Forestry *An International Journal of Forest Research*

Institute of Chartered Foresters

Forestry 2014; **87**, 697–704, doi:10.1093/forestry/cpu030
Advance Access publication 3 August 2014

Western hemlock growth response to increasing intensity of Swiss needle cast on Douglas-fir: changes in the dynamics of mixed-species stands

Junhui Zhao[1]*, Douglas A. Maguire[2], Douglas B. Mainwaring[1] and Alan Kanaskie[2]

[1] *Department of Forest Engineering, Resources and Management, College of Forestry, Oregon State University, Corvallis, OR 97331, USA*
[2] *Oregon Department of Forestry, Salem, OR 97310, USA*

*Corresponding author. Tel.: +1 5416024610; E-mail: junhui.zhao@oregonstate.edu

Received 13 March 2014

Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) is a major commercial tree species in western Oregon and Washington and is often associated with coast Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var *menziesii*) and other species in coniferous forests of the Coast Ranges and Cascade Mountains. Growth of Douglas-fir in many coastal forests has been negatively affected by Swiss needle cast (SNC), a foliar disease caused by the ascomycete *Phaeocryptopus gaeumannii* (T. Rohde) Petr. and characterized by premature foliage loss on severely infected Douglas-fir trees. The effect of SNC on stand dynamics in mixed Douglas-fir-western hemlock stands was tested by constructing a diameter increment model for western hemlock that quantified its growth response to varying SNC severity in Douglas-fir. Diameter increment of western hemlock in any given growth period increased with increasing initial SNC severity as measured by Douglas-fir foliage retention (FR), here defined as the number of annual needle cohorts held by the tree. Furthermore, a decline in Douglas-fir FR during the growth period was associated with an additional increase in diameter increment of western hemlock trees. Assuming no change in FR over the growth period, western hemlock trees in stands with severely impacted Douglas-fir (initial FR $\leq$1.5 years) averaged 79 per cent greater diameter growth than that in relatively healthy stands (initial Douglas-fir FR $\geq$3.5 years). The implied annual diameter growth response of a western hemlock with initial diameter at breast height of 10, 20, 30 or 40 cm was 0.29, 0.52, 0.65 and 0.68 cm year^{-1}, respectively. Compensatory growth by western hemlock in mixed-species stands alters stand dynamics by allowing this species to surpass the growth of Douglas-fir experiencing severe SNC.

Introduction

Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) is a major commercial tree species in coastal forests of the northwestern US and southwestern Canada (Packee, 1990). This native conifer exhibits rapid growth and accumulates large stand-level stem volumes due to its relative shade tolerance, rapid height growth and long lifespan. In mixed-species stands, western hemlock most commonly grows with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var *menziesii*), Sitka spruce (*Picea sitchensis* (Bong.) Carrière), western redcedar (*Thuja plicata* Donn ex D. Don), grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.) and/or red alder (*Alnus rubra* Bong.). The coast variety of Douglas-fir (var. *mensiezii*) is limited to coastal regions of the US and Canada, and it is the variety that has been planted in a number of locations around the world. Because Douglas-fir historically has had greater economic value than western hemlock and any other associated species, it has traditionally been the preferred species within its range of coastal western North America. The proportion of Douglas-fir planted in the coastal fog belt increased in the latter half of the twentieth century and may have been a contributing factor to the current epidemic of Swiss needle cast (SNC), a foliar disease of Douglas-fir caused by the endemic ascomycete *Phaeocryptopus gaeumannii* (T. Rohde) Petr. (Hansen *et al*., 2000). Based on dendrochronological methods, Black *et al*. (2010) concluded that the epidemic intensified during the mid-1980s, but Lee *et al*. (2013) suggested that intensification of SNC has been cyclical at least since the 1590s. In some areas of severe SNC, Douglas-fir plantations have failed, and in other areas, this species has become a smaller component within stands due to a decline in diameter and height growth (Maguire *et al*., 2002) and subsequent overtopping by associated species. With the continued prevalence of SNC, with the apparent compensatory growth response of western hemlock (e.g. Zhao *et al*., 2013), and with the increasing relative economic value of the latter species (Oregon Department of Forestry, 2014), private and public landowners within the coastal belt of the Oregon Coast Ranges have shown increasing interest in western hemlock.

Numerous silvicultural strategies have been considered as a means of mitigating the growth losses suffered by Douglas-fir in the presence of SNC, including thinning (Mainwaring *et al*., 2005a), fertilization (Mainwaring *et al*., 2005b), use of genetically tolerant trees (Johnson, 2002a; Temel *et al*., 2005) and fungicidal treatment (Mainwaring *et al*., 2002; Mainwaring *et al*., 2009). Although these strategies have shown some potential for mitigating growth losses, support for accommodating non-susceptible species such as western hemlock has gained momentum due to the above-mentioned decline in value differential, continued growth losses in Douglas-fir (Maguire *et al*., 2011) and the fluctuating but generally increasing prevalence of the pathogen throughout the Oregon Coast Ranges landscape (Kanaskie and McWilliams, 2012).

In healthy mixed stands of Douglas-fir and western hemlock, Douglas-fir generally exhibits greater early height growth and becomes the dominant species within an even-aged, stratified stand (Wierman and Oliver, 1979). Because western hemlock is shade tolerant, it can persist and grow below the main canopy. In SNC-impacted stands that have suffered significant Douglas-fir foliar loss (foliage retention (FR) $\leq$1.5 years), leaf area index of Douglas-fir has declined up to 31 per cent relative to healthy stands (initial Douglas-fir FR $\geq$3.5 years) (Weiskittel and Maguire, 2007). This degree of Douglas-fir foliar loss in mixed stands would be expected to evoke compensatory growth in western hemlock for two reasons: (1) greater light penetration through the upper Douglas-fir canopy enhances light availability to subordinate species and (2) loss of foliage results in diminished height growth (Garber *et al*., 2007) and reduced crown expansion of Douglas-fir (Weiskittel, 2003), thereby lowering its ability to compete with non-susceptible species.

The objectives of this study were as follows: (1) to test the hypothesis that increasing SNC severity in mixed-species stands stimulates compensatory growth in western hemlock and (2) to quantify western hemlock compensatory growth as the degree of diameter growth release in mixed stands with varying SNC severity. In pursuit of these two objectives, a diameter increment model for western hemlock (Hann *et al*., 2003) was modified and fitted to data from a growth impact study (GIS) (Maguire *et al*., 2011) and from control plots on two thinning studies (Mainwaring *et al*., 2005a) implemented by the Swiss Needle Cast Cooperative (SNCC). SNC effects were represented by two separate covariates, initial Douglas-fir FR at the start of the growth period and periodic annual change in FR over the same growth period. This study aimed to describe the compensatory growth of western hemlock and associated changes in stand dynamics imposed by SNC, with the ultimate goal of assisting silvicultural decision-making in mixed stands of western hemlock and Douglas-fir experiencing a range in SNC severity.

Methods

Studies

Data for this study were compiled from three ongoing studies established by the SNCC to investigate Douglas-fir growth losses associated with SNC and to test for interaction effects between thinning and initial SNC on both growth responses and subsequent change in SNC severity (Table 1). Plots were established in predominantly Douglas-fir stands across a range in topographic position and initial SNC severity. Latitude ranged from 43.5 to 46.22°N, longitude from 124.06 to 122.29°W and elevation from 14 to 312 m above sea level. Over the last 40 years, the mean January (coldest month) minimum temperature for this region was 0°C and the mean July (warmest month) maximum was 25°C. Total annual precipitation averaged 150–300 cm, with ~70 per cent of the total falling between October and March.

Growth Impact Study plots were established in the winter and spring of 1998 within 76 Douglas-fir plantations in north coastal Oregon. These plots were selected to characterize SNC severity and associated growth impacts within young stands located in the Oregon Coast Ranges (Maguire *et al*., 2002, 2011). The sample was drawn randomly from a comprehensive list of stands meeting the following criteria: (1) total age between 10 and 30 years, (2) at least 80 per cent Douglas-fir by basal area and (3) geographic location within 29 km of the Pacific Ocean and between latitudes corresponding to the cities of Newport and Astoria.

Pre-commercial Thinning (PCT) plots were established in 23 Douglas-fir plantations to assess the effects of PCT on SNC symptom development and possible growth deceleration (Kanaskie *et al*., 1998). In April and May of 1998, 23 paired plots were established within 47 km of the Pacific Ocean and within the same latitudinal range as the GIS.

The Commercial Thinning (CT) Study was designed to test the influence of CT on tree growth and SNC symptom development (Mainwaring *et al*., 2004, 2005b). Plots were established in 30 stands scheduled for thinning and therefore had total ages ranging from 25 to 60 years. The CT plots were chosen to fill a sampling matrix based on three levels of SNC severity

Table 1 Summary of tree-level variables used to model periodic annual diameter increment of western hemlock trees growing in mixture with Douglas-fir experiencing varying intensity of SNC

Variable	Definition	Mean	SD	Min	Max
Modelling dataset (3029 trees)					
DBH (cm)	DBH (1.37 m)	15.21	9.27	4.90	100.90
CR	Crown ratio	0.68	0.15	0.29	1.00
BAL (m^2 ha^{-1})	Basal area in larger trees	26.51	16.48	0.00	70.44
CCFL	Crown competition factor in larger trees	169.09	114.04	0.00	524.86
ΔDBH (cm $year^{-1}$)	Periodic annual increment of DBH	0.73	0.55	0.00	3.20
Validation dataset (735 trees)					
DBH (cm)	DBH (1.37 m)	15.78	10.59	5.70	103.40
CR	Crown ratio	0.77	0.13	0.13	1.00
BAL (m^2 ha^{-1})	Basal area in larger trees	22.49	15.26	0.00	58.92
CCFL	Crown competition factor in larger trees	128.96	78.24	0.00	311.62
ΔDBH (cm $year^{-1}$)	Periodic annual increment of DBH	0.76	0.55	0.00	2.50

(severe, moderate and light) and two levels of Douglas-fir stand density (relative density 3–5 and 5–7 m^2 ha^{-1} $cm^{-0.5}$; Curtis, 1982). Twenty-eight of the stands were in the Oregon Coast Ranges, and two were on the west slope of the Cascade Range. Half of the plots were established prior to the 2002 growing season, and the other half were established prior to the 2003 growing season. Paired 0.20-ha fixed area plots, each with a 21-m buffer, were established in each stand, and one plot was thinned and the other left unthinned as a control. Only the unthinned control plots were used in this analysis.

Plot and tree measurements

In the younger GIS and PCT plantations, all trees with diameter at breast height (DBH) of ≥5 cm were tagged on 0.08-ha permanent plots established in 1998. Trees were re-measured in 2000, 2002, 2004 and 2008. Diameter at breast height was recorded for all trees, and total height (HT) and height to lowest live branch (HLB) were measured with an Impulse 200 laser hypsometer on a subsample of 40 Douglas-fir trees across the diameter range. This subsample included the 6 largest and 2 smallest Douglas-fir trees by DBH, with the remaining 34 distributed evenly across the DBH range within the plot. If 15 or fewer western hemlock trees occurred on a plot, all hemlock trees were measured for HT and HLB by laser hypsometer. If >15 western hemlock trees occurred on the plot, then the 6 largest and 2 smallest hemlock trees by DBH were measured for HT and HLB and an additional 7 hemlock height-sample trees were distributed evenly across the DBH range within the plot. Where small trees (DBH < 5 cm) were abundant, a 0.02-ha subplot was established in the centre of the 0.08-ha plot and all trees in this smaller size class were measured for DBH. Ten dominant or co-dominant Douglas-fir trees were scored annually in April or May for SNC severity. On each tree, crown length was divided into thirds and FR estimated visually as the number of annual needle cohorts held by the tree (nearest 0.1 year). Tree-level FR was computed as the average of all crown thirds and plot-level retention as the average of all 10 sample trees.

In the CT plots, all trees with DBH of ≥5 cm were tagged on square 0.2-ha permanent plots established during the winter prior to the 2002 or 2003 growing seasons. Trees were measured before the growing seasons of 2002, 2004 and 2006 on the 15 plots established in 2002 and before the growing seasons of 2003, 2005 and 2007 for the 15 plots established in 2003. All tagged trees were measured for DBH, and a subsample of 40 Douglas-fir trees was measured for HT and HLB. This subsample included the 10 largest Douglas-fir trees by DBH and the 4 smallest by DBH, with the remaining 26 distributed evenly across the DBH range within the plot. On the largest 10 Douglas-fir trees, breast height ages were also obtained by coring the trees. Foliage retention on the 5–10 largest trees per plot provided an estimate of SNC severity. Due to poorer visibility of crowns on these older, larger trees, binoculars were used to estimate FR to the nearest 0.1 years only in the middle of the live crown on the 5–10 largest trees on each plot. True precision of FR on some of the largest CT trees may have approached 0.5 years, but 0.1 year was retained as the appropriate precision for the average of 5–10 scored trees per plot.

Statistical analysis

Periodic annual diameter increment of western hemlock was calculated for all tagged western hemlock trees that survived at least two growth periods. Periodic annual increment, in contrast to mean annual increment, facilitated insight into the influence of initial disease intensity on subsequent 2- to 4-year growth rates and corresponding stand dynamics. For those plots that had 10 or more tree height and height to crown base measurements, missing HTs and heights to crown base for western hemlock trees were estimated as a function of DBH by fitting regression models specific to each plot and growth period. For those plots that had <10 tree height and height to crown base measurements, missing height and height to crown base of individual western hemlock trees were calculated by using equations developed by Johnson (2002b, 2002c). Predictor variables represented initial tree size, relative position of the tree in the stand, stand density, stand age, site quality and SNC severity (see variables defined in Tables 1 and 2).

Many biological processes that influence tree growth are inherently nonlinear. However, before a comprehensive multiple regression analyses is performed, it is often not clear whether the marginal effect of a given variable is best represented with or without transformation within a nonlinear model framework. Likewise, linear regression is a suitable tool for modelling growth curves if a linearizing relationship can be found between the key variables (Curtis, 1967) and biologically reasonable shapes can be determined (Trasobares *et al.*, 2004). Therefore, transformations were tested for all predictor variables in both linear and nonlinear models, including the natural logarithm, square and inverse transformation (Kmenta, 1971). Preliminary analysis revealed that nonlinear models had more reasonable residual distribution as well as higher accuracy. To account for repeated measures over time, a nonlinear model with a random plot effect was estimated using maximum likelihood by PROC NLMIXED in SAS version 9.2 (SAS Institute, Inc., 2008). Different weighting strategies were also tested on the nonlinear models, and alternative variance–covariance structures were tested on a final linearized form of the model. Final models were chosen on the basis of the root mean square deviation (RMSE), Akaike information criterion (AIC), residual analysis and biological interpretability. All parameter estimates were required to be significantly different from zero at $\alpha = 0.05$.

For selecting the most suitable regression model, it is generally advisable to use some measure of lack of fit in combination with one or more test statistics (Kozak and Kozak, 2003). An independent dataset can provide validation of model accuracy (Kariuki, 2008). In this study, a subset of 80 per cent of the plots was randomly selected for initial model development and the remaining 20 per cent was set aside for growth model validation (Table 2). The models were evaluated quantitatively by examining the magnitude and distribution of residuals on all possible combinations of predictor variables to detect any lack of fit or systematic bias. The following statistics were computed on both the modelling and validation datasets:

$$\text{Pseudo } R^2 = 1 - \frac{\sum_{i=0}^{n} (\Delta DBH - \Delta\widehat{DBH})}{\sum_{i=0}^{n} (\Delta DBH - \Delta\overline{\mathrm{DBH}})}, \tag{1}$$

$$\text{RMSE} = \sqrt{\frac{1}{n}\sum_{i=0}^{n} (\Delta DBH - \Delta\widehat{DBH})^2}, \tag{2}$$

$$\text{MD} = \frac{1}{n}\sum_{i=0}^{n} (\Delta DBH - \Delta\widehat{DBH}), \tag{3}$$

$$\text{MAD} = \frac{1}{n}\sum_{i-0}^{n} (|\Delta DBH - \Delta\widehat{DBH}|), \tag{4}$$

where ΔDBH is the observed diameter increment; $\Delta\widehat{\mathrm{DBH}}$ is predicted diameter increment; $\Delta\overline{\mathrm{DBH}}$ is mean measured diameter increment; n is the number of observations; Pseudo R^2 is an analogue to the coefficient of multiple determination; RMSE is the root mean squared error; MD is mean deviation and MAD is mean absolute deviation.

The null hypothesis representing the first objective of this analysis, i.e. that western hemlock diameter increment did not respond to variation in SNC severity in mixed-species stands, was tested by the P-value ($\alpha =$ 0.05) on parameters associated with initial FR and periodic annual change in FR within the final western hemlock diameter growth model (Kmenta, 1971). If both parameter estimates were significantly >0, then the null hypothesis would be rejected in favour of the alternative hypothesis that lower initial FR and greater periodic decline in retention were correlated

Table 2 Summary of plot-level variables used to model periodic annual diameter increment of western hemlock trees growing in mixture with Douglas-fir experiencing varying intensity of SNC

Variable	Definition	Mean	SD	Min	Max
Modelling dataset (128 plots)					
Age (year)	Stand age	26.20	11.53	11.00	69.28
FR (year)	FR	2.32	0.65	1.10	4.63
$\triangle$FR	Annual change in FR	0.04	0.16	−0.36	0.46
Distance (km)	Distance from Pacific Ocean	19.91	21.18	0.97	140.98
BA (m^2 ha^{-1})	Stand basal area per hectare	29.98	12.93	5.81	72.24
CCF	Crown competition factor (Krajicek *et al.*, 1961; using equations from Paine and Hann 1982)	199.64	80.94	63.43	539.64
D100 (cm)	Average diameter of the largest 100 trees per hectare by DBH	29.59	8.49	10.74	54.39
H100 (m)	Average height of the largest 100 trees per hectare by DBH	18.74	7.32	6.32	41.90
TPH (trees ha^{-1})	Trees per hectare	1325.79	883.09	128.00	5187.00
QMD (cm)	Quadratic mean diameter	19.48	7.91	7.34	40.13
SDI	Stand density index (metric form of Reineke, 1933)	666.85	268.04	187.12	1811.41
SI (m)	Bruce's (1981) 50 years site index	42.37	6.36	26.40	63.10
Validation dataset (42 plots)					
Age (year)	Stand age	25.35	10.38	12.00	66.51
FR (year)	FR	2.36	0.54	1.33	3.55
$\triangle$FR	Annual change of FR	0.01	0.16	−0.38	0.34
Distance (km)	Distance from Pacific Ocean	17.42	20.12	1.93	125.85
BA (m^2 ha^{-1})	Stand basal area per hectare	30.23	11.87	3.73	58.94
CCF	Crown competition factor (Krajicek *et al.*, 1961; using equations from Paine and Hann 1982)	196.02	59.35	43.53	313.93
D100 (cm)	Average diameter of the largest 100 trees per hectare by DBH	30.56	9.20	12.39	46.99
H100 (m)	Average height of the largest 100 trees per hectare by DBH	18.31	6.74	8.45	40.71
TPH (trees ha^{-1})	Number of trees per hectare	1243.59	576.11	202.00	2951.65
QMD (cm)	Quadratic mean diameter	19.10	7.16	8.12	37.56
SDI	Stand density index (metric form of Reineke, 1933)	665.34	220.61	114.52	1089.80
SI (m)	Bruce's (1981) 50 years site index	43.38	6.27	27.30	60.40

with greater western hemlock growth. The second objective, to quantify the effect of SNC intensity and intensification on western hemlock diameter growth in mixed stands (i.e. compensatory growth), was achieved by assessing the final model to depict western hemlock growth as a function of initial FR and periodic annual change in FR.

Results

The initial DBH of western hemlock within this dataset had a large range (5.0–103.4 cm), though most trees had DBH between 10 and 40 cm. Periodic annual diameter increment varied between 0.0 and 3.2 cm $year^{-1}$ (Table 1, Figure 1). The average annual change in FR (ΔFR) of Douglas-fir over the multi-year growth periods varied from −0.38 to 0.46 years/year, although the change on most plots ranged from only −0.1 to +0.1 per year (Table 2, Figure 2). The following final diameter increment equation for western hemlock required a weight of 1 DBH^{-2} to homogenize the variance:

$$\begin{aligned}\Delta DBH = \exp[&\beta_0+\beta_1\ln(DBH)+\beta_2 DBH^2\\&+\beta_3\ln(SI)+\beta_4\ln\left(\frac{CR+0.2}{1.2}\right)\\&+\beta_5\frac{BAL^2}{\ln(DBH)}+\beta_6 H100+\beta_7 FR+\beta_8\Delta FR]\\&+\delta+\varepsilon,\end{aligned} \quad (5)$$

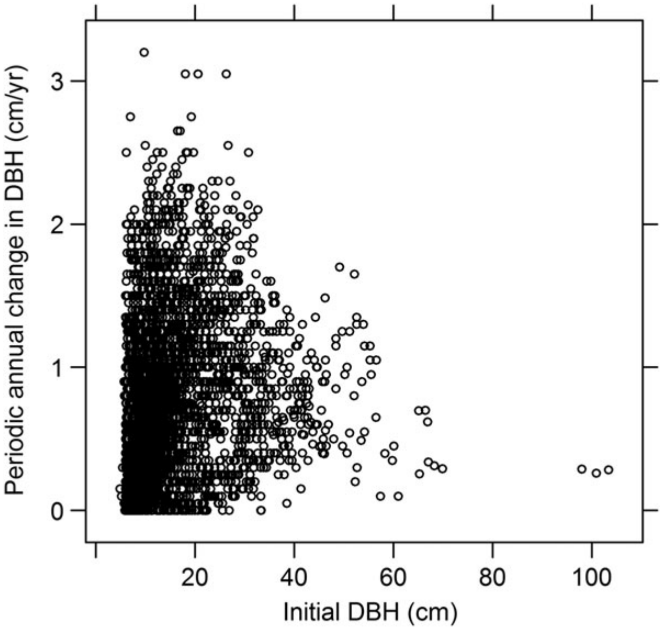

Figure 1 Relationship between periodic annual diameter increment (ΔDBH) and initial DBH for individual western hemlock trees.

where ΔDBH is periodic annual diameter growth of western hemlock (cm year^{-1}); DBH, initial tree diameter of western hemlock subject tree (cm); SI, Bruce 50 years site index (m); CR, crown ratio of western hemlock subject tree; BAL, basal area in trees with larger DBH than subject tree (m^2 ha^{-1}); H100, average height of the largest 100 trees per hectare by DBH (m); FR, initial plot mean FR of Douglas-fir (years); ΔFR, periodic annual change in plot mean FR of Douglas-fir (years/year); β_0– β_8, parameters to be estimated from the data; δ, random plot effect with $\delta\tilde{N}(0,\ \sigma_\delta^2)$; and ε, random error.

The predictor variables represented initial tree size, relative competitive position within the stand, total stand density and SNC severity, and parameter estimates indicated that the direction of each effect was consistent with expectations from silvicultural field trials, other models and stand dynamics observed on these plots (Table 3). At small initial DBH of individual western hemlock trees, diameter increment increased with increasing DBH but reached a peak and then declined with a further increase in initial DBH of the subject tree. As the social position in the stand declined (increasing BAL), western hemlock diameter growth declined. The null hypothesis that FR has no effect on western hemlock growth was rejected; in fact, diameter growth of this species was greater where SNC resulted in low initial Douglas-fir FR. Likewise, western hemlock diameter growth increased as SNC intensified over the growth period, i.e. with further reduction in FR or decreasing ΔFR. The graphical residual analysis represented by residual *vs* predicted diameter growth indicated that the models provided a good fit to the data. On the original un-weighted scale, the western hemlock diameter increment model explained ~70 per cent of the variation in diameter growth (Pseudo $R^2 = 0.7030$), RMSE was 0.2501, MD was −0.0015 and MAD was 0.2143. Validation using 20 per cent of data produced a Pseudo R^2 of 0.6388, RMSE of 0.3290, MD of −0.0807 and MAD of 0.2638. The random plot effect and alternative variance–covariance structures in the linearized mixed-effects version of this model provided no improvement over the model that assumed zero covariance. Different variance–covariance structures, such as AR(1), compound symmetry, Toeplitz, and unstructured variance components, did not improve AIC. In fact, the AIC value was slightly higher with these variance–covariance structures compared with a model assuming zero covariance. Furthermore, residuals indicated better conformity of the nonlinear model to the assumptions of least-squares estimation.

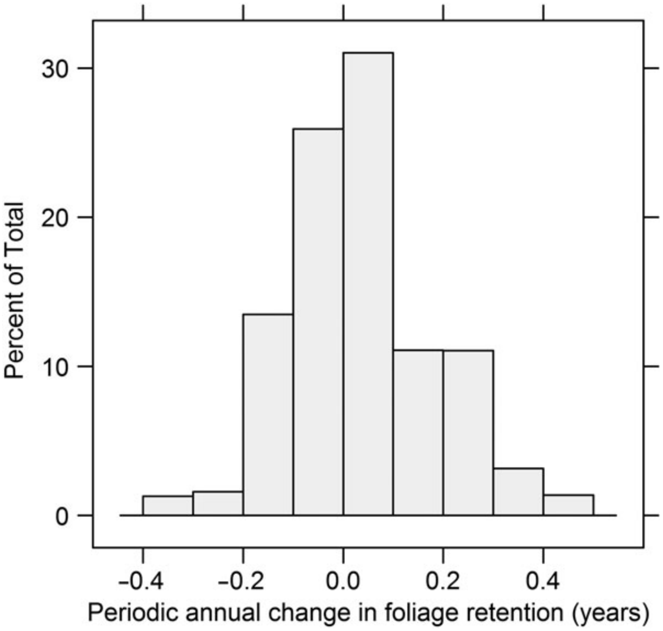

Figure 2 Frequency histogram for individual western hemlock trees by plot-level periodic annual change in FR of Douglas-fir.

In the graphical assessment of model (5), only the FR and ΔFR covariates were of interest; thus, other plot-level predictor variables were set to their mean values, i.e. CR was set at 0.7, H100 at 18.5 m and SI at 43 m. Diameter growth response was then evaluated over a range in initial western hemlock DBH (10–40 cm), initial Douglas-fir FR (1.5–3.5 years) and periodic annual change in Douglas-fir FR (−0.4 to 0.5 year) (Figure 3).

Assuming annual FR change was 0 for the growth period, the diameter increment of a western hemlock tree with initial DBH of 10, 20, 30 and 40 cm in a healthy stand (FR = 3.5 year) was 0.36, 0.66, 0.83 and 0.86 cm year^{-1}. As Douglas-fir FR declined, diameter increment of western hemlock increased to the extent that, for the same initial diameters, increment increased by 16, 34, 55 and 79 per cent, on plots with FR of 3.0, 2.5, 2.0 and 1.5 years, respectively, relative to a healthy stand with FR of 3.5 years. For a given FR, western hemlock diameter increment was also affected by the change in Douglas-fir FR over the growth period. Specifically,

Table 3 Parameter estimates for model describing periodic annual diameter increment of western hemlock (Equation (5))

Parameter	Estimate	Standard error	Pr > |t|	Lower confidence limit	Upper confidence limit
β_0	−3.7171	0.5069	<0.0001	−4.7303	−2.7038
β_1	0.8750	0.05658	<0.0001	0.7619	0.9881
β_2	−0.0003	8.9E−05	0.0004	−0.0005	−0.0002
β_3	0.9365	0.1391	<0.0001	0.6584	1.2146
β_4	0.5061	0.09158	<0.0001	0.3231	0.6892
β_5	−0.0003	0.00007	<0.0001	−0.0005	−0.0002
β_6	−0.0805	0.0064	<0.0001	−0.0933	−0.0677
β_7	−0.2906	0.0367	<0.0001	−0.3640	−0.2173
β_8	−0.6336	0.07341	<0.0001	−0.7803	−0.4868
δ	0.05575	0.0129	<0.0001	0.02996	0.08155

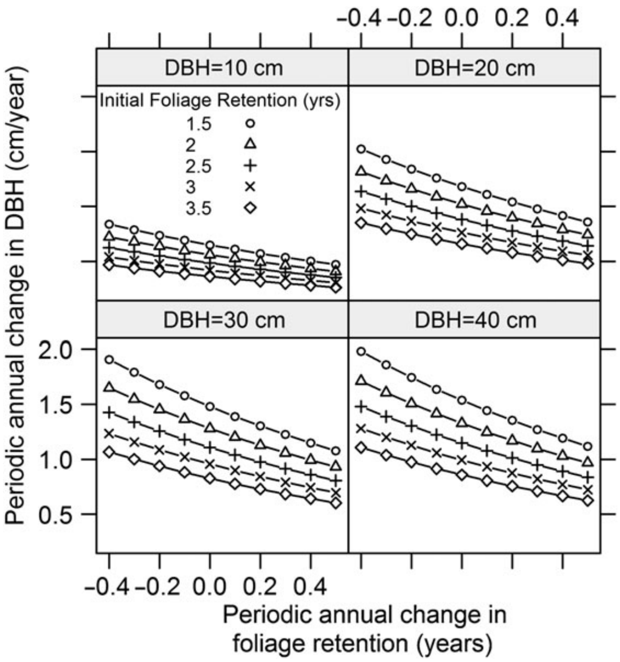

Figure 3 Predicted annual diameter increment of western hemlock at different levels of initial FR of Douglas-fir and different degrees of periodic annual change in FR (other covariates in Equation (5) were set at their mean values, except for BAL, which was allowed to covary with DBH and other predictors; specifically, $\mathrm{BAL} = 68.22262538 - 1.0493416 \times \mathrm{DBH} + 0.00534963 \times \mathrm{DBH2} - 62.29489753 \times \mathrm{CR} + 0.91673381 \times \mathrm{H100}$; $R^2 = 0.6945$).

diameter increment of a western hemlock tree increased by 21, 14 and 7 per cent, respectively, when periodic annual change in Douglas-fir FR was −0.3, −0.2 and −0.1 years/year, respectively. Conversely, diameter increment of a western hemlock tree decreased by 6, 12, 17 and 22 per cent when periodic annual increase in Douglas-fir FR was 0.1, 0.2, 0.3 and 0.4 years/year, respectively.

Discussion

Pathogen-mediated competition is of increasing interest to a broad spectrum of ecologists, due largely to its alteration of vegetation dynamics relative to those in the absence of the pathogen (Holt, 1977; Alexander and Holt, 1998; Brown and Hastings, 2003; Burdon *et al*., 2006; Borer *et al*., 2007; Cobb *et al*., 2010). In this regard, SNC has had a strong influence on stand dynamics of mixed stands of Douglas-fir and western hemlock. Presumably, the diminishing crown density of Douglas-fir trees with severe SNC allowed more light to penetrate further into the canopy and become more available to natural or planted western hemlock, relative to stands with little or no SNC symptoms. Likewise, SNC-induced growth reductions in Douglas-fir can enable hemlock to match or surpass Douglas-fir diameter growth (Zhao *et al*., 2013), diminishing the usual competitive advantage of Douglas-fir (Wierman and Oliver, 1979) and leaving more resources available for compensatory western hemlock growth (Packee, 1990).

The relationships represented within the western hemlock diameter increment model were similar to those found in other diameter growth models that have been fitted to more comprehensive databases; for example, the tree size and stand variables all have effects on diameter increment that were expected from known aspects of stand dynamics (Wierman and Oliver, 1979). The positive growth response of western hemlock trees to a decline in Douglas-fir FR and associated decrease in crown density was likely a direct consequence of greater resource availability to understory western hemlock, including light, water and nutrients.

The phenomenon of increased growth of non-host trees following defoliation of host-tree neighbours has been recorded following other pest outbreaks. Tulip-tree (*Liriodendron tulipifera* L.) and ash (*Fraxinus* spp.) exhibited increased diameter increment following defoliation of species more susceptible to Gypsy moth (*Lymantria dispar* L.) in the northeastern US (Muzika and Leibhold, 1999). The effect of western spruce budworm defoliation on diameter growth of non-host species in the Rocky Mountains depended on species, pre-outbreak stand structure and the degree and duration of defoliation (Hadley and Veblen, 1993), but ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) in particular responded positively to severe or extended outbreaks. These previous observations in other forest systems are consistent with the observed response of western hemlock diameter growth to Douglas-fir foliage loss, both at the scale of annual fluctuations related to recent weather conditions and at the scale of long-term intensification of SNC in response to climatic trends and other possible predisposing factors (e.g. Zhao *et al*., 2011; Figure 3).

This analysis of individual tree growth on GIS, PCT and CT plots from the SNCC quantified the statistically significant growth response of western hemlock to reduced Douglas-fir FR imposed by SNC. However, the gradient of increasing FR on Douglas-fir found in the Oregon Coast Ranges also parallels a gradient of declining hemlock abundance (Ohmann and Spies, 1998; Schrader, 1998) and, to some extent, a gradient in declining productivity (Meurisse, 1976), suggesting that some caution must be exercised in interpreting cause and effect. Site factors related to the decreasing abundance of hemlock on a west-to-east transect include the warmer summer temperatures, lower precipitation and increasing vapour pressure deficits associated with distance from the Pacific Ocean (Taylor and Hannan, 1999). These conditions are manifested in the poor performance of hemlock seedlings relative to Douglas-fir under such conditions (Livingston and Black, 1987). Western hemlock site productivity in the northern Oregon Coast Range has also been found to be negatively correlated with elevation (Meurisse, 1976), a trend that is difficult to separate from all the other environmental factors that vary with distance from the Pacific Ocean. The elevational effect itself is largely climatic, although chemical and physical soil characteristics may also be involved (Meurisse, 1972). Therefore, distance from the Pacific Ocean did not enter the model due to its correlation with FR.

Even in the absence of SNC, an improvement in hemlock growth relative to Douglas-fir would be expected very close to the Pacific Ocean. Although Douglas-fir generally exhibits greater height growth than western hemlock on the same site, this relative growth rate can vary by site type (Steinbrenner, 1976; Nigh, 1995). Regardless, in the presence of SNC, Douglas-fir also suffers height growth loss (Maguire *et al*., 2002); hence, the un-impacted height growth of western hemlock is likely to render it even more competitive as Douglas-fir suffers increasing foliage loss with closer proximity to the Pacific Ocean. Ultimately, the increase in diameter growth of western hemlock relative to Douglas-fir as SNC intensifies is predominantly but perhaps not entirely attributable to the reduced canopy density resulting from Douglas-fir foliar loss. Testing these effects separately would be difficult because geographic patterns in disease intensity are not independent of gradients in various climatic factors that control the growth of western hemlock even in pure stands.

In forests managed for timber production in the Oregon Coast Range, harvested stands are generally replanted to Douglas-fir or western hemlock (Briggs, 2007), with the favoured species dependent on site, market and disease conditions. It would be inappropriate to apply this diameter increment model to stands that do not match the target population for the SNCC studies included in the analysis, i.e. 10- to 60-year-old stands with at least 80 per cent initial Douglas-fir basal area. However, due to the severe impact of SNC on Douglas-fir growth in some of these stands (Maguire *et al*., 2011), and the high fecundity of western hemlock (Packee, 1990), particularly on moister sites occupied by this population, the shift in stand dynamics is important for making silvicultural decisions. Relative growth rate, yield potential and value differentials should all be considered in prescribing residual stand structure, especially with respect to species composition after thinning (e.g. Zhao *et al*., 2013). The information provided by this analysis of western hemlock growth in Douglas-fir stands with varying intensity of SNC should help prioritize stands for silvicultural treatment, as well as guide selection of trees to retain during treatment.

Acknowledgements

We gratefully acknowledge field work performed by many different field crews working for the SNCC and the Oregon Department of Forestry. Discussions and field visits with Jon Wehage of Stimson Lumber Company have provided numerous insights into the silvicultural challenges of managing mixed stands of Douglas-fir and western hemlock in the presence of SNC.

Funding

This project was supported by the Swiss Needle Cast Cooperative (SNCC) hosted at Oregon State University.

Conflict of interest statement

None declared.

References

Alexander, H.M. and Holt, R.D. 1998 The interaction between plant competition and disease. *Perspect. Plant Ecol. Evol. Syst.* **1/2**, 206–220.

Black, B.A., Shaw, D.C. and Stone, J.K. 2010 Impacts of Swiss needle cast on overstory Douglas-fir forests of the western Oregon Coast Range. *For. Ecol. Manag.* **259**, 1673–1680. doi:10.1016/j.foreco.2010.01.047

Borer, E.T., Hosseini, P.R., Seabloom, E.W. and Dobson, A.P. 2007 Pathogen-induced reversal of native dominance in a grassland community. *PNAS* **104**, 5473–5478.

Briggs, D. 2007 Management practices on Pacific Northwest westside industrial forest lands, 1991–2005, with projections to 2010. Stand Management Cooperative. SMC Working Paper #6.

Brown, D.H. and Hastings, A. 2003 Resistance may be futile: dispersal scales and selection for disease resistance in competing plants. *J. Theor. Biol.* **222**, 373–388.

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

Burdon, J.J., Thrall, P.H. and Ericson, L. 2006 The current and future dynamics of disease in plant communities. *Ann. Rev. Phytopathol.* **44**, 19–39.

Cobb, R.C., Meentemeyer, R.K. and Rizzo, D.M. 2010 Apparent competition in canopy trees determined by pathogen transmission rather than susceptibility. *Ecol.* **91**, 327–333.

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

Curtis, R.O. 1982 A simple index of stand density for Douglas-fir. *For. Sci.* **28**, 92–94.

Garber, S., Maguire, D., Mainwaring, D. and Hann, D. 2007 Swiss Needle Cast ORGANON module update. Pages 63–66, in: Shaw, D., ed., Swiss Needle Cast Cooperative Annual Report, College of Forestry, Oregon State University.

Hadley, K.S. and Veblen, T.T. 1993 Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range. *Can. J. For. Res.* **23**, 479–491.

Hann, D.W., Marshall, D.D. and Hanus, M.L. 2003 *Equations for predicting height-to-crown-base, 5-year diameter-growth rate, 5-year height-growth rate, 5-year mortality rate, and maximum size-density trajectory for Douglas-fir and western hemlock in the coastal region of the pacific northwest*. Forest Research Lab., Oregon State University. Research Contribution 40, 83 pp.

Hansen, E.M., Stone, J.K., Capitano, B.R., Rosso, P., Sutton, W., Winton, L. *et al*. 2000 Incidence and impact of Swiss needle cast in forest plantations of Douglas-fir in coastal Oregon. *Plant. Dis.* **84**, 773–778.

Holt, R.D. 1977 Predation, apparent competition, and the structure of prey communities. *Theoret. Pop. Biol.* **12**, 197–229.

Johnson, G.R. 2002a Genetic variation in tolerance of Douglas-fir to Swiss needle cast as assessed by symptom expression. *Silv. Gen.* **51**, 80–86.

Johnson, G.R. 2002b Organon calibration for western hemlock project: height - diameter prediction equation. Willamette Industries, Inc. Internal Research Report, 10 pp.

Johnson, G.R. 2002c *ORGANON Calibration for Western Hemlock Project: Crown Width, and Height to Crown Base Equations*. Willamette Industries, Inc. Internal Research Report, 16 pp.

Kanaskie, A. and McWilliams, M. 2012 Swiss Needle Cast Aerial Survey. Pg. 6–9 in 2012 Annual Report, Swiss Needle Cast Cooperative, College of Forestry, Oregon State University.

Kanaskie, A., Maguire, D., Kavanagh, K. and McWilliams, M. 1998 Growth response to precommercial thinning in Douglas-fir stands with varying intensity of SNC in the Coast Range of Oregon. Pg. 19 in 1998 Annual Report, Swiss Needle Cast Cooperative, College of Forestry, Oregon State University.

Kariuki, M. 2008 Modelling the impacts of various thinning intensities on tree growth and survival in a mixed species eucalypt forest in central Gippsland, Victoria, Australia. *For. Ecol. Manage.* **256**, 2007–2017.

Kmenta, J. 1971 *Elements of econometrics*. MacMillan.

Kozak, A. and Kozak, R. 2003 Does cross validation provide additional information in the evaluation of regression models? *Can. J. For. Res.* **33**, 976–987.

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

Lee, E.H., Beedlow, P.A., Waschmann, R.S., Burdick, C.A. and Shaw, D.A. 2013 Tree-ring analysis of the fungal disease Swiss needle cast in western Oregon coastal forests. *Can. J. For. Res.* **43**, 677–690. dx.doi.org/10.1139/cjfr-2013-0062

Livingston, N.J. and Black, T.A. 1987 Water stress and survival of three species of conifer seedlings planted on a high elevation south-facing clear-cut. *Can. J. For. Res.* **17**, 1115–1123.

Maguire, D.A., Kanaskie, A., Voelker, W., Johnson, R. and 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. and 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., Kanaskie, A. and Maguire, D. 2002 Response of Douglas-fir to Fungicidal Suppression of *Phaeocryptopus gaeumannii*: Volume Growth, Branch Elongation, and Foliage Dynamics, pp 82–86. In Filip, G. (ed.). 2002 Swiss Needle Cast Cooperative Annual Report.

Mainwaring, D.B., Maguire, D.A., Kanaskie, A. and Brandt, J. 2004 Interactive effects of Swiss needle cast and commercial thinning on Douglas-fir growth and development in North coastal Oregon: Results from the first 15 permanent plots. In Annual Report 2004. Mainwaring, D. (eds). Swiss Needle Cast Cooperative, College of Forestry, Oregon State University, pp. 80–90.

Mainwaring, D.B., Maguire, D.A., Kanaskie, A. and Brandt, J. 2005a Growth responses to commercial thinning in Douglas-fir stands with varying intensity of Swiss needle cast. *Can. J. For. Res.* **35**, 2394–2402.

Mainwaring, D.B., Maguire, D.A., Fletcher, R., Hristiansen, N., Gourley, M., Moyer, C. *et al*. 2005b Growth response of young Douglas fir to balanced fertilization in Western Oregon, pp. 51–60. In Mainwaring, D. and Shaw, D. (eds). 2005 Swiss Needle Cast Cooperative Annual Report.

Mainwaring, D., Maguire, D. and Gourley, M. 2009 Growth Responses to Sulfur Application in Douglas-fir Stands with Swiss Needle Cast, pp 82–86. In Shaw, D. and Wooley, T. (eds). 2009 Swiss Needle Cast Cooperative Annual Report.

Meurisse, R.T. 1972 Site quality of western hemlock and chemical characteristics of some western Oregon Andic soils. Ph.D. dissertation. Oregon State University. 164 p.

Meurisse, R.T. 1976 Some chemical and other properties of western hemlock soils in Oregon: their relationship to productivity. In *Western Hemlock Management Conference*. Atkinson, W.A. and Zasoski, R.J. (eds). University of Washington, pp. 49–55.

Muzika, R.M. and Leibhold, A.M. 1999 Changes in radial increment of host and nonhost tree species with gypsy moth defoliation. *Can J. For. Res.* **29**, 1365–1373.

Nigh, G.D. 1995 The geometric mean regression line: a method for developing site index conversion equations for species in mixed stands. *For. Sci.* **41**, 84–98.

Ohmann, J.L. and Spies, T.A. 1998 Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. *Ecol. Mon.* **68**, 151–182.

Oregon Department of Forestry. 2014 http://www.oregon.gov/ODF/pages/state_forests/timber_sales/logpage.aspx (accessed on 2 June).

Packee, E.C. 1990 *Tsuga heterophylla* (Raf.) Sarg. Western hemlock. In *Silvics of Forest Trees of North America. Vol. 1. Conifers*. Technical coordinators: Burns, R.M. and Honkala, B.H. U.S. Dep. Agric. Agric. Handb. 654. pp. 613–622.

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

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.

Schrader, B.A. 1998 Structural development of late successional forests in the central Oregon Coast Range: abundance, dispersal, and growth of western hemlock (*Tsuga heterophylla*) regeneration. Ph.D. Dissertation. Oregon State University.

Steinbrenner, E.C. 1976 Soil-site relationships and comparative yields of western hemlock and Douglas-fir. In *Western Hemlock Management Conference*. Atkinson, W.A. and Zasoski, R.J. (eds). University of Washington, pp. 49–55.

Taylor, G.H. and Hannan, C. 1999 *The Climate of Oregon: From Rain Forest to Desert*. Oregon State University Press, 211 pp.

Temel, F., Johnson, G.R. and Adams, W.T. 2005 Early genetic testing of coastal Douglas-fir for Swiss needle cast tolerance. *Can. J. For. Res.* **35**, 521–529.

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

Weiskittel, A.R. 2003 Alterations in Douglas-fir crown structure, morphology, and dynamics imposed by the Swiss needles cast disease in the Oregon Coast Range. M.S. Thesis. Oregon State Univ.

Weiskittel, A.R. and Maguire, D.A. 2007 Response of Douglas-fir leaf area index and litterfall dynamics to Swiss needle cast in north coastal Oregon, USA. *Ann. For. Sci.* **64**, 121–132.

Wierman, C.A. and Oliver, C.D. 1979 Crown stratification by species in even-aged mixed stands of Douglas-fir – western hemlock. *Can. J. For. Res.* **9**, 1–9.

Zhao, J., Mainwaring, D.B., Maguire, D.A. and Kanaskie, A. 2011 Regional and annual trends in Douglas-fir foliage retention: correlations with climatic variables. *For. Ecol. Manage.* **262**, 1872–1886.

Zhao, J., Maguire, D.A., Mainwaring, D., Wehage, J. and Kanaskie, A. 2013 Thinning mixed-species stands of Douglas-fir and western hemlock in the presence of Swiss needle cast: Guidelines based on relative basal area growth of individual trees. *For. Sci.* **60**. doi:http://dx.doi.org/10.5849/forsci.12-528.