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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.

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 retention: (1) Model 1: plot-level foliage retention (PlotFR); (2) Model 2: tree-level foliage retention (TreeFR); and (3) Model 3: combination of plot-level foliage retention and the difference between tree-level and plot-level foliage retention (DiffFR = TreeFR–PlotFR, Fig. 1). Variables from the following four classes of additional explanatory variables were also tested:

1. *Tree size*: diameter at breast height, DBH (cm); total height, HT (m); height to crown base defined as the lowest live branch, HCB (m); crown ratio, CR.
2. *Stand density*: trees per ha, TPH (trees/ha); average diameter and average height of the 100 largest (by diameter) trees per ha, D100 (cm) and H100 (m), respectively; stand density index, SDI; quadratic mean diameter, QMD (cm); basal area, BA (m^2/ha); crown competition factor (Krajicek et al., 1961) using the maximum crown width equations described by Paine and Hann (1982), CCF (%).
3. *Tree social position*: basal area in trees with DBH greater than the subject tree, BAL (m^2/ha); crown competition factor in trees with DBH greater than the subject tree, CCFL (%).
4. *Site quality*: Bruce's (1981) site index, SI (m at 50 years).

In addition to the untransformed variables, the natural logarithm, square, and inverse of each were also tested.

2.2. Model development

The biological processes that influence tree growth are inherently non-linear. However, linear regression is a suitable tool for modeling growth curves if a linearizing relationship can be found between the key variables (Curtis, 1967) and biologically reasonable shapes are determined (Trasobares et al., 2004). Various linear and nonlinear regression models were fitted to the data to develop a series of equations describing diameter increment. Preliminary analysis revealed that nonlinear models tended to have more reasonable residual distribution as well as higher accuracy. Therefore, nonlinear regressions were adopted in this analysis.

Repeatedly measured growth and yield data are typically correlated, and they usually exhibit heteroskedasticity in model residuals as well (Gregoire, 1987). Preliminary analysis revealed that model residuals were not homogeneous and that the residual variance increased monotonically with increasing tree diameter. Although the logarithmic transformation was examined to correct for heteroskedasticity (Calama and Montero, 2005; Yang et al., 2009), the models continued to show a trend of increasing residual variance with tree diameter. Therefore, weighted nonlinear regression was used to homogenize the variance in residuals. A weight of DBH^{-m} was tested, with $m = 0, 1, 2, 3,$ and 4.

To account for correlations among trees within a plot, a non-linear model with a random plot effect was estimated with PROC NLMIXED in SAS version 9.2 (SAS Institute 2008). A set of promising model forms was selected by a combination of all-subsets exploratory analyses on linearized models and numerous existing nonlinear diameter growth models. The final model for each of the three representations of foliage retention were nonlinear and chosen on the basis of residual analysis, minimization of AIC, and biological interpretability. Alternative variance–covariance matrices, including unstructured, compound symmetry, Toeplitz, and AR(1) structures, were tested on the linearized form of the final non-linear model. All parameter estimates were required to be significantly different from zero at $\alpha = 0.05$.

Table 1
Means and ranges of tree-level attributes from the Swiss needle cast growth impact study. See text in Section 2 for variable definitions.

Variable	Unit	*N*	Mean	Std Dev	Minimum	Maximum
dbh	cm	2469	26.77	8.23	3.90	57.30
ht	m	2469	16.78	4.88	3.32	35.40
hcb	m	2469	4.20	3.13	0.00	19.69
BAL	m^2/ha	2469	8.90	8.85	0.00	49.31
CCFL	%	2469	46.04	45.26	0.00	289.88
CR	–	2469	0.77	0.14	0.26	1.00
TreeFR	years	2469	2.39	0.58	0.67	4.77
DiffFR	years	2469	−0.01	0.40	−1.59	1.71

Table 2
Means and ranges of plot-level attributes from the Swiss needle cast growth impact study. See text in Section 2 for variable definitions.

Variable	Unit	*N*	Mean	Std Dev	Minimum	Maximum
SI	m	282	43.69	7.12	13.80	63.10
PlotFR	years	282	2.38	0.45	1.01	3.85
Age	years	282	22.67	5.93	11.00	38.00
D100	cm	282	29.44	8.08	5.58	49.00
H100	m/ha	282	17.25	4.76	4.01	34.14
BA	m^2	282	27.65	10.72	1.71	65.37
CCF	%	282	184.44	63.25	38.33	539.64
TPH	trees/ha	282	1121.57	548.90	345.80	4705.35
QMD	cm	282	18.71	5.76	4.12	35.76
SDI	25-cm trees/ha	282	611.98	213.07	69.20	1298.65
Douglas-fir BA	m^2/ha	282	21.77	9.50	0.62	48.35
Other conifer BA	m^2/ha	282	4.19	6.99	0.00	46.98
Hardwood BA	m^2/ha	282	1.70	2.66	0.00	17.29
% Douglas-fir BA	%	282	80	23	12	100
Douglas-fir TPH	trees/ha	282	118.59	14.33	37.05	135.85

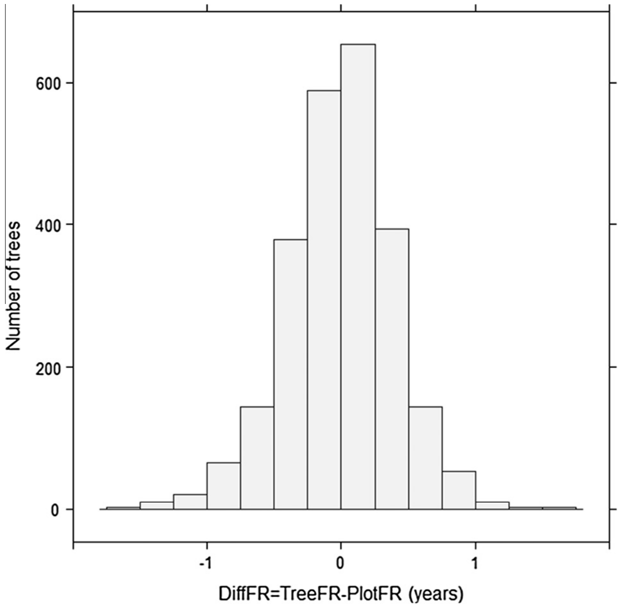

Fig. 1. Frequency of sample trees in each class of DiffFR, or deviation of tree-level foliage retention (TreeFR) from plot-average foliage retention (PlotFR) in the Swiss needle cast growth impact study.

2.3. Model evaluation

The models were evaluated by examining the magnitude and distribution of residuals plotted against the response variable and each of the separate predictor variables. The aim was to detect any obvious dependencies or patterns that indicated systematic biases. To determine the accuracy of model predictions, bias and precision of the models were computed directly. Mean difference (MD), mean squared difference (MSD), mean absolute difference (MAD), and R^2 were calculated on the original (unweighted) scale (including any corrections for log bias from log-transformed models) as follows (Palahí et al., 2003):

$$\mathrm{MD} = \sum_{i=1}^{n}\left(\Delta\mathrm{dbh}_i - \widehat{\Delta\mathrm{dbh}}\right)\bigg/ n$$

$$\mathrm{MSD} = \sum_{i=1}^{n}\left(\Delta\mathrm{dbh}_i - \widehat{\Delta\mathrm{dbh}}\right)^2\bigg/ n$$

$$\mathrm{MAD} = \sum_{i=1}^{n}\left|\Delta\mathrm{dbh}_i - \widehat{\Delta\mathrm{dbh}}\right|\bigg/ n$$

$$R^2_{\mathrm{pseudo}} = 1 - \frac{\sum_{i=1}^{n}\left(\Delta\mathrm{dbh}_i - \widehat{\Delta\mathrm{dbh}}\right)^2}{\sum_{i=1}^{n}\left(\Delta\mathrm{dbh}_i - \overline{\Delta\mathrm{dbh}}\right)^2}$$

where $\Delta\mathrm{dbh}$ was the observed periodic annual diameter increment, $\widehat{\Delta\mathrm{dbh}}$ was the predicted periodic annual diameter increment, $\overline{\Delta\mathrm{dbh}}$ was the average value of observed periodic annual diameter increment, and i referred to the ith tree with $i = 1, 2, \ldots, n$.

2.4. Model application: growth multiplier

The greatest tree-level foliage retention (4.77 years) and plot-level foliage retention (3.85 years) were assumed to represent the most "healthy" condition of Douglas-fir trees and plots, respectively. The diameter growth impact and basal area growth impact for individual plots with foliage retention between 1.0 and 3.85 years, or for trees with average foliage retention between 1.0 and 4.77 years, were calculated using the model based on plot-level foliage retention (Model 1) or tree-level foliage retention (Model 2), respectively. Within a plot, the difference between TreeFR and PlotFR typically ranged between −0.75 and +0.75 years. Therefore, the SNC multiplier from the model based on both plot-level foliage retention and the deviation of tree-level from plot-level foliage retention (Model 3) was plotted across the range of PlotFR from 1 to 3.85 years under three different conditions of TreeFR: (1) TreeFR − PlotFR = −0.75 years; (2) TreeFR − PlotFR = 0 years; and (3) TreeFR − PlotFR = +0.75 years.

2.5. Within-stand variability in foliage retention

Little analysis has been done to date to test the hypothesis that foliage retention declines with lower or greater social status within a stand. Foliage retention values on more than 700 trees from more than 70 plots and four different measurement periods were available to test this hypothesis. Individual-tree foliage retention was regressed on the ratio of individual-tree dbh (D) to plot-level quadratic mean diameter of the Douglas-fir component (Q), treating plot as a random effect. This analysis was intended to facilitate interpretation of the final growth models relative to initial tree size versus initial foliage retention. As a means of illustrating the within-plot variation of foliage retention, the standard deviation in estimated foliage retention for the ten trees within each plot was calculated for each year of SNC rating, and an average value for each plot was determined as the average of all years during which SNC severity was rated for that plot.

3. Results

3.1. The model

The diameter increment models based on plot-level and tree-level foliage retention were as follows:

$$\Delta\mathrm{dbh} = \exp\left(\beta_{10} + \beta_{11}\cdot\log(\mathrm{dbh}) + \beta_{12}\log\left(\frac{\mathrm{CR}+0.2}{1.2}\right) + \beta_{13}\cdot\mathrm{CCFL} + \beta_{14}\cdot\mathrm{age} + \beta_{15}\cdot\mathrm{SDI} + \frac{\beta_{16}}{\mathrm{PlotFR}}\right) + \delta_1 + \varepsilon_1 \qquad (1)$$

$$\Delta\mathrm{dbh} = \exp\left(\beta_{20} + \beta_{21}\cdot\log(\mathrm{dbh}) + \beta_{22}\cdot\log\left(\frac{\mathrm{CR}+0.2}{1.2}\right) + \beta_{23}\cdot\mathrm{CCFL} + \beta_{24}\cdot\mathrm{age} + \beta_{25}\cdot\mathrm{SDI} + \frac{\beta_{26}}{\mathrm{TreeFR}}\right) + \delta_2 + \varepsilon_2 \qquad (2)$$

$$\Delta\mathrm{dbh} = \exp\left(\beta_{30} + \beta_{31}\cdot\log(\mathrm{dbh}) + \beta_{32}\cdot\log\left(\frac{\mathrm{CR}+0.2}{1.2}\right) + \beta_{33}\cdot\mathrm{CCFL} + \beta_{34}\cdot\mathrm{age} + \beta_{35}\cdot\mathrm{SDI} + \frac{\beta_{36}}{\mathrm{PlotFR}} + \beta_{37}\cdot\log(\mathrm{DiffFR}+2)\right) + \delta_3 + \varepsilon_3 \qquad (3)$$

where dbh was diameter at breast height (cm); CR was crown ratio (live crown length/total tree height); CCFL was crown competition factor in larger trees (%); age was total stand age (years); SDI was stand density index (Reineke, 1933); PlotFR was plot-level foliage retention (years); TreeFR was tree-level foliage retention (years); DiffFR was the difference between tree-level foliage retention and average plot-level foliage retention (TreeFR − PlotFR); β_{10}–β_{16}, β_{20}–β_{26}, and β_{30}–β_{37} were parameters to be estimated from the data; δ_1, δ_2, and δ_3 were random plot effects assuming $\delta_i \sim N(0, {\sigma_{\delta i}}^2)$, with $i = 1, 2$, or 3; and ε_i are random errors assuming $\varepsilon_i \sim N(0, {\sigma_{\varepsilon i}}^2)$ with $i = 1, 2$, or 3. A weight of DBH^{-2} was used in all three of the above models. Variance covariance structures AR(1) and compound symmetry were significant in the linear form of these models, however, they had a slightly higher AIC. Therefore, the final model did not specify a variance covariance structure.

The above three models were evaluated with R^2_{pseudo}, MD, MSD, and MAD (Table 3). The model using tree-level foliage retention [2] had a greater R^2_{pseudo} than the model with plot-level foliage retention [1], as well as a lower MD, MSD, and MAD, indicating that tree-level foliage retention predicted Douglas-fir diameter increment more accurately. Model [3], incorporating both plot-level foliage retention and the deviation of tree-level retention from plot-level retention, performed almost as well as model [2], but with slightly less precision. However, all three models had similar accuracy, e.g., R^2_{pseudo} of Model [2] was only 0.0049 higher than that of Model [1] and only 0.0011 higher than Model [3]. Similarly, MAD of Model [2] was only 0.00190 lower than that of Model [1] and only 0.00044 lower than that of Model [3].

Parameter estimates in the final models were all significantly different from zero at $\alpha = 0.05$ (Table 4). In all models, diameter growth was positively correlated with dbh and crown ratio, and negatively correlated with SDI, CCFL, age, and the reciprocal of foliage retention. In general, diameter growth increased with increasing tree size, crown size and foliage retention, and decreased with higher stand density, lower social position, and greater age. Weighted residuals showed no serious departures from constant variance or biases across predictor variables (not shown). The random plot effect and alternative variance–covariance structures in

Table 3
Statistics for evaluation of diameter growth models for Douglas-fir trees from the Swiss needle cast growth impact study. See equations in Section 2 for exact definition of statistics.

Variable	Definition	Model [1]	Model [2]	Model [3]
MD	Mean difference	−0.000007	−0.000115	−0.000143
MSD	Mean squared difference	0.073561	0.072404	0.072667
MAD	Mean absolute difference	0.208572	0.206675	0.207118
R^2_{pseudo}	Pseudo-R^2	0.687629	0.692551	0.691441

the linearized mixed-effects version of this model provided no significant improvement over the model without these potential refinements, and residuals indicated better conformity of the nonlinear model to the assumptions of least squares estimation.

3.2. Growth multiplier

Given the model forms and parameter estimates, the trends in implied diameter growth multipliers (DMOD) over initial foliage retention were as follows:

$$\begin{aligned}\mathrm{DMOD}_{\mathrm{model1}} &= \frac{\exp\left(\frac{-0.4772}{\mathrm{plotFR}}\right)}{\exp\left(\frac{-0.4772}{3.85}\right)} \\ &= \exp\left[-0.4772\left(\frac{1}{\mathrm{plotFR}}-\frac{1}{3.85}\right)\right]\end{aligned} \tag{4}$$

$$\mathrm{DMOD}_{\mathrm{model2}} = \frac{\exp\left(\frac{-0.4529}{\mathrm{treeFR}}\right)}{\exp\left(\frac{-0.4529}{4.77}\right)} = \exp\left[-0.4529\left(\frac{1}{\mathrm{treeFR}}-\frac{1}{4.77}\right)\right] \tag{5}$$

$$\begin{aligned}\mathrm{DMOD}_{\mathrm{model3,0}} &= \left(\frac{0+2}{2}\right)^{0.1597}\left[\frac{\exp\left(\frac{-0.5069}{\mathrm{plotFR}}\right)}{\exp\left(\frac{-0.5069}{3.85}\right)}\right] \\ &= \left(\frac{0+2}{2}\right)^{0.1597}\exp\left[-0.5069\left(\frac{1}{\mathrm{plotFR}}-\frac{1}{3.85}\right)\right] \\ &= \exp\left[-0.5069\left(\frac{1}{\mathrm{plotFR}}-\frac{1}{3.85}\right)\right]\end{aligned} \tag{6}$$

$$\begin{aligned}\mathrm{DMOD}_{\mathrm{model3,-0.75}} &= \left(\frac{-0.75+2}{2}\right)^{0.1597}\left[\frac{\exp\left(\frac{-0.5069}{\mathrm{plotFR}}\right)}{\exp\left(\frac{-0.5069}{3.85}\right)}\right] \\ &= \left(\frac{-0.75+2}{2}\right)^{0.1597}\exp\left[-0.5069\left(\frac{1}{\mathrm{plotFR}}-\frac{1}{3.85}\right)\right]\end{aligned} \tag{7}$$

$$\begin{aligned}\mathrm{DMOD}_{\mathrm{model3,+0.75}} &= \left(\frac{+0.75+2}{2}\right)^{0.1597}\left[\frac{\exp\left(\frac{-0.5069}{\mathrm{plotFR}}\right)}{\exp\left(\frac{-0.5069}{3.85}\right)}\right] \\ &= \left(\frac{+0.75+2}{2}\right)^{0.1597}\exp\left[-0.5069\left(\frac{1}{\mathrm{plotFR}}-\frac{1}{3.85}\right)\right]\end{aligned} \tag{8}$$

where PlotFR ranged from 1 to 3.85 years, and TreeFR ranged from 1 to 4.77 years.

The tree-level foliage retention multiplier exhibited a greater range for a given initial foliage retention than did the plot-level multiplier (Fig. 2). Where SNC was most severe, (PlotFR = TreeFR = 1 year), the value of the diameter growth multiplier was 0.70 for both plot-averages and individual-trees. As SNC became less severe, the multipliers for models [1] and [2] approached a value of 1 at foliage retention levels indicative of little to no SNC impact. A tree with a foliage retention that was 0.75 years greater than the plot average foliage retention (model [3], TreeFR = PlotFR + 0.75) was implied to have a diameter increment 5% larger than a tree with the plot-average foliage retention. In contrast, a tree with a foliage retention that was 0.75 years less than that of the plot average foliage retention (model [3], TreeFR = PlotFR-0.75) was implied to have a diameter increment 7% less than a tree with the plot-average foliage retention.

Table 4
Parameter estimates from the model for predicting diameter increment from plot-average foliage retention (Model 1; PlotFR), individual-tree foliage retention (Model 2: TreeFR), and the combination of individual-tree and plot-average foliage retention (Model 3: TreeFR + PlotFR). All parameters are significantly different from zero at α = 0.05.

	Model [1]		Model [2]		Model [3]	
	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.
β_{i0}	0.6723	0.1227	0.6524	0.09537	0.5797	0.1243
β_{i1}	0.3301	0.03811	0.3306	0.03601	0.3233	0.03802
β_{i2}	1.4187	0.09225	1.3888	0.09103	1.3848	0.09154
β_{i3}	−0.00246	0.00028	−0.00228	0.000265	−0.00235	0.000277
β_{i4}	−0.0399	0.004106	−0.03989	0.004029	−0.03978	0.004041
β_{i5}	−0.00056	0.000087	−0.00055	0.000086	−0.00054	0.000086
β_{i6}	−0.4772	0.113	−0.4529	0.06101	−0.5069	0.1142
β_{i7}					0.1597	0.02624
μ_i	0.03336	0.0062	0.03326	0.00616	0.03338	0.0062

3.3. Within-stand variability in foliage retention

The trees selected for SNC severity rating within this dataset were limited to dominant and co-dominant trees, so the average D/Q was 1.4 with a standard deviation of 0.37. Regardless, the mixed-effects model indicated that foliage retention increased significantly with increasing D/Q even over this limited diameter range. On average, foliage retention would increase by 0.19 years per unit increase in D/Q (Fig 3).

In the 76 plots analyzed, the average standard deviation in tree-level foliage retention for a given year and a given plot of scoring varied from 0.04 to 0.90 years, with an average of 0.39 years. The standard deviation in tree level foliage retention for each plot and year increased with increasing average tree height (Fig 4), indicating that as the stands matured and differentiated, the variation in foliage retention was increasing

4. Discussion

The diameter growth models (Eqs. (1–3)) were consistent with previously constructed diameter and basal area increment models (Wykoff, 1990; Monserud and Sterba, 1996; Hann and Hanus, 2002; Uzoh and Oliver, 2008); i.e., dbh and crown ratio (CR) were positively correlated with diameter increment, but stand age, crown competition factor in larger trees (CCFL), and stand density index (SDI) were negatively correlated with diameter increment. As expected, foliage retention was positively correlated with diameter increment at both the plot-level and tree-level. To date, all SNC-related growth impacts have been assessed using plot-average foliage retention. Although there is significant variation in tree-level foliage retention within a stand, plot-level averages have nonetheless provided a useful means of determining regional

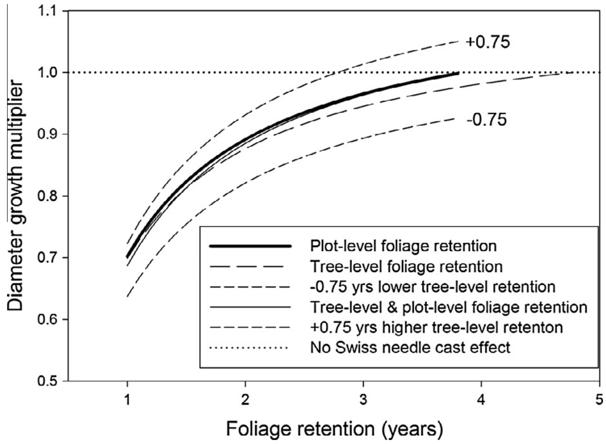

Fig. 2. Inferred diameter growth multipliers from the diameter increment model using plot-average foliage retention (Model 1; PlotFR), individual-tree foliage retention (Model 2: TreeFR), and the combination of individual-tree and plot-average foliage retention (Model 3: TreeFR + PlotFR).

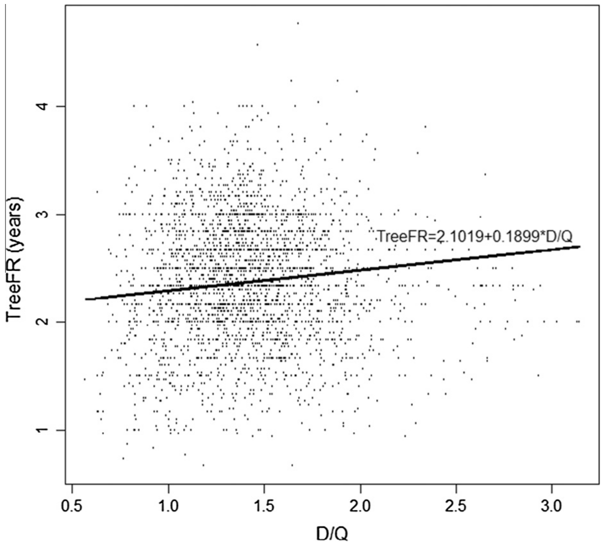

Fig. 3. Relationship between TreeFR and D/Q.

impacts of the disease and stand-level growth losses (Maguire et al., 2011). However, given the variation of foliage retention among trees within a plot and the correlation between tree-level foliage retention and individual-tree growth, plot-level averages mask the portion of within-stand variability in tree growth imposed by differences in SNC severity among individual trees. Accounting for this additional source of variation in individual tree growth increases the accuracy of simulated stand dynamics where significant tree-level differences in SNC severity persist, specifically by better representing the intensity of size differentiation. Likewise, this variation provides an opportunity to improve growth responses to thinning by considering foliage retention as a criterion for selecting retained trees.

In a previous analysis, Garber et al. (2007) applied plot-level foliage retention to the same growth data used in this analysis to calculate multiplicative adjustment factors. These SNC multipliers were intended to enable users of the growth and yield model ORGANON to simulate growth dynamics of SNC-impacted stands. Garber et al. (2007) found that a foliage retention of one year at the plot level implied diameter and height growth averaging only 33% and 60%, respectively, of that expected in a healthy stand. Although these growth multipliers seemed to imply plot-level growth impacts that were consistent with volume growth losses estimated at the stand level (Maguire et al., 2011), the variability in multipliers observed in this analysis suggests that a constant multiplier across all trees within the stand will generate inaccuracies in simulated stand dynamics and resulting stand structure (e.g., diameter distributions). This inaccuracy will be compounded by corresponding effects on stand-structural covariates that are designed to represent relative social position in the stand (e.g., CCFL) and that therefore depend on the degree of size differentiation. In this case, a silvicultural regime selected to achieve a given stand management objective may not produce the expected stand structure if based on simulations that do not consider individual-tree variation in SNC effects.

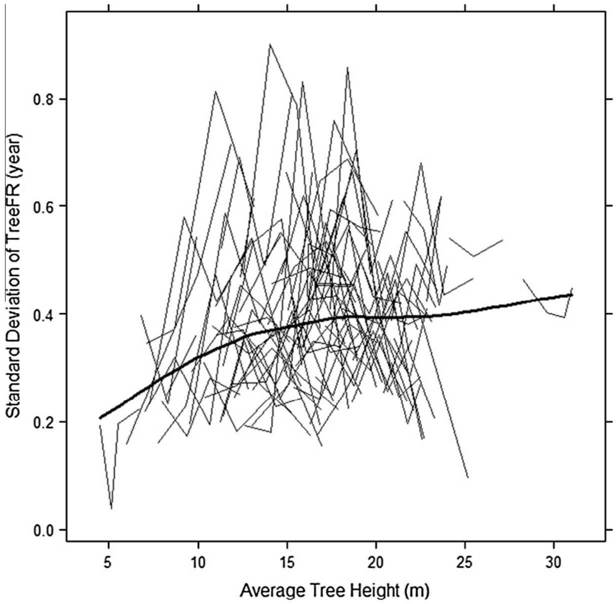

Fig. 4. Standard deviation and lowess trend line of tree-level foliage retention for all plot and measurement year combinations in the SNCC growth impact study. Lines connect time series for each individual plot.

In addition to these implications for stand dynamics and silvicultural manipulation of stand structure, the size distribution of trees and logs underlying a given stand volume has a strong influence on stand valuation. Product recovery and value will vary by log size, but further variation is introduced by the SNC effects on wood stiffness (Johnson et al., 2005). The effects of SNC on wood quality and stem form have not been fully quantified, but trees subjected to fungicidal exclusion of the fungus are known to grow significantly different wood than trees without fungicidal protection (Johnson et al., 2003). Likewise, SNC-impacted stems are generally more slender for a given dbh and height (Weiskittel and Maguire, 2004). Both these responses to SNC affect product recovery and value of Douglas-fir in regions where SNC is prevalent.

Plot-level average foliage retention is based on estimates from dominant and co-dominant trees only, so the full range of variability within the stand was probably not captured by this protocol. However, this stand component contributes the most to growth and value (O'Hara, 1988), so the practical implication of any bias introduced by extrapolating to lower crown classes may be minimal. Although foliage retention was generally estimated on dominant and codominant trees, foliage retention exhibited a significant increase with increasing relative diameter even over this limited diameter range. The degree to which this relationship is cause versus effect, and the degree to which it can be extrapolated to intermediate and suppressed trees, is unknown. Dendrochronological work attempting to identify historical fluctuations in SNC in the Oregon Coast Ranges included trees that make up part of the suppressed component of current stands (Black et al., 2010). Black et al.'s (2010) analysis showed that at the most severely impacted sites Douglas-fir radial growth was reduced by as much as 85%. In the current study, the largest diameter growth reduction was only 30% for the most severely impacted trees. Part of the difference may have resulted from comparing the effect of SNC between different stand components in the two studies, i.e., among dominants and co-dominants in the Swiss Needle Cast Cooperative growth impact study, but among all crown classes in Black et al.'s (2010) study. However, it is impossible to know retrospectively whether the greater growth impact of SNC in Black et al.'s (2010) dendrochronological study was largely or partly an effect of lower foliage retention by lower crown classes.

The link between foliage retention and crown position, and between foliage retention and growth is consistent with observations previously made within SNC-infected stands, i.e., that SNC is one of numerous drivers of differentiation within coastal Douglas-fir stands (Mainwaring et al., 2005). In severely impacted stands, it has been recommended that density be kept low to ensure long crowns, thereby sustaining sufficient foliar mass and diameter growth. Arguments have also been made that a higher density of trees should be planted in these stands to ensure that enough crop trees produce sufficient volume to maintain net positive revenues from Douglas-fir stand management in SNC-impacted coastal regions. Meeting both of these objectives with a pre-commercial thinning will alter current management guidelines in coastal zones, affecting stand structure by providing more growing space and opportunity for recruitment and persistence of other under- and overstory species.

This growth analysis of plots from the Swiss Needle Cast Cooperative relied on our ability to accurately assess tree-level foliage retention. Measurement error in estimating foliage retention for a given crown third and the average for a given tree may reduce the appeal of accounting for within-stand variation in foliage retention. As the trees on these permanent plots become taller and foliage visibility declines, maintenance of estimation accuracy necessitated that the method for estimating tree-level foliage retention shift to estimating foliage retention on the southernmost branch pruned off the fifth whorl from the tip of the tree. Initial comparisons to the more conventional ground based visual estimates when needle cohorts were still visible from the ground indicated close agreement between the two approaches. Especially in older stands, visual estimates are easiest to get for dominant trees, because they tend to have some open space around them, and their branches can be more readily seen against the sky. However, intermediate and suppressed trees are more difficult to assess from the ground, due primarily to the low contrast in color between needles on a specific branch and those on neighboring branches. Incorporation of tree-level foliage retention values for predictive purposes on a large scale and on taller trees would probably necessitate further analysis of sampling strategies to ensure the required estimation accuracy.

Finally, it is widely recognized that other factors related to site quality, stand structure, and silvicultural history influence foliage retention, complicating efforts to quantify pure SNC impacts (Maguire et al., 2011). Both earlier and current work on *P. gaeumannii* indicate that this endemic fungus has been virtually ubiquitous on Douglas-fir foliage (Boyce, 1940; Hood, 1982; Stone et al., 2008). In fact, pseudothecia counts on foliage samples indicated the presence of the fungus at all the plots included in this study (unpublished data). Slower growth associated with lower fertility in unmanaged stands has been considered a cause of greater foliage retention rather than an effect (Reich et al., 1995; Shoettle, 1990), and foliage retention has been observed to decline as a result of positive growth responses to fertilization (Balster and Marshall, 2000). Because these trends are opposite to growth patterns observed over the range in SNC intensity characterizing the growth impact study, growth reductions quantified in this analysis are attributed predominantly to direct effects of *P. gaeumannii* on gas exchange and foliage retention (Manter et al., 2003).

5. Conclusion

Within-stand variation in individual-tree foliage retention has influenced individual-tree growth rates and stand dynamics. The most severely impacted plots exhibited 30% diameter growth loss for dominant and co-dominant trees. Within a plot, diameter growth averaged about 12% higher on dominant and co-dominant trees with the greatest foliage retention relative to trees with the least foliage retention. Results from this analysis indicated that use of a plot-average foliage retention will introduce bias into individual-tree growth predictions. Bias would result both from the projected growth of individual trees, and from the compounding effects over multiple growth periods on covariates that represent the relative size and social position of the tree in the stand. Furthermore, lack of knowledge about differential SNC growth effects on individual trees forfeits the opportunity to include foliage retention as a criterion for selecting trees for removal during thinnings.

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References

Balster, N.J., Marshall, J.D., 2000. Decreased needle longevity of fertilized Douglas-fir and grand fir in the northern Rockies. Tree Physiol. 20, 1191–1197.

Black, B.A., Shaw, D.C., Stone, J.K., 2010. Impacts of Swiss needle cast on overstory Douglas-fir forests of the western Oregon coast range. For. Ecol. Manage. 259, 1673–1680.

Boyce, J.S., 1940. A needle cast of Douglas-fir associated with *Adelopus gaeumannii*. Phytopathology 30, 649–659.

Bruce, D., 1981. Consistent height-growth and growth-rate estimates for remeasured plots. For. Sci. 27, 711–725.

Calama, R., Montero, G., 2005. Multilevel linear mixed model for tree diameter increment in stone pine (*Pinus pinea*): a calibration approach. Silva Fenn. 39, 37–54.

Curtis, R.O., 1967. Height diameter and height-diameter-age equations for second-growth Douglas-fir. For. Sci. 13, 356–375.

Garber, S., Maguire, D., Mainwaring, D., Hann, D., 2007. Swiss Needle Cast ORGANON module update. In: Shaw, D., (Ed.). 2007 Swiss Needle Cast Cooperative Annual Report. College of Forestry, Oregon State University, Corvallis, OR, pp. 63–66.

Gregoire, T.G., 1987. Generalized error structure for forestry yield models. For. Sci. 33, 423–444.

Hann, D.W., Hanus M.L., 2002. Enhanced diameter-growth-rate equations for undamaged and damaged trees in southwest Oregon. Forest Research Lab., Oregon State University, Corvallis, Oregon. Research Contribution 39, 54p.

Hansen, E.M., Stone, J.K., Capitano, B.R., Rosso, P., Sutton, W., Winton, L., Kanaskie, A., McWilliams, M., 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., 1982. *Phaeocryptopus gaeumannii* on *Pseudotsuga menziesii* in southern British Columbia. New Zealand J. For. Sci. 12, 415–424.

Johnson, G.R., 2002. Genetic variation of Douglas-fir to Swiss needle cast as assessed by symptom expression. Silvae Genetica 51, 80–86.

Johnson, G.R., Gartner, B.L., Maguire, D., Kanaskie, A., 2003. Influence of Bravo fungicide applications on wood density and moisture content of Swiss needle cast affected Douglas-fir trees. For. Ecol. Manage. 186, 339–348.

Johnson, G.R., Grotta, A.T., Gartner, B.L., Downes, G., 2005. Impact of the foliar pathogen Swiss needle cast on wood quality of Douglas-fir. Can. J. For. Res. 35, 331–339.

Kanaskie, A., McWilliams, M., 2013. Swiss Needle Cast aerial survey, 2013. In: Shaw, D., (Ed.). 2013 Swiss Needle Cast Cooperative Annual Report. College of Forestry, Oregon State University, Corvallis, OR, pp. 5–8.

Kimberley, M.O., Hood, I.A., Knowles, R.L., 2011. Impact of Swiss needle-cast on growth of Douglas-fir. Phytopathology 101, 583–593.

Krajicek, J.E., Brinkman, K.E., Gingrich, S.F., 1961. Crown competition: a measure of density. For. Sci. 7, 35–42.

Maguire, D.A., Kanaskie, A., Voelker, W., Johnson, R., Johnson, G., 2002. Growth of young Douglas-fir plantations across a gradient in Swiss needle cast severity. West. J. Appl. For. 17, 86–95.

Maguire, D.A., Mainwaring, D.B., Kanaskie, A., 2011. Ten-year growth and mortality in young Douglas-fir stands experiencing a range in Swiss needle cast severity. Can. J. For. Res. 41, 2064–2076.

Mainwaring, D.B., Maguire, D.A., Kanaskie, A., 2005. Interactive effects of Swiss needle cast and commercial thinning on Douglas-fir growth and development in north coastal Oregon: two year response from 30 permanent monitoring plots. In: Mainwaring, D., Shaw, D., (Eds.). Swiss Needle Cast Cooperative 2005 Annual Report. College of Forestry, Oregon State University, Corvallis, OR, pp. 23–33.

Manter, D.K., Bond, B.J., Kavanagh, K.L., Stone, J.K., Filip, G.M., 2003. Modelling the impacts of the foliar pathogen, *Phaeocryptopus gaeumannii*, on Douglas-fir physiology: net canopy carbon assimilation, needle abscission and growth. Ecol. Model. 164, 211–226.

Manter, D.K., Reeser, P.D., Stone, J.K., 2005. A climate-based model for predicting geographic variation in swiss needle cast severity in the oregon coast range. Phytopathology 95, 1256–1265.

Monserud, R.A., Sterba, H., 1996. A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. For. Ecol. Manage. 80, 57–80.

O'Hara, K.L., 1988. Stand structure and growing space efficiency following thinning in an even-aged Douglas-fir stand. Can. J. For. Res. 18, 859–866.

Paine, D.P., Hann, D.W., 1982. Maximum crown-width equations for southwestern Oregon tree species. Oregon State University, Forest Research Laboratory, Corvallis, OR, Research Pap. 46, 20p.

Palahí, M., Pukkala, T., Miina, J., Montero, G., 2003. Individual-tree growth and mortality models for Scots pine (*Pinus sylvestris* L.) in north-east Spain. Ann. For. Sci. 60, 1–10.

Reich, P.B., Koike, T., Gower, S.T., Schoettle, A.W., 1995. Causes and consequences of variation in conifer leaf life-span. In: Smith, W.K., Hinckley, T.M. (Eds.), Ecophysiology of Coniferous Forests. Academic Press, New York, USA, pp. 225–254.

Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46, 627–638.

SAS Institute Inc., 2008. SAS/STAT® 9.2 User's Guide. SAS Institute Inc., Cary, NC.

Schoettle, A.W., 1990. The interaction between leaf longevity and shoot growth and foliar biomass per shoot in *Pinus contorta* at two elevations. Tree Physiol. 7, 209–214.

Stone, J.K., Capitano, B.R., Kerrigan, J.L., 2008. The histopathology of *Phaeocryptopus gaeumannii* on Douglas-fir needles. Mycologia 100, 431–444.

Trasobares, A., Tomé, M., Miina, J., 2004. Growth and yield model for *Pinus halepensis* Mill. in Catalonia, north-east Spain. For. Ecol. Manage. 203, 49–62.

Uzoh, F.C.C., Oliver, W.W., 2008. Individual tree diameter increment model for managed even-aged stands of ponderosa pine throughout the western United States using multilevel linear mixed effects models. For. Ecol. Manage. 256, 438–445.

Weiskittel, A.R., Maguire, D.A. 2004. Influence of Swiss needle cast on Douglas-fir stem properties. In: Mainwaring, D., (Ed.). Swiss Needle Cast Cooperative 2004 Annual Report. College of Forestry, Oregon State University, Corvallis, OR, pp. 91–97.

Weiskittel, A.R., Maguire, D.A., Garber, S.M., Kanaskie, A., 2006. Influence of Swiss needle cast on foliage age class structure and vertical distribution in Douglas-fir plantations of north coastal Oregon. Can. J. For. Res. 36, 1497–1508.

Wykoff, R.W., 1990. A basal area increment model for individual conifers in the northern Rocky Mountains. For. Sci. 36, 1077–1104.

Yang, Y., Huang, S., Meng, S.X., Trincado, G., VanderSchaaf, C.L., 2009. A multilevel individual tree basal area increment model for aspen in boreal mixedwood stands. Can. J. For. Res. 39, 2203–2214.