
Growth of Young Douglas-Fir Plantations Across a Gradient in Swiss Needle Cast Severity

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ABSTRACT: During the past decade, Swiss needle cast (SNC) damage has intensified in many Douglas-fir plantations in the Coast Range of Oregon, particularly along the immediate north coast. In plantations with severe symptoms, growth losses and reduced tree vigor are evident, but the magnitude of growth losses associated with varying intensities of damage is not known. A growth impact study was conducted in 1997 to quantify retrospectively the relationship between growth losses and visual symptoms in 10- to 30-yr-old Douglas-fir plantations in coastal northwestern Oregon, a population totaling 75,700 ha. A random sample of 70 Douglas-fir plantations was selected from the population and evaluated for Swiss needle cast severity. One 0.02 ha plot was destructively sampled in each plantation to reconstruct past height and basal area growth trends and to characterize foliage loss and distribution. The SNC "effect" was assessed by comparing growth of plantations with varying degrees of Swiss needle cast to growth of those that retained maximal amounts of foliage, after correcting for initial stand density, Douglas-fir growing stock, age, and site index. Of numerous possible SNC indices, mean needle retention (yr) explained the largest amount of variation in both basal area and top height growth. Prior to 1990, top height growth was similar across all plantations after correcting for site quality and plantation age; but, by 1992, top height growth losses appeared and were proportional to apparent foliage losses. In 1996, top height growth was reduced by up to 25% relative to plantations with little or no SNC. Basal area growth reductions began to appear around 1990, and in 1996 basal area growth of the most heavily damaged plantations was 35% less than the growth that would be expected in absence of SNC damage. The inferred volume growth loss for 1996 averaged 23% for the 75,700 ha target population, but this loss averaged as high as 52% for the most severely impacted plantations. *West. J. Appl. For.* 17(2):86–95.

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Approximately 2 1/2 million ha of commercial timberland in the Pacific Northwest are occupied by young stands (≤ 40 yr) of Douglas-fir, *Pseudotsuga menziesii* (Greg Latta and Darius Adams, pers. comm., Adams et al. 1992, Oswald et al. 1986). The growth, yield, and overall health of these plantations are tremendously important to the economy and environmental quality of Oregon and Washington. Unfortunately, Swiss needle cast (SNC) has recently emerged as a serious problem for many Douglas-fir plantations in coastal Oregon (Kanaskie and McWilliams 2000, Hansen et al. 2000). Although the disease was first observed in Europe after establishment of Douglas-fir plantations in Switzerland (Anonymous 1939, Boyce 1940), the fungus causing SNC, *Phaeocryptopus gaeumannii*, has since been recognized as endemic throughout the range of coast Douglas-fir (Anonymous 1939, Meinecke 1939, Boyce 1940). Only recently has concern arisen about the potential adverse effects of SNC within the natural range of Douglas-fir, primarily in response to the increasing severity of SNC symptoms observed over the last 6–10 yr. SNC is now regarded as such an urgent

problem that a major research effort has been launched to gain a better understanding of its basic biology, its geographic distribution, and its growth impact; much of this research is coordinated through the Swiss Needle Cast Cooperative (SNCC) at Oregon State University (Filip 2000).

Symptoms of SNC include premature loss of foliage, abundant fungal pseudothecia (fruiting bodies) on needles, yellowing of foliage, small average needle size, and apparent reduction in diameter and height growth. Although a range in symptom severity can be observed, the magnitude of growth loss associated with various foliar symptoms has been largely uncertain. Growth losses are quite apparent upon casual observation in severely impacted plantations but are more subtle in zones with fewer or less severe visual symptoms. The problem is particularly critical in young plantations (10–30 yr) since trees have not yet attained merchantable size and, under severe SNC, may never attain merchantable size given the observed declines in growth rate. Without the option of commercial harvest, re-establishment of productive stands consisting of resistant varieties of Douglas-fir or alternative species would constitute a net expense; yet, without direct intervention, significant yield losses may continue to accrue. Estimation of potential growth losses for varying levels of infection severity would allow economic analysis of management alternatives, ranging from no treatment to complete stand replacement. Without a quantitative link between easily observed SNC symptoms and tree growth, both local and regional growth impacts of SNC would be at best difficult to assess.

Damage from SNC has been frequently observed on Douglas-fir grown outside of its natural range, first, as mentioned above, in Europe in the early part of the century (Boyce 1940) and more recently in both Christmas tree plantations throughout North America (Michaels and Chastagner 1984, Bergdahl and French 1976, Merrill and Longnecker 1973) and timber stands in New Zealand (Hood and Kershaw 1975, Hood et al. 1990). Although some European research was motivated by concern about growth losses, relatively little work has been accomplished to date on estimation of growth impact, especially within the natural range of Douglas-fir and across a gradient in infection severity. Height growth of SNC-affected Douglas-fir in the Pacific Northwest has been estimated at 50–70% of normal, corresponding to as much as a 30% volume growth loss (Hansen et al. 2000). In New Zealand, basal area growth of stands experiencing “Douglas-fir decline” was as low as 50% of the basal area growth of stands exhibiting no decline (Beekhuis 1978). At that time, forest scientists in New Zealand noted that, although the Swiss needle cast fungus (*Phaeocryptopus gaeumannii*) was associated with declining Douglas-fir stands, it was uncertain as to whether this pathogen was the cause of the decline or an after-effect of other predisposing factors (see discussion of Decline in Growth, FRI 1978). In Finland, another needle cast disease of Douglas-fir caused by *Rhabdocline pseudotsugae* was reported to impose radial growth reductions that increased with increasing foliage loss, although losses fluctuated over time and ranged between 25–75% (Kurkela 1981).

Given the urgent concern about Swiss needle cast in coastal Oregon and the lack of knowledge about the range and variation in growth losses, a retrospective growth analysis was initiated in 1997 to meet the following objectives: (1) to screen various tree and foliage attributes that may serve as indices of SNC severity and corresponding growth losses; (2) to estimate current growth losses across the observed range in SNC severity; and (3) to gain some insight into past growth trends of plantations that are currently experiencing varying levels of SNC (while remaining cognizant of the limitations and pitfalls of retrospective analysis).

Methodology

Target Population

The target population for the growth impact study was defined by geographic location, species composition, and plantation age. The approximate geographic center of the region experiencing the most severe SNC was Tillamook, OR (N45°25', W123°50'). Rainfall in the study area varies from approximately 180 to 300 cm/yr, and January mean minimum and July mean maximum temperatures range from –2 to +2°C and from 20 to 28°C, respectively. Patterns in precipitation and temperature are strongly correlated with elevation and proximity to the coast. The stands of greatest concern were relatively young plantations, due both to the relative severity of symptoms that were observed and to the submerchantable stature of the stands. Hence, the target population for initial growth impact work was defined as: (1) Douglas-fir plantations between 10 and 30 yr of total age in 1996; and (2) Plantations located within 29 km of the coast, north of Newport (N44°35', W124°00') and south of Astoria (N46°10', W123°50') (see Figure 1).

A list of plantations meeting these criteria was assembled. Plantations were then selected from this list with probability proportional to area since potential growth losses were proportional to total plantation area. The target population included 4,504 plantations covering 75,929 ha, and the sample included 70 plantations covering 2,620 ha. Each plantation was assessed for SNC intensity and was measured intensively to establish the link between SNC ratings and growth loss.

Field Work

Stands were first visited and rated for SNC during March and April, 1997. A five-point transect was established from a random location along an access road. Sample points were separated by 15 m, resulting in a 75 m transect. Color attributes and needle retention were estimated on the two dominant or codominant Douglas-fir trees nearest to each sample point and on opposite sides of the transect line. Needle retention was estimated by dividing the live crown into thirds, with the base of the live crown defined as the lowest live branch, and by examining secondary or lateral branches on a primary or main branch in the center of each third. The average number of needle age classes present at time of sampling was estimated for each third of the live crown to the nearest 0.5 yr. Likewise, discoloration (yellowness) in each third of the live crown was rated on a scale of 0–3 for each



Figure 1. Locations of sample plantations included in the Swiss needle cast growth impact study.

tree, with 0 representing no discoloration and 3 representing the most severe discoloration. Slope, aspect, elevation, and other site information were also compiled for all plantations.

The third sample point on the sample transects was flagged, marked with a PVC stake, and subsequently used as the center of a 0.02 ha plot (radius = 8.01 m) on which all conifers and hardwoods were measured for dbh (diameter outside bark at 1.37 m, nearest 0.1 cm). The four Douglas-fir trees with the largest dbh and two with the smallest dbh were felled, as were the two Douglas-fir closest to the midrange of the diameter distribution. Each felled tree, with the exception of the two smallest Douglas-fir, was measured to the nearest 0.01 m for total height, height to live crown base, and annual cumulative height growth (height of each bud scale scar at or just above each annual branch whorl). Identification of annual whorls was verified by cutting the stem and counting rings below every fifth whorl. Two stem disks were removed from each of the felled Douglas-fir trees, one at breast

height and one at crown base. These disks were labeled and stored in a plastic bag for transport to the lab.

Finally, a sample branch was collected from the fourth largest Douglas-fir tree on each plot. This sample branch was identified as the southern-most branch in the fifth whorl from the top of tree. After measuring its diameter, the branch was cut from the tree flush with the stem, and one of the secondary branches in the third whorl down from the primary branch tip was removed, placed in a plastic bag, stored on ice for up to 4 days, then frozen in the lab. The remaining portions of the branch were placed in a plastic bag and transported to the lab for drying and weighing.

All initial field work was completed in the spring of 1997, prior to budbreak. Supplementary field work on a subset of plots was completed during the following summer (June–September, 1997). During this supplementary field work, the 0.02 ha plots at point 3 of the sample transects were revisited, and all standing live Douglas-fir trees were measured for height to crown base and total height (nearest 0.01 m), ignoring any 1997 leader growth. Past height growth (nearest 0.01 m) of the two smallest trees felled during the initial field work was also reconstructed from branch whorls and bud scale scars. An increment core was then removed from each standing Douglas-fir tree to estimate annual radial growth. 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. Four sapwood widths (nearest 0.5 mm) were recorded on the same two axes. Increment cores from the supplementary field work were likewise transported to the laboratory and measured for annual radial growth and sapwood width (nearest 0.5 mm).

Secondary branches were kept frozen until they could be analyzed for specific leaf area by measuring projected area (nearest 0.001 cm²) and dry weight (nearest 0.0001 g) of 50-needle subsamples of 1-, 2-, and 3-yr-old foliage separately. Pseudothecia of *P. gaeumannii* were also counted on 10 needles from each 50 needle subsample, and length of each of these 10 needles was recorded (nearest 0.1 mm). Pseudothecia counts represented the number of occluded stomates out of the centermost 100 in the second row to the right of the needle midrib, with the petiole pointing downward. Because each of these secondary branches was removed from the third whorl down from the branch tip, each contained three different age classes of shoots and needles.

The remaining branch samples were clipped by age class, dried, and separated into foliage and wood + bark. The samples were then redried for at least 24 hr and weighed (nearest 0.01 g).

Growth Reconstruction

Patterns in past basal area and height growth were reconstructed from the annual height increments and stem section

radial growth measurements. The cross-sections of heartwood and the entire stem both inside and outside bark were assumed to be elliptical in shape, and basal area growth and sapwood area were computed accordingly from cumulative radial growth and sapwood widths. In the case of single increment cores extracted from standing trees, cross-sections were assumed to be circular.

Initial height and height growth for each annual growth period were reconstructed for all felled Douglas-fir trees. Similarly, initial diameter outside bark (dob) and inside bark basal area growth for each annual growth period were estimated on all Douglas-fir trees from which a breast height disk or increment core was removed. Key stand-level variables were then computed for each plot, with the following assumptions: (1) No trees died from suppression mortality or were removed by thinning since the year in which the stands reached breast height; and (2) Relative basal area growth of other conifer and hardwood species was proportional to relative basal area growth of the sectioned and cored Douglas-fir trees on that plot.

The analysis was not expected to suffer seriously from the assumption of no mortality in these young plantations, since very little evidence of mortality, especially in Douglas-fir, was observed in these intensively managed plantations. However, landowner records indicated that at least half of the sampled plantations had been thinned. As a result, some of the past stand densities computed by back-dating diameters of trees alive in 1997 are underestimates. Possible ramifications of this latter bias in estimated stand densities are discussed briefly in the Conclusions section. It is also quite possible that the basal area of different species developed more rapidly or more slowly than Douglas-fir basal area, causing a respective over- or under-estimate of its contribution to total stand basal area in any one year. The assumption that all species conformed to the pattern in relative basal area growth observed in Douglas-fir measurement trees implied that

$$BA_{j,k} = relBA_{k-1} \cdot BA_{j,1996}$$

where

$BA_{j,k}$ = initial basal area for species j in year k , or at the end of year $k-1$ (m^2/ha)

$relBA_{k-1}$ = relative cumulative basal area growth of measured Douglas-fir trees through year $k-1$

$$= \frac{\sum^k \Delta BA_i}{\sum^{1996} \Delta BA_i} = \frac{\text{basal area in year } k}{\text{basal area in } 1996}$$

ΔBA_i = basal area growth of all Douglas-fir measure trees on the plot in year i ($m^2/ha/yr$)

$BA_{j,1996}$ = basal area for species j at end of 1996 (m^2/ha)

Stand density measures for the total stand and for species groups were computed as initial conditions for each annual growth period.

The four largest trees on each plot were assumed to represent the site tree component of the stands. Site index was estimated yearly for each site tree by solving Bruce's (1981) equations iteratively for each height-age pair. Plot site index at the start of each annual growth period was estimated as the mean of the four site trees.

Data Analysis

Height growth and basal area growth, the two major components of volume growth, were analyzed separately since it was evident early in the study that the onset of growth reductions in these two components was quite possibly asynchronous and that their relative magnitudes were different. Top height growth of the plots was related to a set of potential predictor variables, including potential height growth (given the estimate of site index from the previous year), basal area of Douglas-fir, basal area of competing species, various Swiss needle cast indices, elevation, and slope-aspect transformations (Stage 1976). The response variable was the logarithm of annual height growth, and models were screened in an all-subsets regression analysis for two separate datasets: all years combined, and 1996 only. Because the logarithmic transformation of height growth implied a multiplicative effect of predictor variables, interactions were implicit. A subset of models that exhibited biologically rational behavior, included Bruce's (1981) potential height growth, and provided strong predictive power was selected for further analysis.

Basal area growth data from all Douglas-fir measure trees, whether estimated from disks or cores, were combined to assess the "effect" of SNC. As with top height growth, all-subsets regression analyses were run to screen for the potentially most powerful variables for predicting the logarithm of plot basal area growth. Predictor variables included basal area of Douglas-fir, basal area of competing species, various Swiss needle cast indices, site index, and other site variables including elevation and slope-aspect transformations (Stage 1976). The most promising models were selected based on their ability to explain variation in basal area growth and on their consistency with current principles about stand density effects on tree and stand diameter growth. Screening runs were implemented on both the entire dataset representing all years combined and on the 1996 growth data only, but the final model was fitted on a year-by-year basis.

In the final models, the annual "effect" of SNC was assessed by computing percentage of expected growth for several levels of SNC and graphing this percentage of expected growth for all years between 1982 and 1996 in which the SNC index was a statistically significant variable in the regression model ($\alpha = 0.05$). In this approach, growth of the plantations with the least severe SNC ratings served as the expected growth rate, after correcting for the effects of other covariates in the regression model (that is, holding all other variables such as site quality, stand density, and age constant).

Table 1. Attributes of the 70 plots and 788 Douglas-fir trees sampled in 1996 for retrospective growth impact analysis.

| Attribute | Mean | SD | Min | Max |
|---|-------|-------|------|---------|
| Plot level | | | | |
| Douglas-fir basal area growth (m ² /ha/yr) | 1.72 | 0.81 | 0.49 | 3.95 |
| Douglas-fir basal area (m ² /ha) | 15.77 | 9.02 | 2.03 | 37.24 |
| Douglas-fir trees/ha | 688 | 347 | 148 | 1,927 |
| Douglas-fir quadratic mean dbh (cm) | 17.81 | 6.63 | 5.52 | 33.56 |
| Basal area in other conifers (m ² /ha) | 2.39 | 6.14 | 0 | 43.37 |
| % basal area in other conifers | 1.5 | 3.7 | 0 | 20.0 |
| Basal area in hardwoods (m ² /ha) | 1.09 | 2.63 | 0 | 15.31 |
| % basal area in hardwoods | 9.5 | 15.1 | 0 | 63.8 |
| Total basal area (m ² /ha) | 19.25 | 10.96 | 2.84 | 54.97 |
| Average breast-height age (yr) | 12.2 | 4.9 | 3.3 | 28.33 |
| Average foliage retention (yr) | 2.21 | 0.53 | 1.09 | 3.65 |
| Site index* (height at 50 yr, in m) | 41.0 | 5.1 | 24.4 | 52.1 |
| Conifer relative density [†] | 4.52 | 2.50 | 1.04 | 15.48 |
| Conifer stand density index ^{††} | 426.7 | 234.6 | 90.7 | 1,430.2 |
| Tree level | | | | |
| Dbh (cm) | 14.8 | 7.7 | 0.4 | 40.3 |
| Height (m) | 11.28 | 4.83 | 2.09 | 31.08 |
| Height to crown base (m) | 2.70 | 2.75 | 0 | 14.16 |
| Crown length (m) | 8.58 | 3.62 | 0.16 | 20.34 |
| Crown ratio (%) | 78.8 | 18.1 | 1.5 | 100 |

* Bruce (1981).

† Curtis (1982).

†† Reineke (1933); trees/ha at mean dbh of 25.4 cm.

Results

The 70 growth impact plots ranged between 8 and 30 yr of total age, and all were Douglas-fir plantations with varying amounts of naturally regenerated western hemlock (*Tsuga heterophylla*) and other conifer and hardwood species (Table 1). Basal area of other conifers averaged a little less than 2% of the total, and basal area of hardwoods averaged a little less than 10%, although maxima were 20 and 64%, respectively. In addition to variations in stand structure, sampled plantations covered a wide range in individual tree condition and SNC status (Tables 1 and 2). Many of the alternative SNC indices were correlated to some degree (Table 3), yet the implied symptoms probably reflect varying effects of the disease, from declining nutritional status of foliage (for example, yellowness and needle length) to premature foliage loss (for example, needle retention and percent foliage mass in 2-yr-old foliage).

In the final model for top height growth, expected top height growth (HG) was a function of current breast height age and site index (Bruce 1981). Site index for 1990 was

selected as the measure of site quality for all analyses in an effort to maximize the probability that this index was not depressed by the cumulative effects of SNC. Average years of foliage retention (*retx*) proved to be one of the best SNC indices among those tested for predicting height growth (Table 2), yielding the following final model:

$$\ln(\Delta H) = a_0 + a_1 \cdot HG + a_2 \cdot \ln(\text{retx}) \quad (1)$$

where

$\ln(\cdot)$ = natural logarithm

ΔH = annual top height growth (m/yr)

retx = average years of foliage retention

HG = Bruce's (1981) predicted top height growth (m)

$$0.3048 \cdot \ln(\text{hite} \cdot b_2 \cdot b_3 \cdot (\text{piage} + 13.5 - (SI_{90} / 0.3048) / 20)^{(b_3-1)})$$

piage = average initial breast height age at the start of the growth period

Table 2. Indices of Swiss needle cast considered in growth impact analysis.

| Index | Definition | Mean | Range |
|-------|--|-------|--------------|
| LEN1 | Ave. length of 1-yr-old needles (mm) | 23.4 | 13.9–30.9 |
| LEN2 | Ave. length of 2-yr-old needles (mm) | 24.2 | 16.9–33.6 |
| SLA1 | Specific leaf area of 1-yr-old needles (cm ² /g) | 69.6 | 56.5–96.7 |
| SLA2 | Specific leaf area of 2-yr-old needles (cm ² /g) | 61.1 | 46.5–94.0 |
| FM1 | Foliage mass on 1-yr-old shoots (g) | 92.6 | 7.74–255.70 |
| FM2 | Foliage mass on 2-yr-old shoots (g) | 50.0 | 0.50–143.18 |
| FM3 | Foliage mass on 3-yr-old shoots (g) | 20.7 | 0–90.38 |
| TFM | Foliage mass on 1-5-yr-old shoots (g) | 164.9 | 25.38–439.21 |
| PFM1 | Percent foliage mass in 1-yr-old needles | 58.7 | 17.5–98.9 |
| PFM2 | Percent foliage mass in 2-yr-old needles | 28.9 | 0.8–45.5 |
| PFM3 | Percent foliage mass in 3-yr-old needles | 11.2 | 0–38.4 |
| P1 | Pseudothecia count on 1-yr-old needles | 3.8 | 0–28.6 |
| P2 | Pseudothecia count on 2-yr-old needles | 34.8 | 0–80.2 |
| FBA | Ratio of branch foliage mass to branch basal area (g/mm ²) | 42.2 | 10.6–108.7 |
| YX | Yellowness | 1.28 | 0–2.9 |

Table 3. Pearson product-moment correlations among indices of Swiss needle cast (bold indicates statistical significance at $\alpha = 0.05$).

| | RETX | YX | LEN1 | LEN2 | SLA1 | SLA2 | FM1 | FM2 | FM3 | TFM | PFM1 | PFM2 | PFM3 | P1 | P2 | FBA |
|------|--------------|--------------|--------------|--------------|--------------|--------------|-------------|--------------|--------------|--------------|--------------|-------------|--------------|--------------|--------------|-----|
| RETX | 1 | | | | | | | | | | | | | | | |
| YX | -0.70 | 1 | | | | | | | | | | | | | | |
| LEN1 | -0.07 | 0.07 | 1 | | | | | | | | | | | | | |
| LEN2 | -0.04 | 0.07 | 0.70 | 1 | | | | | | | | | | | | |
| SLA1 | -0.08 | 0.03 | -0.40 | -0.25 | 1 | | | | | | | | | | | |
| SLA2 | -0.21 | 0.11 | -0.23 | -0.39 | 0.78 | 1 | | | | | | | | | | |
| FM1 | 0.35 | -0.25 | 0.38 | -0.27 | -0.50 | -0.52 | 1 | | | | | | | | | |
| FM2 | 0.43 | -0.34 | 0.32 | 0.46 | -0.29 | -0.43 | 0.75 | 1 | | | | | | | | |
| FM3 | 0.37 | -0.24 | 0.20 | 0.21 | -0.06 | -0.15 | 0.40 | 0.64 | 1 | | | | | | | |
| TFM | 0.44 | -0.32 | 0.37 | 0.36 | -0.39 | -0.47 | 0.92 | 0.92 | 0.69 | 1 | | | | | | |
| PFM1 | -0.22 | 0.20 | -0.02 | -0.28 | -0.20 | -0.02 | 0.07 | -0.48 | -0.64 | -0.29 | 1 | | | | | |
| PFM2 | 0.21 | -0.24 | 0.10 | 0.41 | 0.07 | -0.08 | 0.02 | 0.56 | 0.31 | 0.28 | -0.79 | 1 | | | | |
| PFM3 | 0.16 | -0.11 | 0.02 | 0.14 | 0.18 | 0.04 | -0.05 | 0.35 | 0.81 | 0.29 | -0.86 | 0.40 | 1 | | | |
| P1 | -0.36 | 0.34 | 0.02 | -0.06 | 0.26 | 0.44 | -0.11 | -0.24 | -0.37 | -0.23 | 0.35 | -0.19 | -0.38 | 1 | | |
| P2 | -0.39 | 0.30 | -0.01 | -0.09 | 0.32 | 0.45 | -0.19 | -0.31 | -0.43 | -0.32 | 0.37 | -0.18 | -0.42 | 0.75 | 1 | |
| FBA | 0.27 | -0.18 | 0.28 | 0.29 | -0.28 | -0.36 | 0.58 | 0.69 | 0.64 | 0.73 | -0.45 | 0.32 | 0.48 | -0.36 | -0.42 | 1 |

$hite =$

$$SI_{90} \cdot \exp(b_2 \cdot ((piage + 13.25 - (SI_{90} / 0.3048) / 20) b_3) - (63.25 - (SI_{90} / 0.3048) / 20) b_3)$$

$b_3 =$

$$- 0.447762 - 0.894427 \cdot ((SI_{90} / 0.3048) / 100) + 0.793548 \cdot ((SI_{90} / 0.3048) / 100)^2 - 0.171666 \cdot ((SI_{90} / 0.3048) / 100)^3$$

$b_2 =$

$$\ln(4.5 / (SI_{90} / 0.3048)) / ((13.25 - (SI_{90} / 0.3048) / 20) b_3 - (63.25 - (SI_{90} / 0.3048) / 20) b_3)$$

SI_{90} = Bruce's (1981) site index computed from plot data backdated to 1990 (m at 50 yr)

and a_0 , a_1 , and a_2 are regression parameters estimated from the data for each year of backdated height growth.

Across years, the regression model accounted for 14–63% of the variation in top height growth, and the foliage retention variable ($retx$) was statistically significant in 1992 and 1996 only. The plantations implied to be most severely impacted by SNC according to the foliage retention index ($retx$) were growing at only 75% of the rate observed in “unaffected” plantations in 1996; that is, growth was reduced 25%. Top height growth trends prior to 1992 appeared totally unrelated to the 1997 SNC ratings. The equation for 1996 was (parameter estimate standard errors in parentheses):

$$\ln(\Delta H) = -0.738497 + 1.426510 \cdot HG + 0.213098 \cdot \ln(retx) \\ (0.218829 \quad (0.646926) \quad (0.113089))$$

Approximately 14% of the variation in top height growth was accounted for by the model, and the root mean squared error was 0.221. Although foliage retention ($retx$) was statistically significant ($\alpha = 0.05$), its marginal effect accounted for only 5% of the original variation.

The final model for plot basal area growth contained features that were typical of growth and yield equations developed for pure even-aged plantations in other parts of the world (Clutter et al. 1983). Variables representing Douglas-fir growing stock (BA_{DF}), competition from other species (BA_{TOT}), and stand age ($BHAGE$) comprised the basic growth model, and the marginal effect of SNC was evaluated by including mean foliage retention:

$$\ln(\Delta BA) = c_0 + c_1 \cdot \ln(BA_{DF}) + c_2 \cdot \ln(BA_{TOT}) + c_3 \cdot BHAGE + c_4 \cdot \ln(retx) \quad (2)$$

where

$\ln(\cdot)$ = natural logarithm

ΔBA = Douglas-fir basal area growth for the plot ($m^2/ha/yr$)

BA_{DF} = Douglas-fir basal area (m^2/ha)

BA_{TOT} = total basal area (m^2/ha)

$BHAGE$ = average initial breast-height age (yr)

$retx$ = average foliage retention (yr)

and c_0 , c_1 , c_2 , c_3 , and c_4 are regression parameters estimated from the data for each year of backdated basal area growth.

Site index was not included in the model because it was never statistically significant at $\alpha = 0.05$. The basal area growth model accounted for 74–97% of the variation in plot basal area growth in any given year. As expected, basal area growth increased with higher initial Douglas-fir basal area (greater growing stock), but decreased with higher total basal area (competition from other species). Increasing initial plot age was associated with reduced growth, and growth also declined with a reduction in foliage retention. Those plantations with lower foliage retention in 1997 started to slow in basal area growth around 1990. Growth losses have been as high as 48% relative to the expected growth for plantations with a maximum foliage retention of 3.65 yr; for example, in 1992, plantations with only a single age class of needles ($retx = 1$) grew 52% of the basal area expected for similar plantations with “normal” foliage retention ($retx = 3.65$ yr). The equation for 1996 was (parameter estimate standard errors in parentheses):

Table 4. Estimated volume growth losses 1990 through 1996 by level of 1996 foliage retention.

| Foliage retention in 1996 (yr) | Estimated % volume growth loss by year | | | | | | | |
|-----------------------------------|--|------|------|------|------|------|------|----------------|
| | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | Ave. 1990–1996 |
| 3.65 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3.0 | 8 | 8 | 13 | 7 | 7 | 5 | 10 | 8 |
| 2.5 | 15 | 15 | 23 | 13 | 13 | 9 | 18 | 15 |
| 2.0 | 23 | 23 | 35 | 20 | 20 | 13 | 27 | 23 |
| 1.5 | 32 | 32 | 47 | 28 | 28 | 19 | 37 | 32 |
| 1.0 | 42 | 42 | 60 | 38 | 37 | 27 | 49 | 42 |

$$\ln(\Delta BA) = -0.082462 + 1.014086 \cdot \ln(BA_{DF}) - 0.404472 \cdot \ln(BA_{TOT})$$

$$(0.17856986) \quad (0.09746455) \quad (0.10595974)$$

$$-0.096863 \cdot BHAGE + 0.300946 \cdot \ln(retx)$$

$$(0.01007467) \quad (0.13186040)$$

Approximately 74% of the variation in 1996 basal area growth was accounted for by the model, yielding a root mean squared error of 0.257. Although foliage retention was statistically significant ($\alpha = 0.05$), its marginal effect accounted for only 2% of the original variation.

Volume growth is controlled predominantly by basal area growth and height growth. Although stem form changes are possible due to the reduced foliage density imposed by SNC, they would be very subtle compared to changes induced by large differences in live crown length as may result, for example, from variation in stand density. Hence, changes in stem form would not substantially change the growth loss estimated from diameter and height growth effects alone. Taking the values of 75.9 and 67.7% for the percentages of

expected height and basal area growth, respectively, associated with the most severe SNC symptoms observed in 1997, the corresponding volume growth for 1996 was estimated at approximately 51% of expected growth:

$$\Delta V = k \cdot \Delta BA \cdot \Delta H$$

$$= k \cdot (0.677 \cdot \Delta BA_{exp}) \cdot (0.759 \cdot \Delta H_{exp})$$

$$= 0.513 \cdot k \cdot \Delta BA_{exp} \cdot \Delta H_{exp}$$

where ΔBA_{exp} and ΔH_{exp} are expected plot basal area growth and top height growth, respectively, at maximum foliage retention. In other words, plantations retaining only a single age class of needles were estimated to have experienced a 49% volume growth loss in 1996 (Table 4). Growth losses prior to 1990 are assumed to have been negligible based on the retrospective analysis, since neither basal area growth nor top height growth varied significantly with foliage retention values measured in 1997. Cubic volume growth losses estimated for individual years between 1990 and 1996 ranged from 27 to 60% of expected growth (Figure 2 and Table 4).

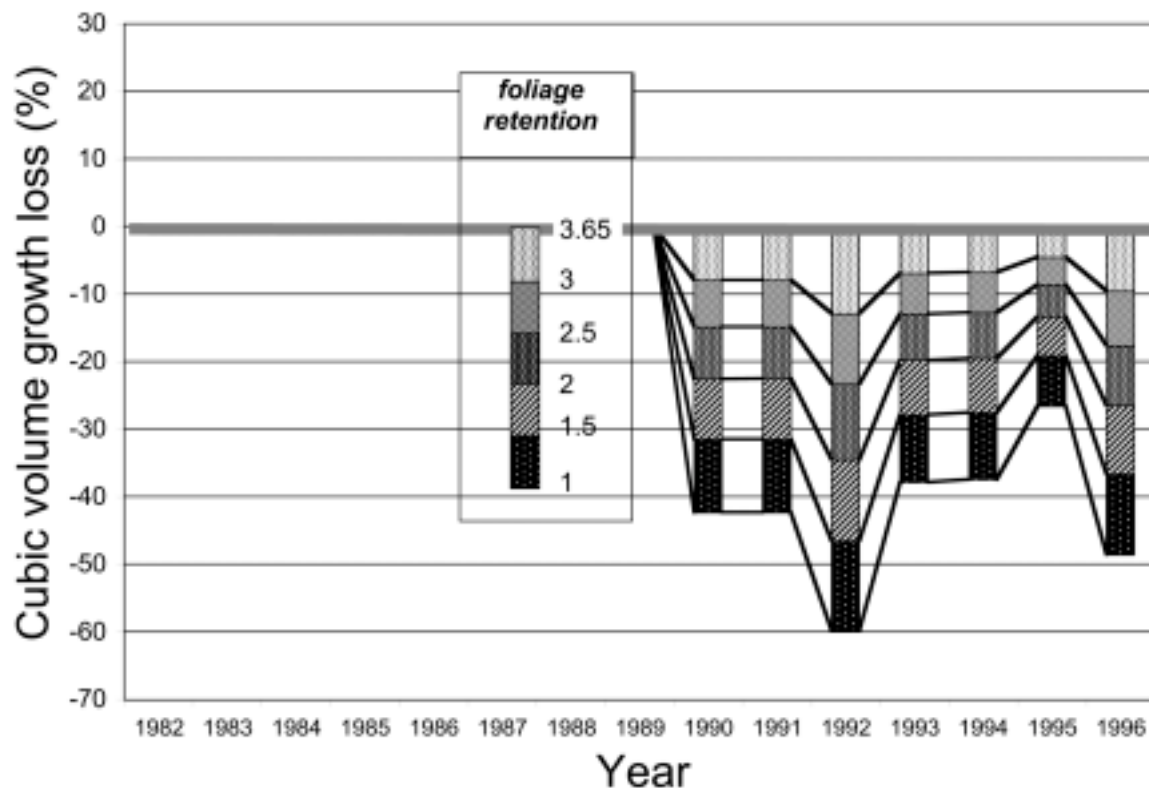


Figure 2. Trends in estimated cubic volume growth loss (%) for the range in average foliage retention (yr) observed on 70 sample plots in 1996. Growth was not significantly related to foliage retention in any year prior to 1990.

Discussion

Different SNC indices no doubt reflect the various mechanisms by which *P. gaeumannii* exerts its growth impact. For example, variables such as mean foliage retention are expected to represent the effects of foliage loss in the growth analysis, while pseudothecia counts are expected to signal direct physiological disruption of photosynthesis by the presence of fungal hyphae or pseudothecia (Manter et al. 2000). As a result, SNC indices cannot be considered mutually exclusive. On the other hand, the various indices are correlated with one another, complicating interpretation of any one index with respect to a single associated mechanism. For example, foliage retention is correlated, but not perfectly, with relative and absolute foliage mass by age class, but it is also correlated with pseudothecia counts; hence, foliage retention cannot be strictly interpreted as a surrogate for foliage amount. Results from this analysis do indicate that loss of foliage was the predominant mechanism by which SNC reduces growth but also that foliage retention may perform better than actual foliage mass variables because it also serves as an effective integrator of numerous other mechanisms. The relatively strong correlations between foliage retention and three other groups of variables—yellowness, foliage mass in the three age classes, and pseudothecia counts—underscore the difficulty of isolating the effects of specific mechanisms in this type of observational study.

Several assumptions must be considered when interpreting results of the growth analysis. Some of these assumptions are a direct consequence of the retrospective design, while others are simplifications necessary for initial interpretation of results. In retrospective analyses, estimating past stand conditions such as basal area of individual species can be particularly tenuous given the inevitable uncertainty in past mortality. This uncertainty is further augmented by incomplete information on past thinning treatments. Departures from either the assumption of no mortality or the assumption of no recent thinning would lead to underestimates in past stand density and, hence, to lower growth rates than would be expected for the residual Douglas-fir trees. When hindcasting basal area of other species, rates of basal area growth that differ substantially from Douglas-fir could either lower or raise Douglas-fir growth relative to expectations, depending on whether basal area of those species developed earlier and slower or later and faster, respectively, than Douglas-fir. Probably the most glaring weakness of the retrospective design is the fact that SNC condition could only be assessed in the spring of 1997. No information is available on how long a given plantation has had SNC, how quickly SNC may have increased to its present level, or the degree to which SNC severity may have fluctuated over the past several decades at a given site. As a result, the growth trends described are conditional on the final SNC level in 1997 rather than on initial SNC level at the beginning of a growth period.

Other potentially problematic assumptions in the analysis do not necessarily arise from the retrospective nature of the study. Perhaps the most influential assumption in the growth analysis is that all variation in foliage retention is a direct result of needle cast caused by *P. gaeumannii*. Surprisingly

little is known about the natural variation of needle retention on Douglas-fir. SNC severity may be confounded with site or other factors contributing to reduced tree vigor, although *P. gaeumannii* and other foliar fungi likely mediate the effect of site on foliage retention virtually everywhere. Although conventional site descriptors were included in the analysis, site quality is complex in both a static and dynamic sense and, hence, may not be well-represented simply by site index and slope-aspect transformations. Furthermore, site index is notoriously difficult to assess in young plantations because of the influence of intensive silvicultural treatments and the large variance associated with predicting height at age 50 yr from height at very young ages.

Douglas-fir in the Coast Range of Oregon is thought normally to hold 4 to 5 yr of foliage, yet none of the plantations sampled in the SNC growth impact study held foliage longer than 4 yr. On eight sites in the Coast Range and Cascade foothills, Mitchell (1974) only rarely found young Douglas-fir with more than 5 yr of needles, yet frequently observed 7 yr of needles on older trees. Although this finding suggests that foliage retention may be confounded with tree age, the extent to which other differences, such as variation in nutrient availability, may have influenced the results is not clear. It is important to note that many if not most of the young trees in his study were essentially open-grown, while the branches on the older tree that held 7 yr of needles were apparently shaded. Standardization of foliage retention ratings by crown thirds, as applied in the SNC growth impact study, may therefore be quite important. Similarly, inclusion of stand and tree covariates is essential in determining the relationship between the ratings and growth behavior.

In contrasting studies from British Columbia, Brix (1981) documented at least 6 yr of foliage retention on 24-yr-old Douglas-fir at Shawnigan Lake, and Silver (1962) found foliage up to 10 yr old on four 80-yr-old Douglas-fir trees near Victoria. Foliage retention in other species has been found to be correlated with nutritional status (Balster and Marshall 2000), water availability (Raison et al. 1992), and various other environmental factors (Reich et al. 1996). The assumption applied in the SNC analysis, specifically that 3.65 yr was the maximum background retention for the study population, could easily be an underestimate of the healthy condition, in turn leading to underestimates of growth loss. Clearly, greater understanding of foliage dynamics in Douglas-fir and other species would be very helpful for more accurately assessing this type of needle cast disease.

Although 90% of the foliage on trees examined by Silver (1962) consisted of 5-yr-old or younger needles, the amounts of 6- and 7-yr-old foliage were considerable. Given the relatively low photosynthetic efficiency of older foliage, the relative importance of this older foliage to each tree's total photosynthetic capacity is probably low (Brix 1971, Woodman 1971, Salo 1974). Woodman (1971) measured net photosynthetic rates ($\text{mg CO}_2/\text{g/h}$) for 1-, 2-, 3-, and 4-yr-old needles that were 72, 50, 30, and 12% of the rates observed for current foliage in Douglas-fir. In a growth modeling context, Mitchell (1975) assumed that 2-, 3-, 4-, and 5-yr-old foliage had relative photosynthetic efficiencies that were 86, 75, 63, and

53%, respectively, of 1-yr-old foliage. These efficiencies were incorporated into weights applied to conceptual shells of crown volume representing relative amount of foliage by age class and yielded reasonable growth predictions. In contrast, others have found the relationship between measured assimilation rates over short periods and cumulative diameter or height growth to be rather ambiguous (e.g., Sulzer et al. 1993).

Artificial defoliation studies seem to support the relatively greater importance of younger foliage, although many of these studies do not distinguish between differences in total amount of foliage and net photosynthetic rates among the age classes. For example, Linzon (1958) removed entire age classes of needles from small saplings of eastern white pine (*Pinus strobus*) and then monitored growth over two subsequent growing seasons. Based on both diameter and height growth, he concludes that 1-yr-old foliage in white pine is more important to growth than current or 2-yr-old foliage. However, probable differences in the total amount of needles in each age class were not addressed, making it difficult to assess the relative influence of net assimilation rate. Also, diameter growth rather than basal area growth was analyzed, with no correction for initial tree diameter. To the extent that we can extrapolate from eastern white pine to Douglas-fir, the treatment in which 2-yr-old foliage was removed and the treatment in which both 2-yr-old and 1-yr-old foliage were removed (leaving current foliage) would mimic patterns of foliage loss from Swiss needle cast. For these treatments, the growth reductions relative to control trees were 55 and 91%, respectively, for basal area growth (estimated from the diameter and diameter growth averages presented), and 45 and 64%, respectively, for height growth. As was the case for Swiss needle cast responses, basal area and height growth responded differently to the defoliation treatments. Osman and Sharrow (1993) similarly demonstrated a relative insensitivity of height growth to artificial defoliation of current-year needles, although basal diameter growth did decline continuously with increasing intensity of defoliation.

In both the top height and basal area growth analyses, pseudothecia counts (P1 and P2) were not able to account for a significant portion of growth variability when other SNC indices were already in the models. This result may not be too surprising given that a majority of the growth loss can probably be attributed to premature foliage loss rather than to direct effects of the fungus on surviving foliage and secondarily to the fact that pseudothecia counts were significantly correlated with foliage retention. Some other indices performed as well as or slightly better than average foliage retention, for example, the percent of total foliage mass in 2-yr-old foliage (PFM2) for top height growth and percent of total foliage mass in 1-yr-old foliage (PFM1) for basal area growth; however, given the meager gain from these variables and the fact that destructive sampling is required to estimate them, foliage retention was judged preferable from a practical standpoint. By convention, SNC is assessed just prior to budbreak (approximately May 1 in the Coast Range of Oregon), primarily because discoloration reaches its peak during this period and because foliage retention is typically

at its lowest; hence, SNC is maximally detectable from both the ground and air. Similarly, because the range in indices such as foliage retention tends to be maximal, spring sampling has the greatest potential for discriminating among stands with varying levels of SNC. However, this sampling strategy also underscores the fact that foliage retention is only an index of SNC rather than an estimate of foliage quantity available for photosynthesis during the growing season.

Finally, it is important to note that the growth losses associated with the observed level of foliage retention in 1997 have fluctuated over the 7 yr period (1990–1996) during which this SNC index was significantly correlated with growth. Growth losses after 1996 are therefore likely to vary as well, because of interactions with annual weather fluctuations, the cumulative effects of past losses in foliage and growth vigor, and the anatomical and physiological changes imposed by the disease.

Conclusions

1. Past basal area growth losses in Douglas-fir plantations with the most severe SNC in 1997 were as high as 48%, and basal area growth reductions appeared to have started in 1990.
2. Past top height growth losses in Douglas-fir plantations with the most severe SNC in 1997 were as high as 25%; significant top height growth reductions appeared to have started in 1992.
3. Plantations with the most severe SNC in 1997 lost on average 49% of their potential volume growth in 1996.
4. Failure to detect statistically significant SNC effects prior to 1990 may reflect the recent emergence of SNC as a primary determinant of growth; however, the following possible artifacts of the applied retrospective approach cannot be totally dismissed:
 - a. Uncertainty in reconstructed initial stand conditions for annual growth periods;
 - b. Uncertainty and possible changes in intensive plantation management practices that were not accounted for in the present analysis;
 - c. Lack of any knowledge about SNC intensities prior to the spring of 1997, and possible shifts in SNC intensity in any one plantation over time;
5. Thinning effects have not been addressed explicitly in the analyses, but because most of the plantations were thinned within the last 12 yr, the reconstructed initial stand densities almost certainly were underestimates. It is also possible that the thinnings could have promoted a temporary decline in stand vigor to some degree (thinning shock, *sensu* Harrington and Reukema 1983) or an alteration in microclimate, thereby predisposing Douglas-fir at least temporarily to *P. gaumannii* and SNC under the prevailing climatic conditions and inoculum levels. If so, the expected growth based on a given site index estimate would be too low, and growth loss would

be underestimated. Conversely, SNC may have made the trees more sensitive to weather fluctuations.

6. Height and diameter growth of stands exhibiting severe SNC symptoms were tested only against those stands in the sample with no apparent symptoms, that is, those with the longest needle retention. Needle retention is likely influenced by factors other than SNC, so the relative effect of SNC per se on growth as estimated in this analysis is tentative.

With respect to this last conclusion, SNC growth impacts would be additive to other (positive or negative) departures of the “unaffected” plantations from a given landowner’s growth expectations, regardless of the cause of the departures or the source of the expectation.

Literature Cited

- ADAMS, D.M., R.J. ALIG, D.J. ANDERSON, J.A. STEVENS, AND J.T. CHMELIK. 1992. Future prospects for western Washington’s timber supply. Coll. of For. Resour., Univ. of Washington, Seattle. Inst. of For. Resour. Contrib. No. 74. 201 p.
- ANONYMOUS. 1939. The Swiss leaf-cast of Douglas-fir. For. Abstr. 1:69–70.
- BALSTER, N.J., AND J.D. MARSHALL. 2000. Decreased needle longevity of fertilized Douglas-fir and grand fir in the northern Rockies. *Tree Physiol.* 20:1191–1197.
- BEEKHUIS, J. 1978. Growth decline in Douglas-fir. Pp. 119–125 in *A review of Douglas-fir in New Zealand*. James, R.N., and E.H. Bunn (eds). FRI Symp. No. 15, For. Res. Inst., Rotorua, NZ.
- BERGDAHL, D.R., AND D.W. FRENCH. 1976. Swiss needlecast of Douglas-Fir in Minnesota. *Plant Dis. Rep.* 60:148.
- BOYCE, J.S. 1940. A needle-cast of Douglas-fir associated with *Adelopus gaumanni*. *Phytopathology* 30:649–659.
- BRIX, H. 1971. Effects of nitrogen fertilization on photosynthesis and respiration in Douglas-fir. *For. Sci.* 17:407–414.
- BRIX, H. 1981. Effects of thinning and nitrogen fertilization on branch and foliage production in Douglas-fir. *Can. J. For. Res.* 11:502–511.
- Bruce, D. 1981. Consistent height-growth and growth-rate estimates for remeasured plots. *For. Sci.* 27:711–725.
- CLUTTER, J.L., J.C. FORTSON, L.V. PIENAAR, G.H. BRISTER, AND R.L. BAILEY. 1983. *Timber management: A quantitative approach*. Wiley, New York. 333 p.
- CURTIS, R.O. 1982. A simple index of stand density for Douglas-fir. *For. Sci.* 28:92–94.
- FILIP, G.M. 2000. Swiss Needle Cast Cooperative Annual Report. For. Res. Lab. Coll. of For., Oregon State Univ., Corvallis, OR. 52 p.
- FOREST RESEARCH INSTITUTE. 1978. Discussion on decline in growth. P. 23–36 in *A review of Douglas-fir in New Zealand*, James, R.N., and E.H. Bunn (eds). FRI Symposium No. 15. For. Res. Inst., Rotorua, NZ.
- HARRINGTON, C.A., AND D.L. REUKEMA. 1983. Initial shock and long-term stand development following thinning in a Douglas-fir plantation. *For. Sci.* 29:33–46.
- HANSEN, E.M., J.K. STONE, B.R. CAPITANO, P. ROSSO, W. SUTTON, L. WINTON, A. KANASKIE, AND M. MCWILLIAMS. 2000. Incidence and impact of Swiss needle cast in forest plantations of Douglas-fir in coastal Oregon. *Plant Dis.* 84:773–778.
- HOOD, I.A., AND D.J. KERSHAW. 1975. Distribution and infection period of *Phaeocryptopus gaeumannii* in New Zealand. *N.Z. J. For. Sci.* 5(2):201–208.
- HOOD, I.A., C.J. SANDBERG, C.W. BARR, W.A. HOLLOWAY, AND P.M. BRADBURY. 1990. Changes in needle retention associated with the spread and establishment of *Phaeocryptopus gaeumannii* in planted Douglas-fir. *Eur. J. For. Path.* 20:418–429.
- KANASKIE, A., AND M. MCWILLIAMS. 2000. 2000 Swiss Needle Cast Aerial Survey. Oregon State Dep. of For., Salem. 3 p.
- KURKELA, T. 1981. Growth reductions in Douglas fir caused by Rhabdocline needle cast. *Comm. Inst. For. Fenn.* 102:1–16.
- LINZON, S.N. 1958. The effect of artificial defoliation of various ages of leaves upon white pine growth. *For. Chron.* 34:49–56.
- MANTER, D.K., B.J. BOND, K.L. KAVANAGH, P. ROSSO, AND G.M. FILIP. 2000. Timing and mechanism of impact of the Swiss needle cast fungus, *Phaeocryptopus gaeumannii*, on Douglas-fir needle gas exchange and rubisco activation. *New Phytologist* 148:481–491.
- MEINECKE, E.P. 1939. The Adelopus needle cast of Douglas fir on the Pacific coast. *Cal. Dep. of Natur. Resour., Div. of For. Sacramento.* 6 p.
- MERRILL, W., AND J. LONGNECKER. 1973. Swiss Needlecast of Douglas-fir in Pennsylvania. *Plant Dis. Rep.* 57:984.
- MICHAELS, E., AND G.A. CHASTAGNER. 1984. Distribution, severity, and impact of Swiss needle cast in Douglas-fir Christmas trees in western Washington and Oregon. *Plant Dis.* 68:939–942.
- MITCHELL, R.G. 1974. Estimation of needle populations on young, open-grown Douglas-fir by regression and life table analysis. *USDA For. Serv. Res. Pap. PNW-181.* 14 p.
- MITCHELL, K.J. 1975. Dynamics and simulated yield of Douglas-fir. *For. Sci. Monogr.* 17. 39 p.
- OSMAN, K.A., AND S.H. SHARROW. 1993. Growth response of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) to defoliation. *For. Ecol. Manage.* 60:105–117.
- OSWALD, D.D., F. HEGYL, AND A. BECKER. 1986. The current status of coast Douglas-fir timber resources in Oregon, Washington, and British Columbia. P. 26–31 in *Douglas-fir: Stand management for the future*, Oliver, C.D., D.P. Hanley, and J.A. Johnson (eds.). Coll. of For. Resour., Univ. of Washington, Seattle. Inst. of For. Resour. Contrib. No. 55.
- RAISON, R.J., P.K. KHANNA, M.L. BENSON, B.J. MYERS, R.E. MCMURTRIE, AND A.R.G. LANG. 1992. Dynamics of *Pinus radiata* foliage in relations to water and nitrogen stress: I. Needle loss and temporal changes in total foliage mass. *For. Ecol. Manage.* 52:159–178.
- REICH, P.B., J. OLEKSYN, J. MODRZYNSKI, AND M.G. TJOELKER. 1996. Evidence that longer needle retention of spruce and pine populations at high elevations and high latitudes is largely a phenotypic response. *Tree Physiol.* 16:643–647.
- REINEKE, L.H. 1933. Perfecting a stand-density index for even-aged forests. *J. Agric. Res.* 46:627–638.
- SALO, D.J. 1974. Factors affecting photosynthesis in Douglas-fir. Ph.D. thesis, Univ. of Washington, Seattle.
- SILVER, G.T. 1962. The distribution of Douglas-fir foliage by age. *For. Chron.* 38:433–438.
- STAGE, A.R. 1976. An expression for the effect of aspect, slope, and habitat type on tree growth. *For. Sci.* 22:457–460.
- SULZER, A.M., M.S. GREENWOOD, AND W.H. LIVINGSTON. 1993. Early selection of black spruce using physiological and morphological criteria. *Can. J. For. Res.* 23:657–664.
- WOODMAN, J.N. 1971. Variation of net photosynthesis within the crown of a large forest-grown conifer. *Photosynthetica* 5:50–54.