



The effect of within-stand variation in Swiss needle cast intensity on Douglas-fir stand dynamics



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ABSTRACT

Swiss needle cast (SNC) is a foliar disease of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) caused by the ascomycete *Phaeocryptopus gaeumannii* (Rohde) Petrak. The number of annual needle cohorts retained by a tree indicates SNC severity and associated growth losses. In previous studies growth losses have been predicted on the basis of plot-level foliage retention, and plot-level growth multipliers have been uniformly applied to all trees within a stand to simulate tree growth. In this analysis, the effects of within-stand variation in foliage retention on individual-tree growth impact and implied stand dynamics were analyzed. Models describing diameter increment of Douglas-fir were developed based on three different foliage retention ratings: (1) plot-level foliage retention; (2) tree-level foliage retention; and (3) a combination of plot-level foliage retention and the deviation of tree-level from plot-level foliage retention. Foliage retention at both the plot-level and tree-level was positively correlated with diameter increment, and a significant amount of additional variation in diameter growth was explained by the deviation of individual-tree foliage retention from the plot-level average. The SNC “effect” was assessed by comparing growth of trees with varying degrees of Swiss needle cast to growth of those that retained maximal amounts of foliage. Across all plots in the sampled population, the most severely affected dominant or co-dominant trees exhibited 30% diameter growth loss relative to trees of similar crown position with minimal SNC symptoms. Within a plot, diameter growth averaged about 12% higher on trees with the highest foliage retention relative to trees with the lowest foliage retention, implying that SNC intensifies stand differentiation. Rather than responding to SNC with proportionally uniform growth losses within a plot, these results suggest that individual trees tolerate or resist the disease differentially. Foliage retention should therefore be used as a criterion for selecting trees for removal during thinning operations in Douglas-fir stands with moderate to severe SNC.

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1. Introduction

Swiss needle cast (SNC) is a foliar disease of Douglas-fir (*Pseudotsuga menziesii*) caused by the ascomycete *Phaeocryptopus gaeumannii* (Hansen et al., 2000). This pathogen causes premature loss of older foliage, resulting in needle longevity of only one year in the most severe cases, relative to a maximum of approximately four years in unaffected plantations of similar age and geographic location (Hansen et al., 2000; Maguire et al., 2002). Over the past 20 years, the Swiss needle cast epidemic in the Oregon Coast Range has significantly lowered productivity in affected Douglas-fir forests (Hansen et al., 2000; Maguire et al., 2002; Black et al.,

2010). Aerial surveys conducted by the Oregon Department of Forestry annually since 1996 have detected fluctuating but gradually increasing areas in coastal Oregon with detectable SNC symptoms, amounting to 212,265 ha in 2013 (Kanaskie and McWilliams, 2013). Fruiting bodies of the fungal pathogen interfere with foliage gas exchange by physically blocking Douglas-fir stomata, thereby reducing or halting photosynthesis and leading to premature needle abscission (Manter et al., 2005). The mechanisms leading to growth decline of Douglas-fir include loss of photosynthetic surface area (Weiskittel et al., 2006) and physiological disruption of surviving foliage (Manter et al., 2005).

In plantations with severe symptoms of SNC, growth losses and reduced tree vigor have been evident (Maguire et al., 2002). Maguire et al. (2011) found that maximum periodic annual growth losses in cubic volume ranged between 36% and 59% in north coastal Oregon among four separate growth periods between

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1998 and 2008. In New Zealand, Douglas-fir enjoyed a disease-free period for a number of years after its introduction, providing a basis for estimating growth reductions after the appearance of SNC in 1959. Kimberley et al. (2011) estimated that average growth loss reached 25% for mean top height increment, 27% for basal area increment, and 32% for stem volume increment since 1959. Black et al. (2010) assessed the impacts of SNC by tree-ring analysis of mature Douglas-fir and western hemlock trees in the western Oregon Coast Ranges, concluding that radial growth was reduced by as much as 85% since 1984.

The negative effects of SNC-imposed reductions in foliage retention on Douglas-fir growth is well established, but most studies to date have quantified this relationship at the plot-level. To our knowledge the effects of tree-to-tree variation in foliage retention on stand dynamics and relative tree growth rates have not been quantified. Johnson (2002) observed variation in family tolerance to SNC in 11-year-old Douglas-fir progeny, but foliage retention was not a significant predictor of diameter or height growth. However, foliage retention was measured as the percentage of 2-yr-old or 3-yr-old needles rather than the number of retained annual needle cohorts (Johnson, 2002).

The question of whether within-stand variation in foliage retention induced by SNC has altered stand dynamics by differential effects on diameter increment has not been addressed directly. However, a tree-level analysis of diameter growth within commercially-thinned stands infected with SNC found marginally significant evidence of an interaction between foliage retention and tree diameter, suggesting that larger diameter trees maintain a higher percentage of their full growth potential than smaller trees as foliage retention decreased (Mainwaring et al., 2005). Whether smaller trees had lower levels of foliage retention than the larger trees in the same stand is unknown, leaving open the question of whether variation in foliage retention within a stand influences stand dynamics.

The goal of this study was to gain a better understanding of stand dynamics within SNC-infected stands, particularly by quantifying the effects of SNC on any departures from normal growth differentiation patterns among individual trees. The rate and intensity of these departures would have implications for the timing of thinnings and the selection of trees for removal. Similarly, shifts in the intensity of differentiation would have implications for growth and yield projections, harvest schedules, and harvested tree and log dimensions. The specific objective of this study therefore was to test the hypothesis that tree-to-tree variation in foliage retention (SNC severity) has intensified differentiation of Douglas-fir growth rates. If this hypothesis proves correct, then tree-level foliage retention should account for significantly more of the variation in tree growth than plot-average foliage retention, and the dynamics of SNC-impacted stands are characterized by more extreme differentiation in growth rate and size distribution than unimpacted stands. Three steps were followed in pursuit of this objective: (1) separate diameter increment models were developed for Douglas-fir based on plot-level versus individual tree-level foliage retention; (2) diameter increment models were developed for Douglas-fir that included both plot-level foliage retention and the deviation of individual-tree retention from this plot-level retention; and (3) the relative proportion of variation in Douglas-fir diameter increment explained by plot-level foliage retention, tree-level foliage retention, and the combination of plot-level foliage retention and tree-level deviations from the plot average were quantified and assessed graphically.

2. Methods

The target population for the Swiss Needle Cast Cooperative (SNCC) Growth Impact Study was 10- to 30-yr-old Douglas-fir

plantations in north coastal Oregon (Maguire et al., 2002, 2011). A list of all 10- to 30-yr-old Douglas-fir stands was first compiled in 1996, with geographic bounds defined by Astoria to the north (N46°11', W123°50'), Newport to the south (N44°38', W124°04'), the Pacific Ocean to the west (W124°05'), and the crest of the Oregon Coast Ranges to the east (W123°30'). Over the last 40 years in this region, the mean January minimum temperature was 0 °C and the mean July maximum temperature was 25 °C. Total annual precipitation averaged 150–300 cm, with approximately 70% of the total falling between October and March.

A set of 76 stands was randomly selected from this list with probability proportional to area. The selected sample stands represented a range of SNC severity indicated by a minimum plot-level foliage retention of 1.01 years and a maximum of 3.85 years. The assumption made in this analysis was that SNC was the primary influence on foliage retention. Other factors known to influence foliage retention (Maguire et al., 2011) were controlled to some degree by specifying the target population, as well as by including the covariates described below.

A single, permanent plot was established in each sampled stand in the late winter/early spring of 1998. Plots were square, 0.08 ha in area (31.7 × 31.7 m), and centered on the fifth point of an ODF (Oregon Department of Forestry) transect established in spring 1997 (retrospective plots reported by Maguire et al. (2002) were centered on the third point). On each measurement plot, all trees with diameter at breast height (dbh) greater than 4 cm were tagged and measured (nearest 0.1 cm) at a height of 1.37 m. In addition, at least 40 Douglas-fir (largest 10 and smallest 4 by dbh, and the remaining 26 evenly distributed across the dbh distribution) were measured for total height (nearest 0.01 m) and height to crown base (nearest 0.01 m) at time of plot establishment. After two, four, and six growing seasons, all trees were remeasured for dbh, and all undamaged trees from the original height subsample were remeasured for total height and height to crown base. Some plots contained a significant amount of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), as well as various broad-leaved species, most commonly cascara (*Rhamnus purshiana* D.C.), red alder (*Alnus rubra* Bong.), and red elderberry (*Sambucus racemosa* L.). Other conifers that occurred less frequently included Sitka spruce (*Picea sitchensis* (Bong.) Carr.), western redcedar (*Thuja plicata* Donn.), noble fir (*Abies procera* Rehder), and grand fir (*Abies grandis* (Dougl.) Forbes). Other hardwood species included bitter cherry (*Prunus emarginata* (Dougl.) Walp.) and bigleaf maple (*Acer macrophyllum* Pursh).

Ten dominant or codominant trees on each plot were also scored for SNC at time of plot establishment in 1998, and just prior to bud break in years 1999–2004. Needle retention of individual trees was visually estimated by first dividing the live crown into thirds, with the base of the live crown defined as the lowest live branch. Secondary or lateral branches on a primary or main branch were then examined in the center of each third, and the average number of needle age classes present at time of sampling was estimated to the nearest 0.5 yr (Maguire et al., 2002). The needle retention of the tree was then estimated by averaging these values across crown thirds. Plot-level foliage retention was the average of the ten SNC-scored trees.

2.1. Variables in the model

Diameter increment models were developed from the ten individual Douglas-fir trees that had been scored for foliage retention within each plot and for each growth period that the tree survived without any top damage, resulting in 2469 separate measurements (Tables 1 and 2).

Separate diameter increment models for Douglas-fir were developed using each of three different estimates of foliage

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