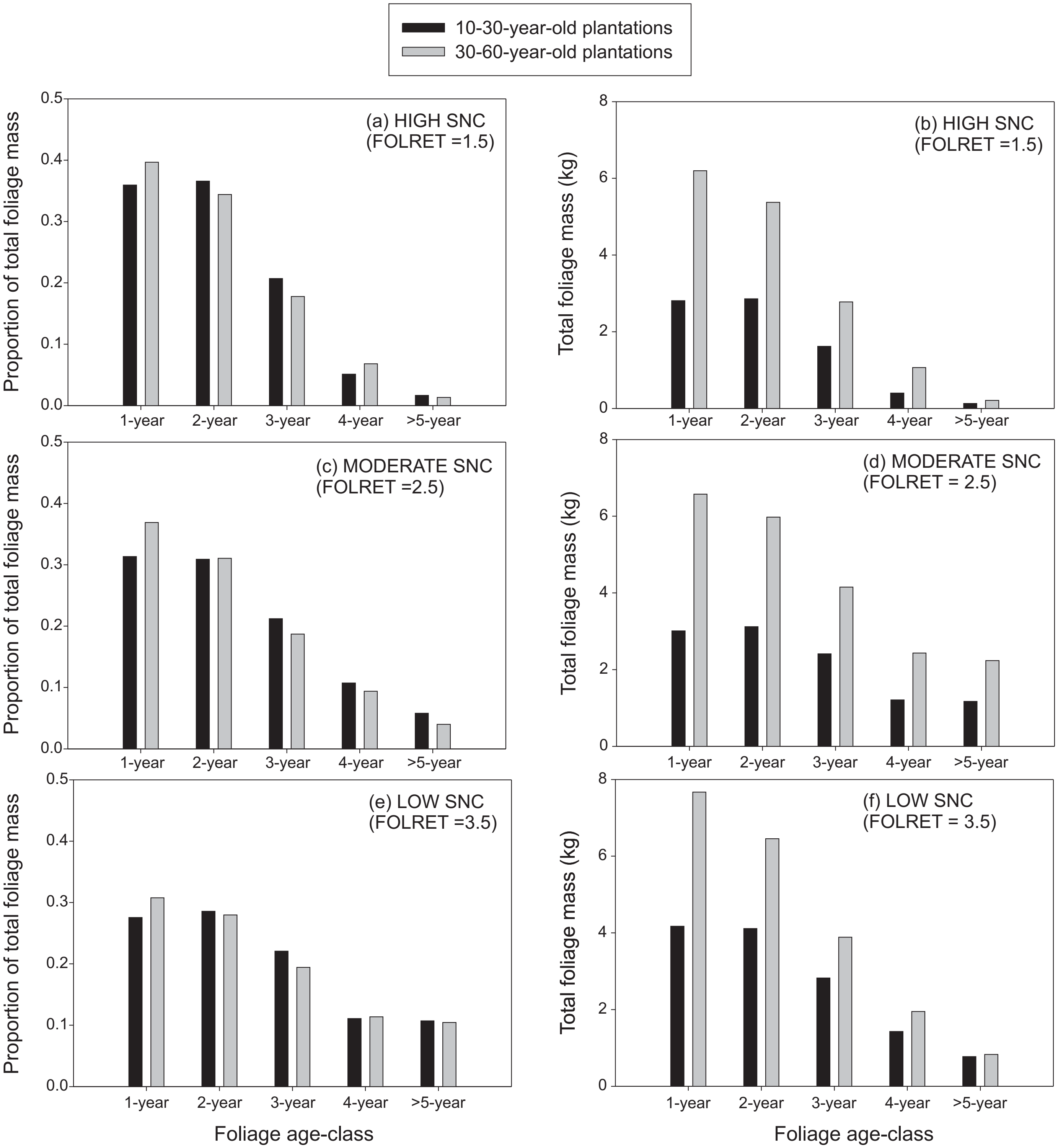
Foliage age-class structure

The models for estimating amount of foliage on an individual tree by age-class explained 47%–72% of the variation in mass (Table 5). In general, the absolute amount of foliage in each age-class increased with greater crown length (CL), diameter/height ratio (DBH/HT), and plot mean foliage retention (FOLRET), but decreased with greater crown sparseness (CLSA). Crown sparseness explained a significant amount of variation in the mass of each foliage age-class, while foliage retention was significant for only the 3-, 4-, and ≥5-year-old foliage age-classes. A tree on a plot with severe SNC (FOLRET = 1.5 years, CLSA = 7.6) had approximately 40%, 34%, 18%, 7%, and 1% of its foliage in 1-, 2-, 3-, 4-, and ≥5-year-old foliage age-classes, respectively. On average, a tree on a plot with low SNC (FOLRET = 3.5 years, CLSA = 6.1) was estimated to have 31%, 28%, 19%, 11%, and 11% of its foliage in 1-, 2-, 3-, 4-, and ≥5-year-old foliage age-classes, respectively (Fig. 1). Overall, severe SNC (FOLRET = 1.5 years) resulted in a 27% reduction in total foliage mass on an averaged-sized tree relative to total foliage mass on a tree with low SNC (FOLRET = 3.5 years). Corresponding reductions in each foliage age-class are 6%, 10%, 33%, 56%, and 91% for the 1-, 2-, 3-, 4-, and ≥5-year-old foliage age-classes, respectively.

Vertical foliage distribution

SNC severity (FOLRET, CLSA, or $\mathrm{CLSA}_{\mathrm{PLOT}}$) explained a significant amount of the variation in relative vertical distribution of foliage, with the latter being represented by beta distribution parameter estimates. Variables representing tree size (HT) and crown dimensions (CL, CR, HCM) also had a statistically significant effect on relative foliage distribution; however, some variables were not statistically significant in

Fig. 1. Predicted relative (left) and total mass (right) by foliage age-class for stands with (*a*, *b*) severe Swiss needle cast (SNC); (*c*, *d*) moderate SNC; and (*e*, *f*) low SNC. Dark bars represent 10- to 30-year-old trees and light bars represent 30- to 60-year-old trees.



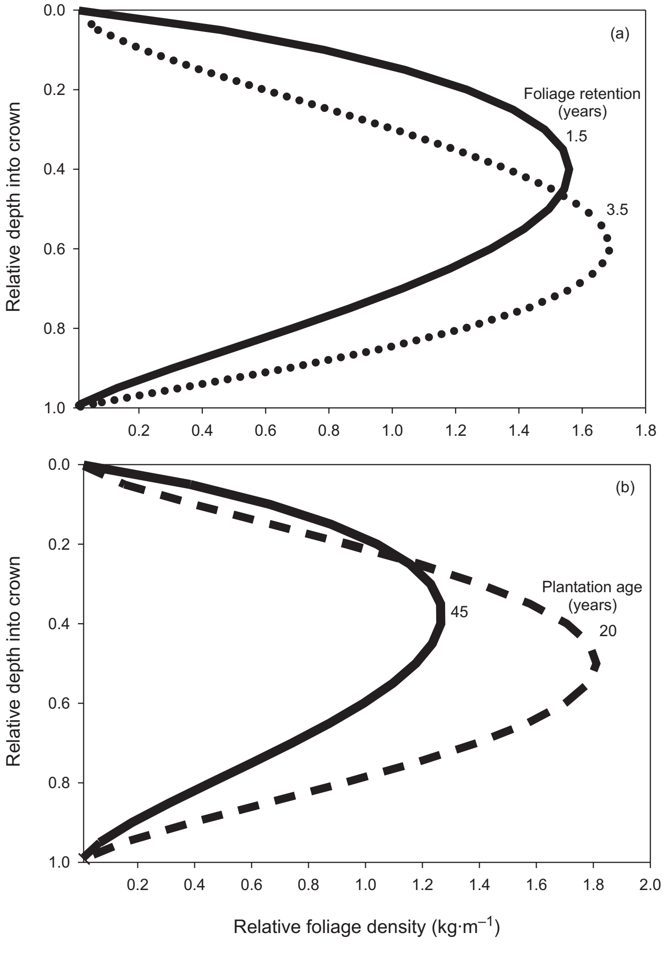
the final fit and were consequently dropped from the system of equations (Table 6). Increasing SNC severity alone tended to shift the mode of vertical distribution upward when all foliage age-classes were lumped, as did increasing stand age, but to a lesser degree (Fig. 2). The amount of variation in the beta parameter estimates explained by SNC severity and tree dimensions ranged from 8% to 69%, and RMSE ranged from 0.52 to 5.19. An increase in the alpha parameter and corresponding downward shift in the mode of the 1-, 2-, and 3-year-old foliage was induced by an increase in FOLRET, although this effect started to reverse gradually beyond 2.7–2.9 years of foliage retention (based on analysis

Table 6. System of linear equations fitted using seemingly unrelated regression for predicting beta-distribution parameters for implied vertical distribution of foliage by age-class (eq. 3).

Foliage age-class	Model form	R^2	RMSE
All	$a = 10.3826 - 3.03789 \times \ln(\mathrm{HT}) + 0.1007 \times \mathrm{HCM} - 1.6075 \times \mathrm{FOLRET} + 4.7411 \times \ln(\mathrm{FOLRET})$	0.47	0.52
	$b = 0.2681 - 1.9205 \times \ln(\mathrm{HCM}) - 3.5215 \times \ln(\mathrm{CR}) + 1.9509 \times \ln(\mathrm{CL}) + 0.0556 \times \mathrm{CLSA}$	0.29	0.75
1	$a_1 = 11.6113 + 0.1249 \times \mathrm{HCM} - 3.5964 \times \ln(\mathrm{HT}) + 2.9666 \times \ln(\mathrm{FOLRET}) - 1.0103 \times \mathrm{FOLRET}$	0.41	0.65
	$b_1 = 6.0315 - 2.5704 \times \ln(\mathrm{CR}) - 1.5675 \times \ln(\mathrm{HCM})$	0.08	1.57
2	$a_2 = 15.4951 + 0.1339 \times \mathrm{HCM} - 4.5845 \times \ln(\mathrm{HT}) + 5.9949 \times \ln(\mathrm{FOLRET}) - 2.1765 \times \mathrm{FOLRET}$	0.65	0.64
	$b_2 = 2.3680 - 3.2489 \times \ln(\mathrm{CR}) - 1.0631 \times \ln(\mathrm{HCM}) + 0.8325 \times \ln(\mathrm{CLSA_{PLOT}})$	0.18	1.08
3	$a_3 = 17.9170 + 0.1357 \times \mathrm{HCM} - 5.050 \times \ln(\mathrm{HT}) + 9.0856 \times \ln(\mathrm{FOLRET}) - 3.409 \times \mathrm{FOLRET}$	0.69	0.71
	$b_3 = 1.4177 - 3.1592 \times \ln(\mathrm{CR}) - 0.7793 \times \ln(\mathrm{HCM}) + 0.7886 \times \ln(\mathrm{CLSA_{PLOT}})$	0.24	1.01
4	$a_4 = 31.0878 - 7.4314 \times \ln(\mathrm{HT}) - 0.8347 \times \mathrm{FOLRET}$	0.31	4.26
	$b_4 = 6.7875 - 5.2776 \times \mathrm{CR} - 1.1167 \times \ln(\mathrm{HCM}) + 0.03732 \times \mathrm{CL} + 0.8325 \times \ln(\mathrm{CLSA_{PLOT}})$	0.25	0.82
≥5	$a_5 = 34.4526 - 7.8717 \times \ln(\mathrm{HT}) + 25.7269 \times \ln(\mathrm{FOLRET}) - 0.8347 \times \mathrm{FOLRET}$	0.33	5.19
	$b_5 = 6.2205 - 4.5574 \times \ln(\mathrm{CR}) - 2.7253 \times \ln(\mathrm{HCM}) + 0.9373 \times \ln(\mathrm{CLSA_{PLOT}})$	0.34	1.56
System		0.42	1.01

Note: All parameter estimates are significant at $\alpha = 0.05$.

Fig. 2. Estimated relative vertical distribution of foliage mass density ($\mathrm{kg \cdot m^{-1}}$) from all age-classes and for trees with different Swiss needle cast severity (*a*) and plantation age (*b*).



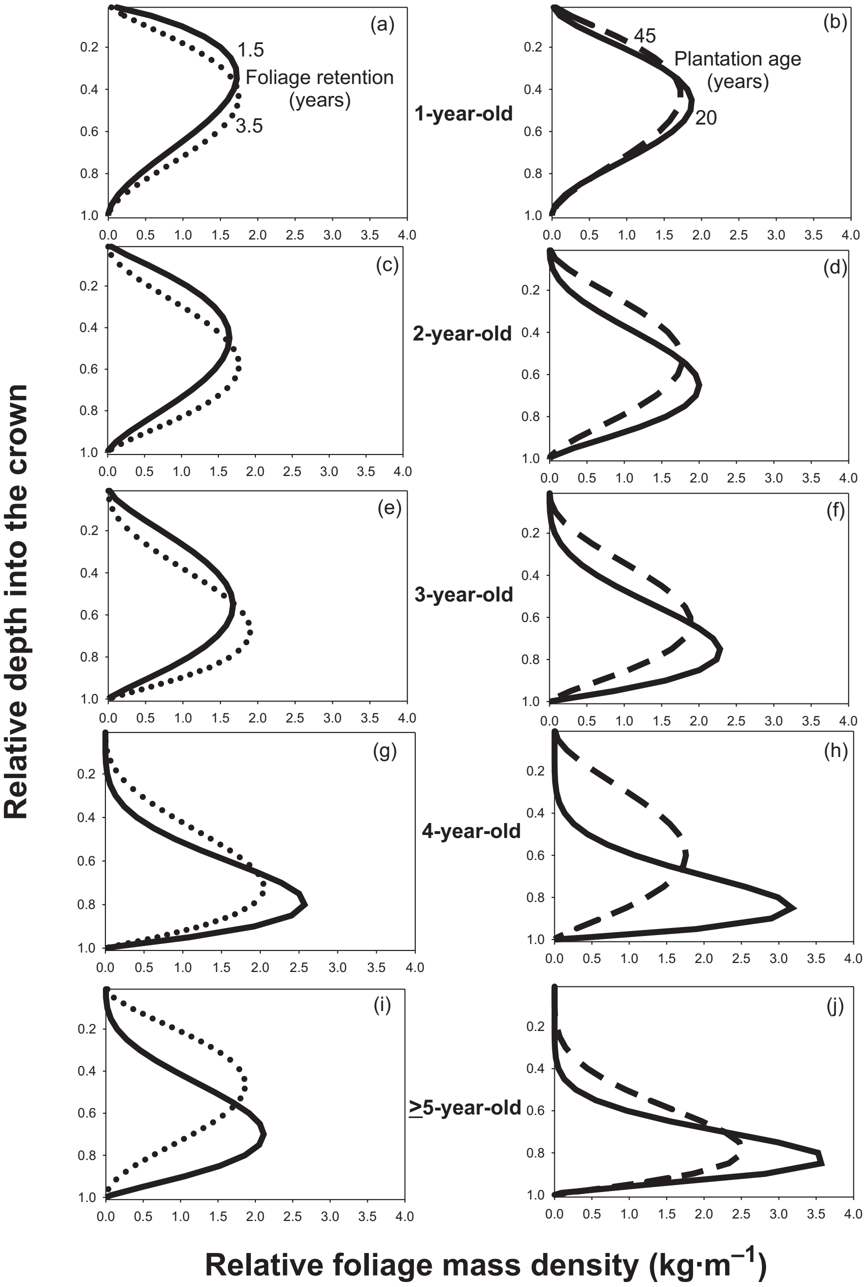
of first derivatives of the alpha parameter equations with respect to FOLRET; Table 6). The ≥5-year-old foliage responded similarly, except that the alpha parameter increased over the full range of observed foliage retention (1.2–4.3 years). In contrast, the alpha parameter for 4-year-old foliage declined monotonically with increasing FOLRET, so the mode would be shifted upward with increasing FOLRET for this age-class. However, because the beta parameter covaries with the alpha parameter, and because crown sparseness (CLSA or $\mathrm{CLSA_{PLOT}}$) was significantly related to the beta parameter, the net of effect of SNC on vertical distribution of each age-class is evident only from the consideration of SNC effects on both parameters simultaneously. For all age-classes, the beta parameter declined or remained constant with declining SNC severity (declining CLSA; Table 6), corresponding to a decrease in the height of the mode. The net effect for the youngest age-classes (1-, 2-, and 3-year-old age-classes) was therefore a shift downward in the mode of vertical distribution with improving stand health or decreasing SNC severity (Fig. 3). This trend was also observed for the ≥5-year-old foliage. However, because increasing SNC severity had opposing effects on vertical distribution of 4-year-old foliage, the net effect of SNC depended on the magnitude and direction of change in both FOLRET and CLSA.

Discussion

Foliage age-class structure

Several recent studies have yielded allometric equations for estimating absolute foliage mass or area by individual age-class at both the branch- and tree-level (Porté et al. 2000; Xiao and Ceulemans 2004; Shibuya et al. 2005). This type of approach worked well for *Pinus* species (Porté et al. 2000; Xiao and Ceulemans 2004), probably because they generally have fewer foliage age-classes on a given branch (Reich et al. 1995). In the Douglas-fir sampled for this study, branch-level allometric equations significantly overestimated the amount of foliage in all five age-classes when compared to a proportional allocation of estimated total mass to different age-classes. The constraint of estimating total branch foliage mass as a function of branch diameter and position in the crown prevented cumulative errors on the scale of individual age-classes. These errors may otherwise

Fig. 3. Estimated relative vertical distribution of foliage mass density (kg·m^{-1}) by 1-year (*a*, *b*); 2-year (*c*, *d*); 3-year (*e*, *f*); 4-year (*g*, *h*); and ≥5 (*i*, *j*) foliage age-classes for an average tree with differing Swiss needle cast severity (left) and plantation age (right).



have caused large over- or under-predictions at the branch level and biased the models describing vertical distribution of foliage mass within the tree. The inclusion of more branch-level variables such as diameter or length did not improve the predictive power of the model describing cumulative proportion of foliage by age-class. This result was consistent with those of other studies in western hemlock, Douglas-fir, and grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.; Kershaw and Maguire 1995).

Schoettle and Smith (1991) found that leaf longevity on individual branches did not differ between crown aspects after accounting for vertical location in the crown. The lack of crown aspect effect in Douglas-fir experiencing severe SNC was unexpected given that Manter et al. (2003*b*) found that SNC fungal colonization was consistently higher in the southern portion of the crown. Colonization was particularly high in branches with a southern exposure in the upper two-thirds of the crown, where needle retention declined by nearly 15% compared to a healthy tree. On the other hand, Manter et al. (2003*b*) were working in younger trees than the 10- to 60-year-old trees in this study. Furthermore, the influence of branch aspect on foliage amount and age-class distribution may have been accounted for by branch diameter. For a given location in the crown, tree size, and level of SNC, maximum branch diameters on the southern portion of the crown were significantly larger than those on the north.

Tree diameter, height, crown length, and age were previously identified as the best predictors for estimating the foliage amount by age-class (Porté et al. 2000; Xiao and Ceulemans 2004). Weiskittel (2003) found that crown surface area performed better as a predictor of foliage age-class structure in young Douglas-fir plantations; however, diameter, height, and crown length were more effective in the older trees of this study, probably in part due to a wider range of tree sizes than in young Douglas-fir plantations. Weiskittel (2003) also found that crown sparseness was a better predictor of total tree foliage mass and that foliage retention better described the relative foliage age-class structure. In the more comprehensive age range of Douglas-fir plantations investigated here, crown sparseness was related both to the total foliage mass on a tree and to the amount of foliage in each age-class, while foliage retention had predictive power only for the amount of foliage in the 3-, 4-, and ≥5-year-old foliage age-classes. These crown condition indices should therefore be considered complementary rather than mutually exclusive or interchangeable. Crown sparseness may be more integrative because it reflects degree of defoliation, tree social position, and probably site quality (Maguire and Kanaskie 2002), so its advantage in characterizing net crown condition may also make it less effective for isolating the effects of SNC alone.

Foliage age-class structure has rarely been assessed across a range of stand conditions. Previous research on foliage longevity indicates that foliage age structure is influenced by stand spacing (Kellomäki et al. 1980; Piene and Fleming 1996; Xiao 2003; Shibuya et al. 2005), site fertility (Gower et al. 1993), and exposure (Kajimoto 1993). Neither site index nor stand density had a significant effect on foliage age-class structure in this age range of Douglas-fir, although when the analysis is restricted to only the younger plantations these variables were identified as influential (Weiskittel 2003). Combinations of other variables such as tree size and crown condition may effectively capture the effects of site fertility and stand density. Comparison with previous work also indicates that younger plantations at both high and low levels of SNC have a greater proportion of their foliage in ≥5-year-old age-class (Weiskittel 2003), although the relative difference is quite small (Fig. 1). Needle longevity is generally positively correlated with tree age (Xiao 2003), possibly because of greater construction costs for needles on older trees (Apple et al. 2002). The changes in needle longevity observed for other species may occur at ages greater than 60 years in healthy Douglas-fir and is certainly complicated in this species by variation in local SNC severity.

Vertical foliage distribution

Tree size and local stand density (as reflected by crown ratio) were important determinants of relative vertical foliage distribution in previous studies (e.g., Maguire and Bennett 1996; Xu and Harrington 1998). Relatively little quantitative work, however, has been done on the vertical distribution of foliage by age-class. Conceptually, the vertical distribution of current-year foliage should be influenced primarily by the prevailing light conditions, while environmental factors other than light (e.g., water supply, nutrients) may become more important as the foliage ages (Kellomäki et al. 1980; Piene and MacLean 1999). Xiao and Ceulemans (2004) found that the mode of the vertical distribution for three foliage age-classes in young Scots pine (*Pinus sylvestris* L.) peaked near the crown midpoint, while Porté et al. (2000) indicated that the mode shifts downward with increasing foliage age in 26-year-old Maritime pine (*Pinus pinaster* Aït.), similar to the pattern observed in this study. On older (53-year-old) SNC-infested Douglas-fir in New Zealand, Kay (1978) found that young needles predominated in the upper crown and older foliage predominated in the lower crown; however, a well-defined maximum mass for each age-class was found in the mid-crown region, in contrast to the results described here for Douglas-fir in the Coast Range of Oregon. With increasing SNC severity, the modes of the youngest three age-classes shifted upwards, while the modes for 4- and ≥5-year-old foliage were located lower in the crown relative to that of healthy trees. This pattern was presumably a result of the biology of the fungus causing SNC, *Phaeocryptopus gaeumannii*. Maguire and Kanaskie (2002) speculated that reduced foliage retention in the upper and middle portion of the crown characterizing SNC might promote longer retention in the bottom of the crown, since more foliage would be illuminated above the light compensation point. However, Weiskittel (2003) found that stands with more severe SNC had significantly shorter crown lengths.

The mode of foliage distribution tends to move to higher relative positions in the crown with stand age (Hashimoto 1991; Kantola and Mäkelä 2004), as might be expected given the concurrent changes in stand height and canopy depth. A similar relative upward shift was found for each foliage age-class across the age range sampled in this study (cf. Weiskittel 2003). These changes, however, may be confounded with stand density manipulations and geographic location. An examination of the changes that occur in the stand-level vertical distribution of foliage would give a better test of the relative influence of stand density and plantation age.

Conclusions

Indices of crown condition often represent different aspects of crown structure and tree and stand health. In this study, mean foliage retention (FOLRET) and crown sparseness (CLSA) were more effective crown indices than crown density and color scores for explaining changes in age-class structure and vertical distribution of foliage on Douglas-fir with varying SNC severity. In particular, crown sparseness proved to be the most effective predictor of total foliage mass and relative age-class distribution, while foliage retention was more closely related to the vertical distribution of foliage. Crown sparseness takes into account the vertical packing of foliage and is more objectively measured than foliage retention (but not necessarily more accurately measured). On the other hand, a large amount of variation in foliage mass, its age-class structure, and its vertical distribution is left unexplained by the combination of foliage retention and crown sparseness. Crown structure is complex and difficult to measure, so it is important to keep in mind the specific aspects of crown structure that various indices are likely to reflect. Aspects of crown structure that are key to understanding and predicting growth loss mechanisms (age-class structure and vertical distribution) are not obvious from using either foliage retention or crown sparseness alone.

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