

SWISS NEEDLE CAST COOPERATIVE



Annual Report 2011

SNCC Income Sources and Expenditures: 2011

Income

Membership dues	70,000
Oregon State Legislature	76,712
Carry-over	<u>54,007</u>
 Total 2009 Budget	 \$200,719

Expenditures

Salaries and wages	103,111
Travel	120
Operating expenses	1,500
Contract Work	1,068
Materials and Supplies	4,894
Indirect Costs	<u>2,456</u>
 Total 2010 Expenditures	 \$113,149

Swiss Needle Cast Cooperative, 2011 Annual Report

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PUBLICATION REPRINTS:

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Ten-year growth and mortality in young Douglas-fir stands experiencing a range in Swiss needle cast severity

Douglas Maguire, Douglas Mainwaring, Alan Kanaskie

2011 Swiss Needle Cast Cooperative Annual Report

Letter to Members from the Director

SNCC Members,

2011 has been a significant year for the SNCC, as this Annual Reports shows; we have focused on providing research, analysis, and publications that further our knowledge of the science and management of Swiss needle cast of Douglas-fir in the Oregon Coast Range. In particular, we have advanced our knowledge concerning forest nutrient applications and SNC, synthesized 10 years of growth and yield data from the Growth Impact Study (GIS) plots, and improved our understanding of the landscape foliage retention patterns and link to climate variables. We have also re-measured the Cascade Mts. plots for the third time, with funds primarily coming from the USFS, Forest Health Monitoring, while the SNCC paid for the climbers. The Annual Report also includes a synthesis of the Tree Improvement efforts, currently led by the Northwest Tree Improvement Cooperative. This is very applied and relevant information for Oregon tree growers.

Although the disease continues to intensify in the Oregon Coast Range, with 2011 total acreage estimated from the aerial survey at an all-time-high, we know more about this disease than perhaps any other foliage disease in the history of science, due to the influence of the SNCC. And we continue.

The membership supports a renewed focus on the landscape pattern of SNC across the Oregon Coast Range. This spring 2012, we will begin the process of determining sites for a new Growth Impact Study (GIS) plot system that will cover the landscape from south of Coos Bay and north to Astoria, and inland along the eastern margin of the Coast Range. This will include the entire range of foliage retention that occurs in Douglas-fir in Coast Range plantations. The plots will be installed in 2013 and measured on a 5 year return interval. The new plot system will also allow for significant collateral studies of the epidemiology of *Phaeocryptopus gaeumannii*, cause of Swiss needle cast.

We all feel that without a significant disease monitoring system, linked to forest growth and yield, it is nearly impossible to know the true impact of the disease and how best to manage for it. The SNCC provides the tree growers of western Oregon with the foundation for an Integrated Pest Management strategy, allowing assessment of current impacts as well as models of predicted landscape patterns. We continue to mix a modest budget for applied and basic research, while funding a monitoring program that includes aerial survey, GIS plots, and Cascades plots. We also provide open access to all information known about SNC on our website, including publications, landscape models, and growth impact assessment tools. The SNCC is a service organization whose goal is to aid forest health management in Oregon.

Sincerely,

David Shaw, Director, SNCC

2011 SNCC Projects

Aerial Survey. ODF/USFS Cooperative Aerial Detection Survey.

Re-measurement of the Cascades SNC Plots

Stand Dynamics of SNC Infected Coast Range Stands

Mycorrhizae

Influence of nutrient additions on SNC disease severity

10 year synthesis of Growth Impact Plots

Relationship of Foliage Retention to Climate Variables

Background and Organization

A major challenge to intensive management of Douglas-fir in Oregon and Washington is the current Swiss Needle Cast (SNC) epidemic. Efforts to understand the epidemiology, symptoms, and growth losses from SNC have highlighted gaps in our knowledge of basic Douglas-fir physiology, growth, and silviculture. The original mission of the Swiss Needle Cast Cooperative (SNCC), formed in 1997, was broadened in 2004 to include research aiming to ensure that Douglas-fir remains a productive component of the Coast Range forests. SNCC is located in the Department of Forest Science within the College of Forestry at Oregon State University. The Membership is comprised of private, state, and federal organizations. Membership dues vary depending on forestland ownership. One annual report, project reports, and newsletters are distributed to members each year. All projects are carried out in cooperation with specific members on their land holdings.

Mission Statement

To conduct research on enhancing Douglas-fir productivity and forest health in the presence of Swiss needle cast and other diseases in coastal forests of Oregon and Washington.

Objectives

- (1) Understand the epidemiology of Swiss needle cast and the basic biology of the causal fungus, *Phaeocryptopus gaeumannii*.
- (2) Design silvicultural treatments and regimes to maximize Douglas-fir productivity and ameliorate disease problems in the Coast Range of Oregon and Washington.
- (3) Understand the growth, structure, and morphology of Douglas-fir trees and stands as a foundation for enhancing productivity and detecting and combating various diseases of Douglas-fir in the Coast Range of Oregon and Washington.

Swiss Needle Cast Aerial Survey, 2011

Alan Kanaskie and Michael McWilliams, Oregon Department of Forestry

Abstract

Aerial surveys to detect and map the distribution of SNC damage have been flown annually since 1996. Although the disease occurs throughout the range of Douglas-fir, damage is most severe in the forests on the west slopes of the Coast range. The 2011 survey mapped 444,228 acres of Douglas-fir forest with obvious symptoms of Swiss needle cast; this was the largest area with damage since the survey began. Most damage occurred within 18 miles of the coast, but it extended up to 28 miles inland in some areas.

Introduction

Swiss needle cast (SNC) is a native disease of Douglas-fir that has intensified dramatically in coastal western Oregon since 1990. The main effect of SNC on forests is reduction of tree growth and vitality. In addition to growth impacts, SNC alters wood properties and affects stand structure and development. This complicates stand management decisions, especially in pure Douglas-fir stands.

Aerial surveys to detect and map the distribution of SNC damage have been flown annually since 1996. Although the disease occurs throughout the range of Douglas-fir, it is most severe in the forests on the west slopes of the Coast range, and in this area it presents a unique aerial survey signature that is highly visible for approximately 6 to 8 weeks prior to bud break and shoot elongation, usually late April to early June.

Methods

The 2011 Oregon Coast Range survey was flown on May 18 & 24 and June 8, 9, & 17, and covered approximately 2.9 million acres of forest. The observation plane flew at 1,500 to 2,000 feet above the terrain, following north-south lines separated by 2 miles. Observers looked for areas of Douglas-fir forest with obvious yellow to yellow-brown foliage, a symptom of Swiss needle cast. Patches of forest with these symptoms (patches are referred to as polygons) were sketched onto computer touch screens displaying topographic maps or ortho-photos and the position of the aircraft. Each polygon was classified for degree of discoloration as either “S” (severe) or “M” (moderate). Polygons classified as “S” had very sparse crowns and brownish foliage, while those classified as “M” were predominantly yellow to yellow-brown foliage with slightly denser crowns than those classified as “S”. The survey area extended from the Columbia River south to Brookings, and from the coastline eastward until obvious symptoms were no longer visible. We did not survey the Cascade Range in 2011, but Swiss needle cast does occur at damaging levels in some areas.

Results and Discussion

The 2011 survey results show an increase in the area of forest with symptoms of Swiss needle cast compared to the previous 3 years and reached an all-time high for the second year in a row. We mapped 444,228 acres of Douglas-fir forest with obvious symptoms of Swiss needle cast (Figure 1). As has been the case for the past several years, the easternmost area with obvious SNC symptoms was approximately 28 miles inland from the coast in the Highway 20 corridor, but most of the area with symptoms occurred within 18 miles of the coast. Figure 2 shows the overall trend in damage from 1996 through 2011. Figure 3 shows damage trends in the north and south half of the Coast range. SNC Damage continues at very high levels despite a shift by many landowners to forest management practices aimed at reducing damage from SNC.

Caution is advised when interpreting aerial survey data. The SNC aerial survey should be considered a conservative estimate of damage because observers can map only those areas where disease symptoms have developed enough to be visible from the air. Permanent plot data and ground checks show that Swiss needle cast occurs throughout the survey area, but that discoloration often is not severe enough to enable aerial detection. Considerable variation from year to year can result from weather patterns which affect both symptom development and timing of the survey. Undoubtedly, the total area of forest affected by Swiss needle cast is far greater than indicated by the aerial survey. Despite these shortcomings the aerial survey provides a reasonable depiction of the extent of moderate and severe damage, and coarsely documents trends in damage over time.

Additional Notes

We appreciate any information regarding the accuracy or usefulness of the maps. If you have a chance to look at some of the mapped areas on the ground, please let us know what you observe. Please call Alan Kanaskie (503-945-7397) or Mike McWilliams (503-945-7395) if you have questions, suggestions or comments.

The GIS data and a .pdf file can be accessed via the ODF web page at:

http://oregon.gov/ODF/PRIVATE_FORESTS/fh.shtml#Survey_Maps___Data

Acknowledgements

The 2011 survey was conducted by the Oregon Department of Forestry Insect & Disease and Air Operations sections, and was funded by the Oregon State University Swiss Needle Cast Cooperative, the USDA Forest Service Forest Health Monitoring Program, and the Oregon Department of Forestry. Trevor Courtney (ODF) piloted the plane. Mike McWilliams (ODF) is the survey coordinator and primary aerial observer; Ben Smith (USFS) and Rob Flowers (ODF) were the other aerial observers.

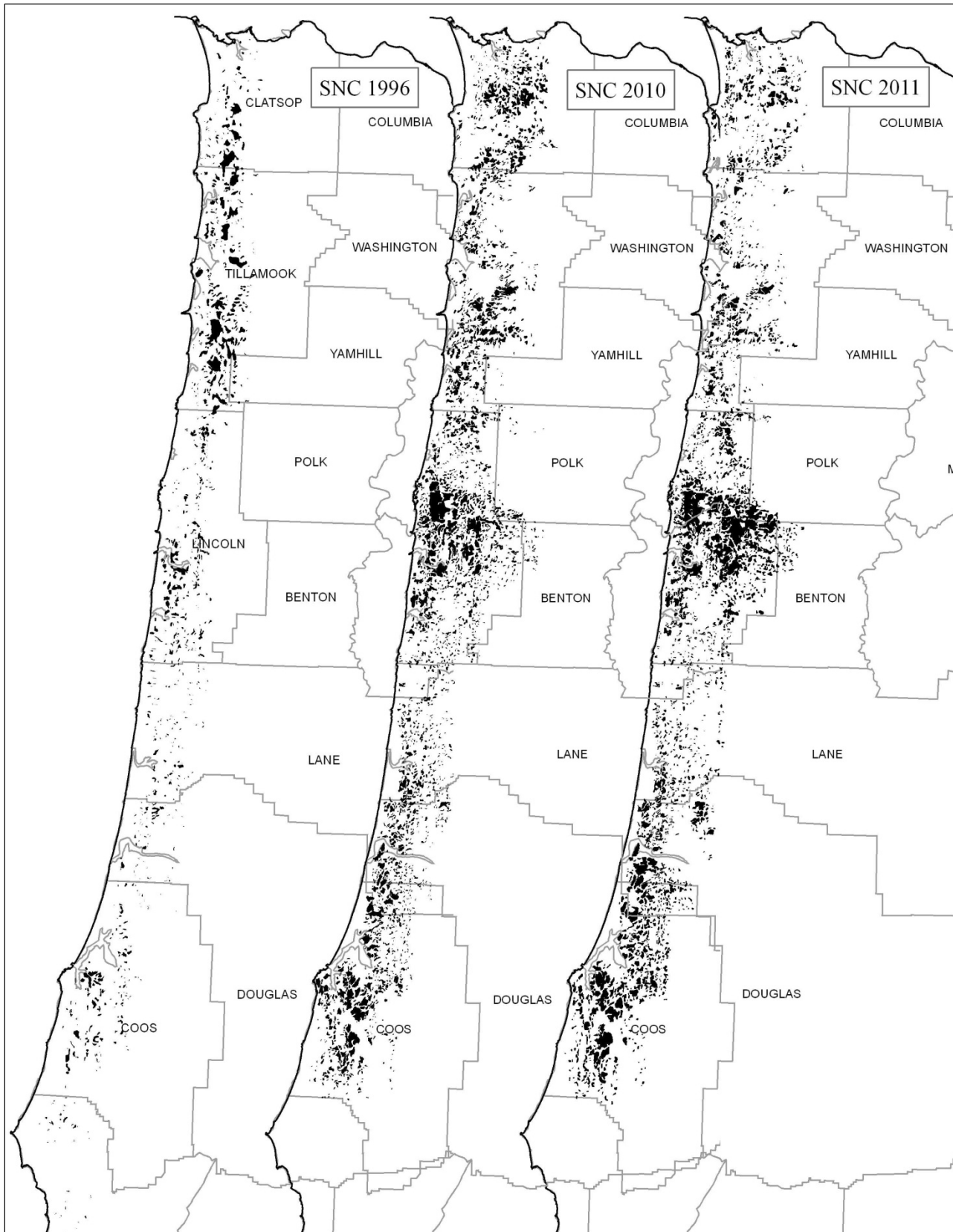


Figure 1. Swiss Needle Cast (SNC) aerial survey: areas of Douglas-fir forest with symptoms of Swiss Needle Cast detected in the 1996, 2010 and 2011 surveys. Solid black polygons (blotches) depict areas with severe or moderate damage from SNC.

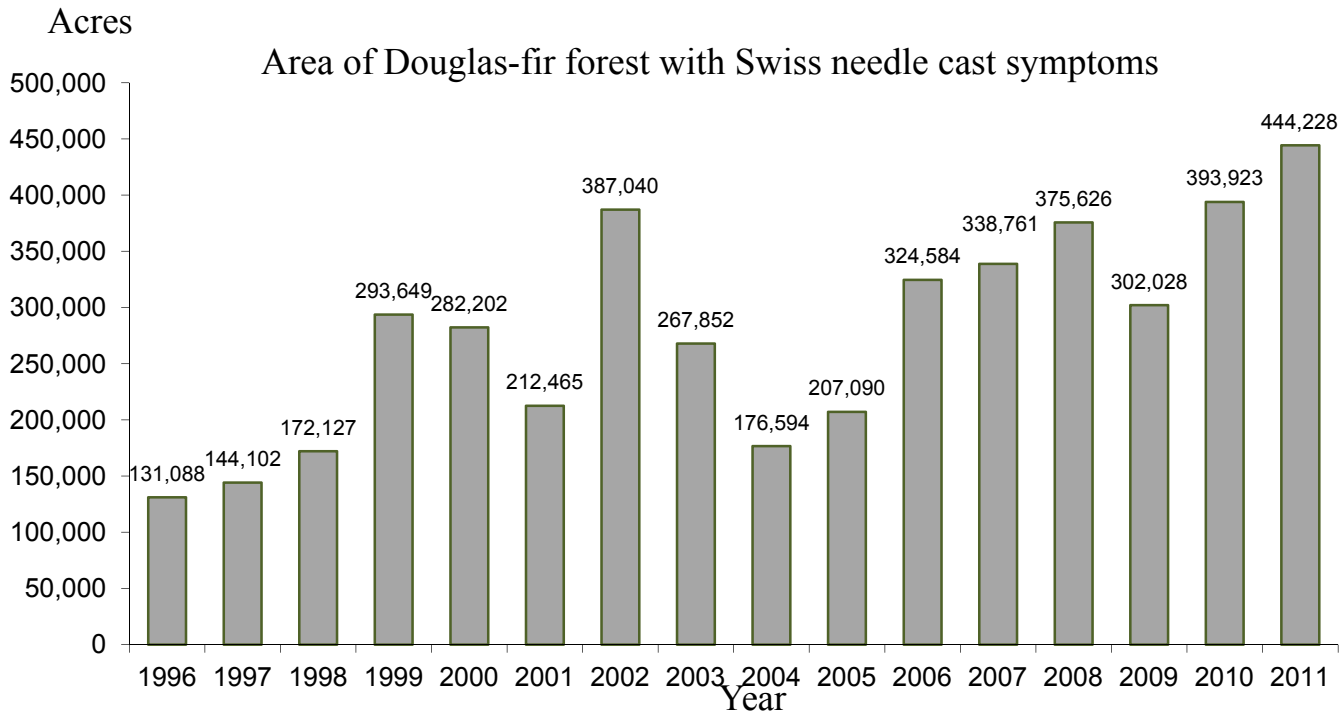


Figure 2. Trend in area of Douglas-fir forest in western Oregon with symptoms of Swiss needle cast detected during aerial surveys in April and May, 1996-2011. Results for 2008 were estimated by extrapolating from 3

sample survey blocks.

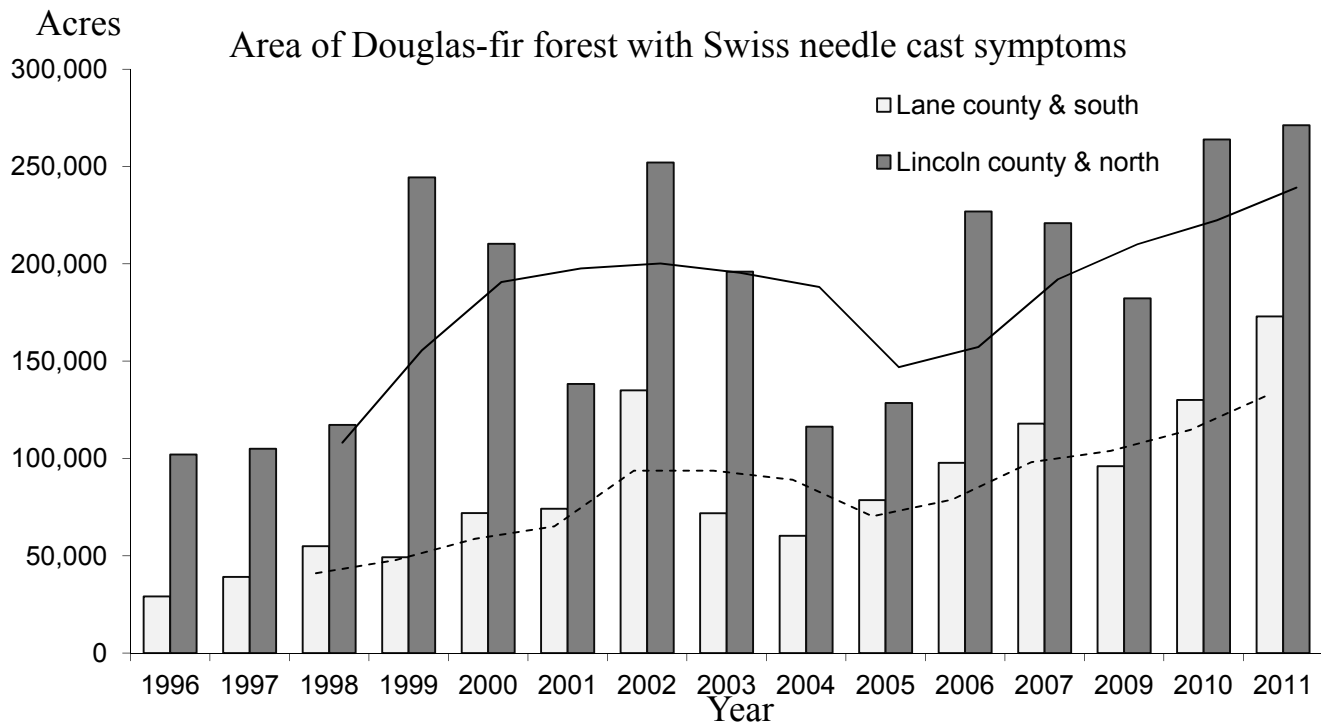


Figure 3. Trend in area of Douglas-fir forest in western Oregon with symptoms of Swiss needle cast detected during aerial surveys in April and May, 1996-2011. North region = Lincoln county & north; South region = Lane county & south. Trend lines are 3-year rolling averages.

Impacts of Swiss Needle Cast on Douglas-fir Growth in the Cascade Foothills of Northern Oregon after Ten Years

Gregory Filip, USDA For. Serv., Portland, OR; **Alan Kanaskie**, Ore. Dept. of For., Salem, OR; **Willis Littke** and **John Browning**, Weyerhaeuser Corp., Federal Way, WA; **Kristen Chadwick**, USDA For. Serv., Sandy, OR; **David Shaw**, Oregon State University, Corvallis, OR; and **Robin Mulvey**, USDA For. Serv., Juneau, AK

Report prepared for the Annual Swiss Needle Cast Cooperative Meeting, December 8, 2011

Abstract

In 2001, 2006, and 2011, we examined 590 Douglas-firs in 59 stands aged initially 10-23 years in the northern Oregon Cascade foothills. Stands ranged in elevation from 500 to 4,200 ft., slope from 0 to 60%, and current total basal area/acre from 34 to 198 ft². Mean 10-year-dbh growth was 4.2 in. (range = 1.8 to 6.0) and total-height growth was 24.7 ft. (range = 8.3 to 31.8). Mean foliage-retention index decreased by 0.4 (range = -15.8 to 8.6) over 10 years. When lab measurements are used, however, foliage-retention index increased by 3.2 over 10 years. Mid-crown foliage increased by 1.2 years (range -0.7 to 3.0). Mean percentage of stomata occluded by pseudothecia were 8.7% for 2009 (2-yr-old) needles sampled in 2011. There were poor correlations ($R^2 < 0.3$) among most variables except for stand elevation where there was a moderate correlation between elevation and either 2011 foliage-retention index ($R^2 = 0.52$) or 2009-stomata occluded ($R^2 = 0.52$), where there was more foliage and fewer pseudothecia at the higher elevations. There was no apparent effect of Swiss needle cast during the latest outbreak on Douglas-fir growth. Based on our results, forest managers do not need to change their current practices in the northern Oregon Cascades because of Swiss needle cast. Managing a mix of Douglas-fir and western hemlock at lower elevations and noble fir at higher elevations will help offset any future stand-growth declines due to Swiss needle cast and other pest outbreaks.

Introduction

Swiss needle cast (SNC), caused by the fungus, *Phaeocryptopus gaeumannii*, is one of the most damaging diseases affecting Douglas-fir in the Pacific Northwest (Hansen et al. 2000, Shaw et al. 2011). Biological impact is particularly acute on the Oregon

and Washington Coast, one of the most productive regions for forest growth in the temperate world. In 2011, the aerial detection survey mapped over 444,000 acres of Douglas-fir forest with obvious symptoms of SNC, the highest acreage recorded since surveys started in 1996. Annual Douglas-fir volume-growth losses from SNC are estimated at about 23% over 187,000 acres with some losses as high as 52% in NW Oregon (Maguire et al. 2002, 2011).

Although defoliation from SNC occurs in the northern Cascade Mountains of Oregon, it is assumed to be less than damage in the Oregon Coast Range. In 2001, baseline monitoring plots were established in 59 stands covering 2 million acres in the Cascade Mountains in Oregon with USFS-Forest Health Monitoring funding. It was essential that these plots be re-measured in order to determine the 5- and 10-year changes and biological impact of SNC on Douglas-fir growth. These plots are the only source of data for SNC impact in the Oregon Cascade Range.

Objectives of our project were to determine changes after 10-years (2001 to 2011) in 1) tree diameter and total-height growth, and live-crown ratio and 2) SNC severity as estimated by needle retention and stomata occlusion in 59 stands in the northern Oregon Cascade Mountains.

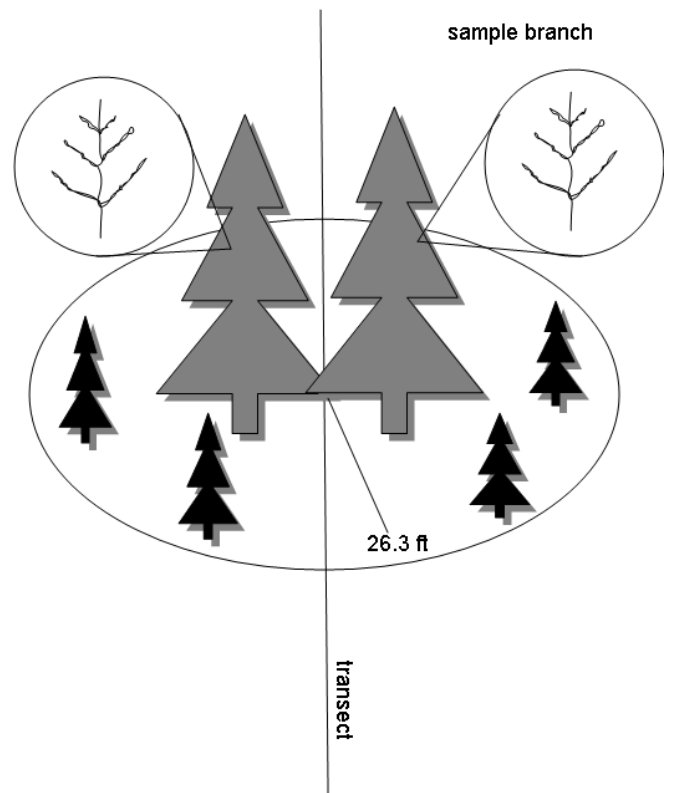


Fig. 1. Diagram of a stand plot where two dominant Douglas-firs were sampled at each of 5 plots per stand. Branches were sampled at mid-crown for foliage-retention index and needle stomata occlusion associated with Swiss needle cast.

Methods

From April to June, 2001, prior to Douglas-fir budbreak, transects were installed in 59 stands according to SNCC protocols (Kanaskie and Maguire 1999). Sampled stands were 10- to 23-years old and contained more than 50% Douglas-fir. Stands were systematically located on public and private lands in the western Oregon Cascade Mountains (Freeman 2001).

Each stand has one transect with five sample plots located at 50-foot intervals (Fig.1). Transects were established in a location representative of the stand. Stand data collected in 2001 included: 1) elevation, 2) slope aspect (8 cardinal points), 3) slope %, and 4) some GPS coordinates at the reference point at the start of the transect.

At each sample plot, the nearest co-dominant or dominant Douglas-fir on each side of the transect was selected for a total of 10 trees per stand. Data collected for each tree in 2001 included: 1) stand, plot, and tree no., 2) dbh (at 4.5 ft. above ground, nearest 0.1 in.), 3) total height (nearest ft.), 4) height to lowest live branch (nearest ft.), 5) ocular estimation of foliage retention in the mid-crown (0 to 8 yrs), and 6) foliage-retention index of a sampled branch. Heights were measured in 2001 with a clinometer. Live-crown ratios for each year were calculated by subtracting height to lowest live branch from total tree height to get live-crown length, and then dividing crown length by total tree height and multiplying by 100.

Foliage-retention index was calculated for each sample tree as follows: a live branch at mid-crown was selected on the south side of the sample tree and cut from the stem with the pole pruner. For trees with a mid-crown height >25 ft. (most trees in 2011), the tree was climbed by a certified climber, and the selected branch was severed at the trunk with a hand saw. From the cut branch, a secondary lateral branch was selected, and the amount of foliage remaining in each needle age class was rated and recorded as: 0 = 0 to 10% of full complement present, 1 = 11 to 20% present, 2 = 21 to 30% present, ..., 9 = 90 to 100% present. Ratings were summed for a minimum score of 0 and a maximum of 36 for each branch. Needle retention has been shown

to be the most reliable and efficient variable when estimating SNC severity in terms of tree volume growth loss (Filip et al. 2000, Hansen et al. 2000, Maguire et al. 2002). Needle retention as estimated from the mid-crown is considered more reliable than upper or lower crown estimates, especially in larger trees.

From April 25 to July 6, 2011, the 59 stands sampled in 2001 and 2006 were relocated using reference maps, aerial photos, and, GPS coordinates collected for all stands in 2006. The same data collected in 2001 and 2006 were collected for each tree in the 59 stands. If a sample tree was dead or severely broken, the cause was recorded, and a live Douglas-fir tree was selected near the dead tree. Total height and height of the lowest live branch were measured with a laser height measurer (Laser Technology, Inc.).

In 2011, for all 10 sample trees per stand, foliage from severed branches was placed in a sample bag, labeled as to stand and tree number; and processed in the Weyerhaeuser laboratory for pseudothecial counts and foliage retention.

Pseudothecia density measured as the percentage of needle stomata occluded is a direct method of determining the presence and severity of the causal fungus of SNC. Measurements were made on 2-year-old needles only except in 2002 where 1-year-old and 2-year-old needles were examined. In 2002, foliage from 10 of 37 stands was sampled for fungal DNA (Freeman 2002, Winton and Stone 2004).

For pseudothecial counts in 2006 and 2011, sampled needles were placed under an imager connected to a

laptop computer, and the percentage of stomata occluded was estimated.

Foliage retention also was calculated in the lab in the same manner as was done in the field on a scale of 0 to 36 for the last 4 years of foliage.

Because some stands were thinned and stand density can influence tree growth, total basal area/acre and basal area/acre of Douglas-fir were calculated in 2006 and 2011 around one tree at each of the five sample points. Total plot basal area was measured around each sample tree by counting all in-trees with a prism and multiplying by the BAF=10. Only trees ≥ 1.0 in. dbh and all tree species including hardwoods were counted.

All data were entered into an Excel spreadsheet where R^2 values were calculated from selected graphed data.

Results and Discussion

We sampled 590 Douglas-firs in 59 stands from April 25 to July 6, 2011. Numbers of sampled stands by management agency were: Salem BLM = 16; Willamette NF = 12; Weyerhaeuser = 9; Mt. Hood NF = 7; Eugene BLM = 6; Port Blakely = 6; Longview Fibre = 2; and Ore. Dept. For. = 1. Stands ranged in elevation from 500 to 4,200 ft. and % slope from 0 to 60 (Table 1). Total basal area per acre averaged 108 ft² with a range of 34 to 198. Douglas-fir basal area per acre averaged 95 ft² with a range of 34 to 198.

Some stands had been precommercially thinned either before or after initial plot establishment in 2001. Forty-six plot trees (8%) were accidentally felled, broke, or died between 2001 and 2011, and these were replaced with other trees. These trees and their replacements were not included in stand means. Other major stand species included western hemlock at the lower elevations and noble fir at the upper elevations.

Mean 10-year-dbh growth was 4.2 in. (range = 1.8 to 6.0) and total-height growth was 24.7 ft. (range = 8.3 to 31.8, Table 2). Mean live-crown ratio (LCR) decreased by 15.5% (range = 3.7% increase to 40.8% decrease) over 10 years; 6 of 43 (14%) stands increased in mean LCR. Sixteen trees were not measured for LCR in 2001. Correlations between total plot basal area and tree growth were poor at $R^2=0.00$ for dbh growth and 0.15 for height growth.

From field measurements, mean foliage-retention index decreased by 0.4 (range = -15.8 to 8.6) over 10 years (Table 2). If lab measurements are used, however, foliage-retention index increased by 3.2 in 10 years. Mid-crown-foliage retention increased by 1.2 years (range -0.7 to 3.1). In 2006 and 2011, many trees had a partial fifth-year complement of needles and some trees as many as 8 years of needles, but these were not reflected in retention indexes that score only the last 4 years of needles. Mid-crown-foliage ratings did capture 5 to 8-year-old needles. Correlations between foliage-retention index and mid-crown foliage years was moderate at $R^2 = 0.68$ in 2001, 0.54 in 2006, and 0.46 in 2011. From field measurements, mid-crown foliage averaged 4.7 years, and only three stands had <3 years of foliage in 2011.

In 2011, foliage retention was measured in the field and again in the lab on a scale of 0 to 36. Correlation between the two sampling methods was moderate

where $R^2 = 0.31$ (Fig. 2). Foliage retention measured in the lab was generally higher than measured in the field (Table 3).

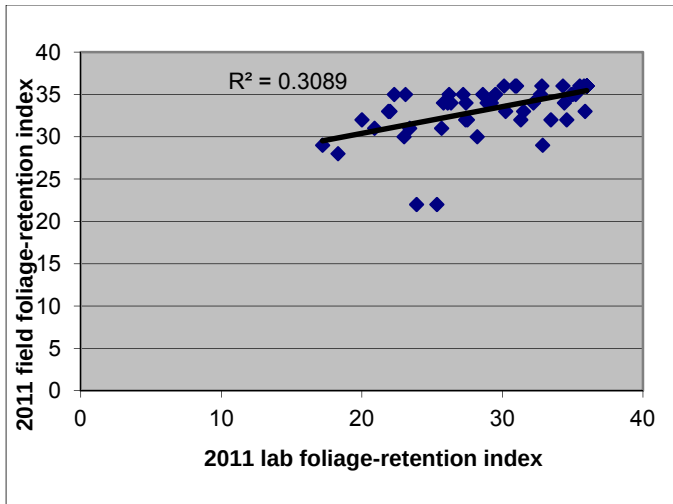


Fig. 2. 2011 field foliage-retention vs. lab foliage retention index

Mean percentage of stomata occluded by pseudothecia was 8.7% for 2009-(2-year-old) needles sampled in 2011 (Table 4). There were no stands with mean stomata occlusions >34%. Correlation between 2009-(2-year-old) needle stomata occlusion and 2004-needle stomata occlusion was moderate at $R^2 = 0.51$ (Fig. 3). Correlation between 2011 field-foliage retention and 2009-(2-year-old) needle stomata occlusion was moderate at $R^2 = 0.25$ (Fig. 4). Correlation between 2011 lab foliage-retention and 2009-needle stomata occlusion also was moderate at $R^2 = 0.25$.

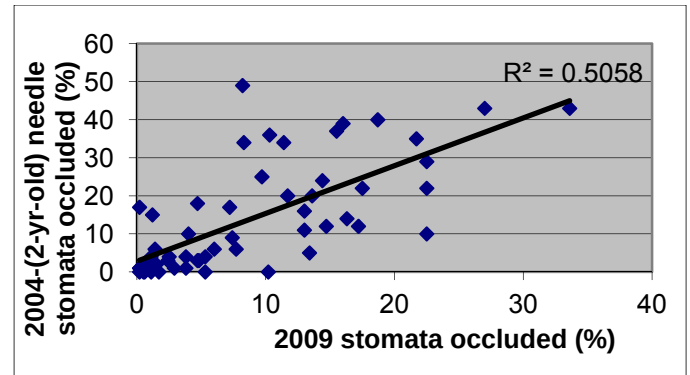


Fig. 3. 2009 pseudothecial density (stomata occluded) vs. 2004 pseudothecial density

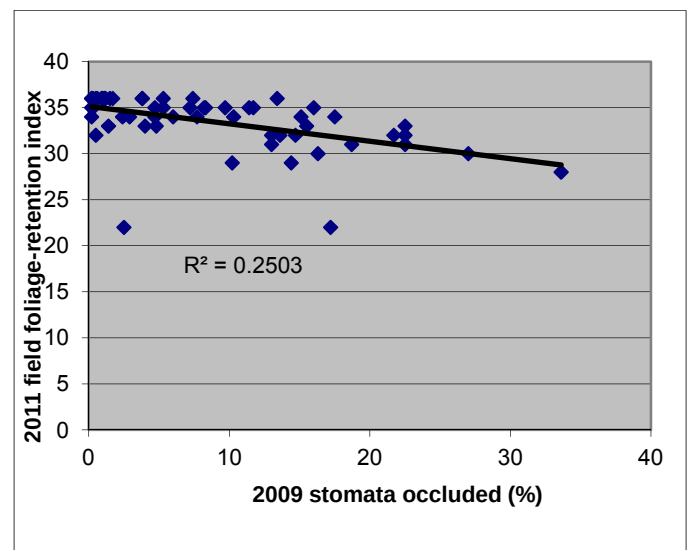


Fig. 4. 2011 field foliage-retention vs. 2009 pseudothecial density

In the Oregon Coast Range, Hansen et al. (2000) showed that increasing proportions of stomata occupied by pseudothecia were associated with increasing

defoliation. They recorded, however, mean pseudothecial densities up to 50% in 1-year-old foliage and foliage retention as low as 1 year, whereas in 2011, our highest mean pseudothecial density was 33.6% in 2-year-old needles, and our lowest mean foliage retention was 2.3 years. All pseudothecia collected in the Cascade Range in 2002 were from lineage 1 (Winton and Stone 2004).

There was a moderate correlation between stand elevation and either 2011 foliage-retention index ($R^2 = 0.52$, Fig. 5) or 2009-stomata occlusion ($R^2 = 0.52$, Fig. 6), where there was more foliage and fewer pseudothecia at the higher elevations.

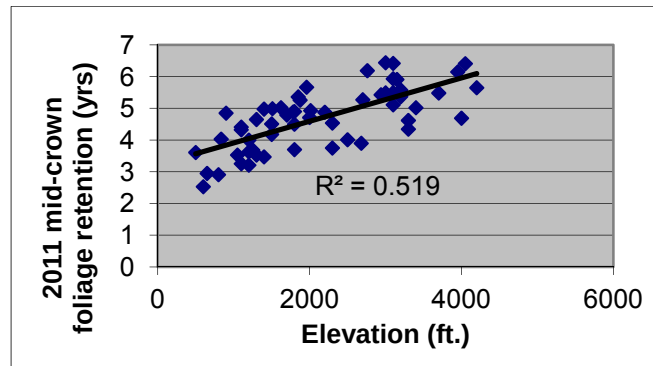


Fig. 5. 2011 mid-crown foliage retention vs. elevation

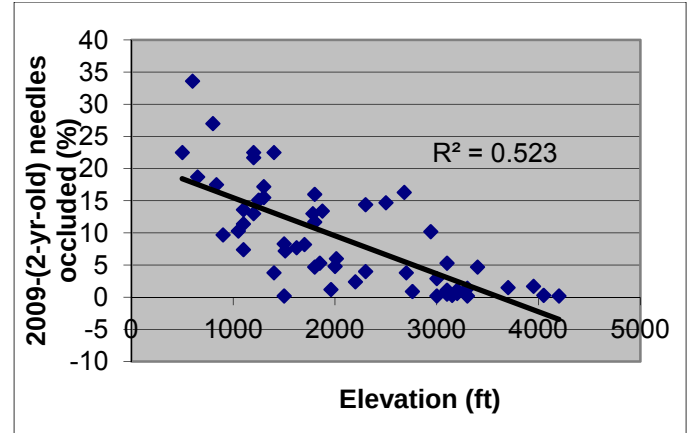


Fig. 6. 2009 pseudothecial density and elevation

There were poor correlations between 2011-mid-crown foliage (yrs) and either 10-year-dbh growth ($R^2 = 0.05$, Fig. 7) or total-height growth ($R^2 = 0.01$, Fig. 8). There were also poor correlations between growth and 2011 foliage-retention index ($R^2=0.02$ and 0.06). Poor correlations occurred between 2009-stomata occlusion and either 10-year-dbh growth ($R^2 = 0.00$) or total-height growth ($R^2 = 0.11$). There appears to be no apparent effect of Swiss needle cast on Douglas-fir growth during the latest outbreak in the Cascade Range.

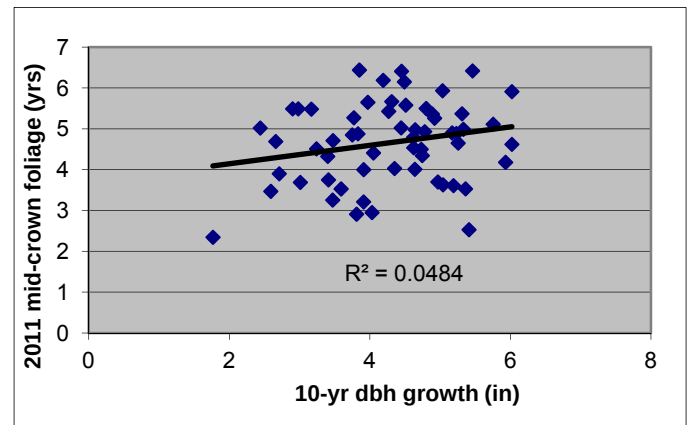


Fig. 7. 2011 mid-crown foliage retention and 10-year dbh growth

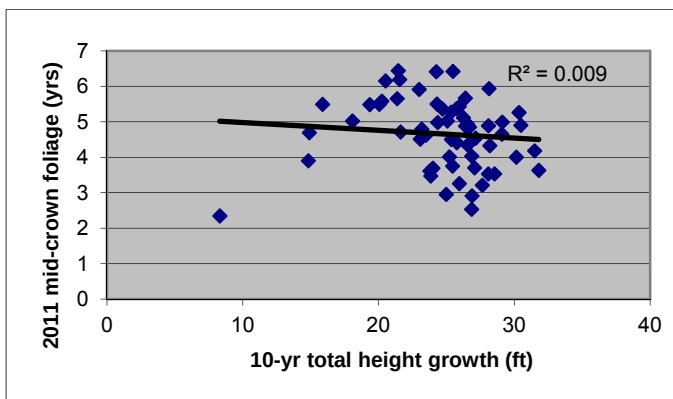


Fig. 8. 2011 mid-crown foliage retention and 10-year total height growth

Conclusions

There are at least three possible reasons why there may be no appreciable effect of Swiss needle cast on Douglas-fir 10-year-diameter and height growth during the latest SNC outbreak in the Cascade Range:

- 1) The SNC outbreak over the past 10 years in the Cascade Range is not as severe as in the Oregon Coast Range. Only a few stands sampled in the

Cascades have foliage retention of less than 3 years. There were no stands with stomata occlusions >50% on 2-year-old needles in 2001, 2006, and 2011.

- 2) Oregon Cascade Range site characteristics, including plant associations, soil chemistry and parent material, air temperatures, and monthly precipitation and leaf wetness, may not be as conducive to elevated populations of the causal fungus, *Phaeocryptopus gaeumannii*, and subsequent severe defoliation, as in the Coast Range.
- 3) The genetics (lineage 1) of isolates of the causal fungus, , in the Oregon Cascades more closely resemble isolates from Idaho, Europe, and New Zealand than isolates from the Oregon Coast Range (Winton and Stone 2004). Also, lineage 2, which is abundant in the Oregon Coast Range, has not been reported in the Cascade Mountains.

Based on our results and their interpretation, forest managers do not need to change their current practices in the northern Oregon Cascades because of Swiss needle cast. Managing a mix of Douglas-fir and western hemlock at lower elevations and noble fir at higher elevations, however, will help offset any future stand-growth declines due to Swiss needle cast or other pest outbreaks.

Acknowledgements: We thank Mike McWilliams, Oregon Dept. of Forestry; Floyd Freeman, USDA Forest Service; and Bob Ohrn and Charlie Thompson, Salem BLM. We also thank Jon Laine, Kevin Nelson, and Michael Thompson from ODF and field crews from the Salem and Eugene BLM and the Mt. Hood and Willamette NF's for data collection; and J.T. Marrs Contract Cutting for tree climbing and sampling.

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Table 1. Characteristics of 59 Douglas-fir stands sampled for Swiss needle cast in 2001, 2006, and 2011 in the northern Oregon Cascade foothills.

Stand no.	Management agency	GPS coordinates ¹		Elev.	Aspect	Slope	2011 Mean BH age	2011 Total BA	2011 D-fir BA
		LAT	LON	(ft)		(%)	(yr)	(ft ² /ac)	(ft ² /ac)
1	Pt. Blakely	45.20393	-122.35942	1100	S	10	23	136	124
2	Pt. Blakely	45.18443	-122.27665	1850	SW	20	17	72	60
3	Pt. Blakely	45.18083	-122.27313	2300	NW	12	17	136	84
4	Pt. Blakely	45.19712	-122.29237	1400	Flat	0	17	142	136
5	Weyerhaeuser	45.09250	-122.31322	3100	SW	15	17	56	46
6	Salem BLM	45.12722	-122.37168	2000	SW	35	15	34	34
7	Pt. Blakely	45.16453	-122.35352	1800	SW	35	22	144	124
8	Salem BLM	45.15162	-122.26048	3200	SE	35	17	92	26
9	Longview	44.69668	-122.71813	650	NE	-	23	128	114
10	Weyerhaeuser	44.68803	-122.63747	1500	NW	-	16	96	76
11	Weyerhaeuser	44.65632	-122.70475	1250	SW	-	25	162	162
12	Weyerhaeuser	44.63193	-122.68848	1100	N	15	23	154	150
13	Salem BLM	44.61547	-122.68780	1200	SW	35	17	100	76
14	Salem BLM	44.59718	-122.65010	1200	SW	50	26	120	112
15	Mt. Hood NF	45.10822	-122.26623	3150	NW	30	19	154	102
16	Salem BLM	44.64317	-122.63410	2500	SW	20	18	84	84
17	Salem BLM	44.58198	-122.67142	1200	NW	40	23	124	116
18	Salem BLM	44.55993	-122.67432	1400	SW	20	27	102	88
19	Weyerhaeuser	44.53648	-122.70077	800	W	20	16	114	106

20	Weyerhaeuser	44.52707	-122.68888	1100	Flat	0	19	172	168
21	Weyerhaeuser	44.52180	-122.69145	1050	NW	-	19	198	198
22	Salem BLM	44.49972	-122.67722	1300	SW	-	24	112	112
23	Pt. Blakely	45.14811	-122.50266	500	-	-	16	102	96
24	Longview	45.25508	-122.18228	1800	-	-	16	126	114
25	Salem BLM	45.27173	-122.45488	900			25	178	178
27	Salem BLM	45.49572	-122.20593	1300	NW	20	22	150	114
28	Ore Dept. For.	44.82132	-122.62608	1800	SW	12	17	138	120
29	Salem BLM	44.80785	-122.45861	1700	NW	25	23	148	144
30	Weyerhaeuser	45.08463	-122.47868	600	Flat	0	17	64	48
31	Weyerhaeuser	45.07693	-122.45002	1500	NW	15	24	138	120
32	Salem BLM	44.63497	-122.61318	3100	SW	20	19	90	66
33	Salem BLM	44.56052	-122.63832	2300	E	15	23	146	138
34	Salem BLM	44.55548	-122.39100	3400	N	50	22	56	48
35	Salem BLM	45.06953	-122.29112	3100	SW	60	19	138	118
36	Salem BLM	44.91057	-122.51382	2700	NE	15	23	136	106
37	Eugene BLM	44.30605	-122.76712	1510	SW	10	19	80	80
38	Eugene BLM	44.28665	-122.88795	2013	S	60	38	122	122
39	Eugene BLM	44.11092	-122.81654	835	NW	15	19	94	86
40	Eugene BLM	43.87277	-122.93720	1622	NW	20	17	72	70
41	Eugene BLM	43.94540	-122.67043	1875	S	20	19	94	86
42	Eugene BLM	43.85107	-122.85082	1782	W	10	21	124	118
43	Mt. Hood NF	45.39463	-122.00180	2940	W	-	18	146	82
44	Mt. Hood NF	45.30740	-122.09143	2680	SW	-	22	116	68

45	Mt. Hood NF	45.10041	-121.92331	2760	W	-	18	92	120
46	Mt. Hood NF	45.07745	-122.02032	1960	NE	-	21	154	100
47	Mt. Hood NF	44.99515	-122.14238	4200	SW	-	16	90	90
48	Mt. Hood NF	44.90790	-121.90334	3000	NE	-	21	92	88
52	Willamette NF	44.81523	-122.28833	4000	SE	60	21	78	56
53	Willamette NF	44.82857	-122.01445	4050	NW	30	17	86	72
54	Willamette NF	44.68762	-122.23912	3000	NE	40	22	78	78
55	Willamette NF	44.64652	-121.92929	3100	W	15	17	56	54
56	Willamette NF	44.54910	-122.26817	3400	W	55	21	66	50
57	Willamette NF	44.55798	-122.03723	3950	S	20	18	64	38
58	Willamette NF	44.47335	-122.17038	3300	SE	10	17	70	70
59	Willamette NF	44.29578	-122.27960	3700	S	40	18	56	50
60	Willamette NF	44.19693	-122.22960	2200	SE	20	23	134	130
61	Willamette NF	44.03618	-122.51863	3300	NW	20	15	66	64
62	Willamette NF	44.03980	-122.43800	3200	SE	55	15	48	42
63	Willamette NF	44.01985	-122.35938	3100	NW	60	20	45	45
Mean				2137		26.6	19.6	107.9	95.2

¹ GPS coordinates are for the reference point at the start of the stand transect. DATUM=WGS1984

Table 2. Changes in 10-year mean dbh, total height, and live-crown ratio for 59 stands sampled for Swiss needle cast in 2001, 2006, and 2011 in the northern Oregon Cascade foothills. Means usually are from 10 trees per stand.

Stand number	Mean dbh (in.)				Mean total height (ft.)				Mean live-crown ratio (%)			
	2001	2006	2011	10-yr growth	2001	2006	2011	10-yr growth	2001	2006	2011	10-yr change
1	8.6	10.9	12.6	4.0	43.9	54.5	69.7	25.8	88.8	71.2	66.0	-22.8
2	3.5	6.1	8.4	4.9	19.8	31.3	44.5	24.7	94.2	96.8	94.7	0.5
3	4.0	6.7	8.6	4.6	24.8	38.4	51.9	27.1	93.8	83.2	67.2	-26.6
4	6.5	8.0	9.1	2.6	39.3	49.4	63.2	23.9	86.4	67.5	58.4	-28.0
5	2.3	3.4	4.1	1.8	13.6	18.6	22.0	8.4	92.5	94.6	89.4	-3.1
6	2.3	4.4	5.8	3.5	15.4	25.9	37.1	21.7	93.4	90.6	82.9	-10.5
7	7.3	10.0	12.0	4.7	40.1	52.0	65.4	25.3	94.1	88.4	78.5	-15.6
8	4.2	7.1	9.5	5.3	23.7	36.2	49.4	25.7	94.3	92.2	88.5	-5.8
9	8.7	11.3	12.8	4.1	44.1	55.1	69.1	25.0	-	68.5	56.5	-
10	4.1	7.5	10.0	5.9	23.5	38.3	55.0	31.5	-	87.0	75.4	-
11	7.8	9.5	10.8	3.0	54.3	66.1	78.3	24.0	-	53.4	42.1	-
12	9.1	11.3	12.5	3.4	52.5	64.0	78.4	25.9	76.2	58.7	46.9	-29.3
13	3.8	6.7	8.8	5.0	21.6	37.1	53.4	31.8	92.0	87.9	77.5	-14.5
14	10.0	12.2	13.9	3.9	53.6	68.4	83.8	30.2	84.7	62.9	61.7	-23.0
15	5.8	9.3	11.8	6.0	31.1	43.1	54.1	23.0	94.7	92.9	88.4	-6.3
16	4.0	6.5	8.6	4.6	24.9	36.4	50.1	25.2	92.9	89.6	82.0	-10.9
17	7.7	10.2	11.6	3.9	43.5	57.4	71.2	27.7	88.5	68.5	57.5	-30.9
18	9.3	11.8	13.9	4.6	46.3	57.5	70.6	24.3	93.4	89.7	79.1	-14.3
19	3.9	6.3	7.7	3.8	24.0	37.2	50.9	26.9	93.1	75.0	52.3	-40.8
20	6.3	8.3	9.7	3.4	37.3	50.6	65.5	28.2	87.7	64.7	47.1	-40.6
21	6.8	9.0	10.4	3.6	38.8	51.7	66.9	28.1	87.1	59.1	46.5	-40.6
22	8.4	11.2	13.7	5.3	42.0	55.4	70.5	28.5	91.9	87.1	70.5	-21.4
23	3.8	7.0	9.0	5.2	21.4	33.4	45.2	23.8	-	85.3	77.6	-
24	4.0	7.0	9.1	5.1	23.7	38.7	54.1	30.4	92.9	88.4	77.9	-15.0
25	9.7	11.8	13.4	3.7	55.9	66.1	82.6	26.7	78.2	50.5	49.9	-28.3
27	6.6	9.6	11.9	5.3	40.5	52.7	69.6	29.1	82.5	64.6	59.0	-23.5
28	4.3	7.2	9.3	5.0	25.2	39.1	52.3	27.1	94.6	83.7	68.6	-26.0
29	7.1	10.1	11.8	4.7	45.2	54.9	68.4	23.2	93.7	82.2	68.3	-25.4
30	3.9	6.9	9.3	5.4	21.8	33.2	48.6	26.8	91.1	82.7	78.0	-13.1
31	7.1	8.7	10.3	3.2	42.5	54.0	65.6	23.1	90.3	75.5	65.4	-24.9
32	4.7	7.5	10.4	5.7	27.8	39.6	54.1	26.3	95.5	87.3	85.3	-10.2
33	7.9	9.8	11.3	3.4	45.2	56.7	70.7	25.5	89.8	70.2	56.8	-33.0
34	4.0	5.3	6.5	2.5	25.8	35.6	43.9	18.1	86.7	74.9	67.4	-19.3
35	6.1	8.7	10.9	4.8	32.4	42.7	56.7	24.3	96.0	91.2	85.8	-10.2
36	6.3	8.3	10.1	3.8	37.0	49.3	62.3	25.3	86.0	76.9	67.8	-18.2
37	5.0	7.9	10.3	5.3	28.4	42.7	57.5	29.1	-	84.4	75.9	-
38	5.3	8.2	10.1	4.8	30.8	45.2	57.4	26.6	-	89.7	74.9	-
39	4.1	6.6	8.4	4.3	25.2	38.8	52.1	26.9	-	83.6	72.1	-
40	3.4	5.9	7.8	4.4	21.4	34.3	46.5	25.1	-	77.7	68.8	-
41	5.1	7.7	10.1	4.9	29.0	43.0	59.3	30.3	-	81.5	72.5	-
42	6.9	10.1	12.1	5.2	37.1	51.1	65.2	28.1	-	84.1	65.2	-
43	4.4	6.6	8.6	4.2	23.1	36.6	49.0	25.9	-	84.7	78.6	-
44	4.5	5.8	7.2	2.7	26.2	33.9	41.0	14.8	-	81.5	80.8	-
45	4.4	6.8	8.6	4.2	25.3	35.3	46.8	21.5	-	95.8	90.7	-
46	4.5	7.0	8.8	4.3	28.2	39.8	54.6	26.4	-	82.7	71.3	-
47	3.0	5.2	7.0	4.0	15.5	26.1	36.9	21.4	-	95.3	89.0	-

48	4.5	6.8	8.4	3.9	25.3	35.0	46.8	21.5	-	93.4	87.6	-
52	4.4	6.0	7.0	2.6	22.4	30.5	37.3	14.9	91.8	94.1	92.5	0.7
53	3.6	6.0	8.1	4.5	17.5	29.2	41.8	24.3	91.1	92.2	90.1	-1.0
54	5.6	7.3	8.6	3.0	31.8	41.5	51.9	20.1	89.4	87.6	85.1	-4.3
55	3.4	6.3	8.8	5.4	18.9	30.9	44.4	25.5	92.4	96.1	94.8	2.4
56	4.5	5.8	7.4	2.9	21.8	28.8	37.7	15.9	86.9	89.2	88.5	1.5
57	4.4	6.9	8.9	4.5	19.5	29.6	40.0	20.5	93.3	96.6	97.0	3.7
58	4.3	6.8	9.1	4.8	24.5	36.0	51.0	26.5	94.6	91.7	94.5	-0.1
59	3.1	4.7	6.3	3.2	17.7	26.8	37.1	19.4	94.2	93.8	92.2	-2.0
60	6.7	9.0	10.5	3.8	37.5	50.5	63.9	26.4	93.3	80.1	69.0	-24.3
61	2.8	5.8	8.8	6.0	15.3	27.6	38.7	23.4	99.0	96.1	91.3	-7.7
62	2.8	5.0	7.3	4.5	17.4	26.5	37.6	20.2	99.4	95.3	93.9	-5.5
63	4.1	6.5	9.1	5.0	25.0	39.8	53.1	28.1	94.7	91.9	95.7	1.0
Mean	5.4	7.8	9.6	4.2	30.3	42.0	55.0	24.7	91.1	82.7	75.1	-15.5
Max.	10.0	12.2	13.9	6.0	55.9	68.4	83.8	31.8	99.4	98.6	97.0	-40.8
Min.	2.3	3.4	4.1	1.8	13.6	18.6	22.0	8.3	76.2	50.5	42.1	4.7

Table 3. Changes in foliage-retention index and mean mid-crown foliage retention for 59 stands sampled for Swiss needle cast in 2001, 2006, and 2011 in the northern Oregon Cascade foothills. Means usually are from 10 trees per stand.

Stand no.	Field foliage-retention index (0-36) ¹				Mid-crown foliage retention (years) ²				Lab foliage retention index (0-36) ¹
	1997 to 2000	2002 to 2005	2007 to 2010	10-year change	1997 to 2000	2002 to 2005	2007 to 2010	10-year change	2007 to 2010
1	32.3	33.4	22.3	-10.0	3.6	4.5	4.4	0.8	35
2	29.2	36.0	35.5	6.3	3.2	4.6	5.4	2.2	36
3	33.1	36.0	21.9	-11.2	3.6	4.5	4.5	0.9	33
4	26.0	33.0	22.0	-4.0	2.9	3.7	3.5	0.6	33
5	27.4	17.0	23.9	-3.5	3.0	1.9	2.3	-0.7	22
6	27.3	36.0	35.9	8.6	2.9	4.6	4.7	1.9	33
7	32.6	36.0	23.1	-9.5	3.6	4.7	4.5	0.9	35
8	34.0	35.8	36.0	2.0	3.7	4.4	5.4	1.7	36
9	23.1	34.3	23.4	0.3	2.4	3.6	3.0	0.6	31
10	27.8	34.1	29.1	1.3	3.0	4.6	4.2	1.2	34
11 ²	26.4	-	28.9	2.5	2.9	4.2	3.7	0.8	34
12	24.2	36.0	20.0	-4.2	2.5	4.1	3.3	0.8	32
13	24.5	35.9	31.3	6.8	2.7	4.4	3.6	0.9	32
14	34.1	36.0	25.7	-8.4	4.0	4.4	4.0	0.0	31
15	33.2	35.8	32.7	-0.5	3.7	5.2	5.9	2.2	35
16	27.7	35.8	34.6	6.9	3.1	4.7	4.0	0.9	32
17	35.4	32.0	20.9	-14.5	3.7	4.1	3.2	-0.5	31

18	32.9	36.0	30.1	-2.8	4.0	4.9	5.0	1.0	36
19	22.9	31.9	23.0	0.1	2.5	3.7	2.9	0.4	30
20	33.8	35.1	30.9	-2.9	3.7	5.1	4.3	0.6	36
21	34.7	29.7	27.4	-7.3	3.9	4.6	3.5	-0.4	34
22	25.8	35.2	31.5	5.7	2.8	4.3	3.5	0.7	33
23	25.4	35.8	33.4	8.0	2.7	5.0	3.6	0.9	32
24	29.2	35.6	28.6	-0.6	3.1	4.8	4.9	1.8	35
25	32.8	36.0	26.2	-6.6	3.6	4.3	4.9	1.3	35
27	31.2	32.8	25.3	-5.9	3.3	4.4	4.6	1.3	22
28	29.8	35.2	34.9	5.1	3.2	4.2	3.7	0.5	35
29	29.1	36.0	35.0	5.9	3.5	5.6	4.8	1.3	35
30	21.0	31.6	18.3	-2.7	2.3	3.4	2.5	0.2	28
31	30.3	34.9	27.2	-3.1	3.3	4.5	4.5	1.2	35
32	34.3	36.0	29.5	-4.8	3.9	5.2	5.1	1.2	35
33	33.0	35.3	17.2	-15.8	3.9	4.5	3.8	-0.1	29
34	34.0	36.0	34.4	0.4	3.9	5.0	5.0	1.1	34
35	33.3	35.6	27.4	-5.9	4.0	4.6	5.5	1.5	32
36	32.6	34.5	31.0	-1.6	3.6	5.1	5.3	1.7	36
37	29.7	36.0	29.5	-0.2	3.5	5.1	5.0	1.5	35
38	30.2	35.4	26.1	-4.1	3.7	5.0	4.9	1.2	34
39	27.1	36.0	25.8	-1.3	2.9	4.5	4.0	1.1	34
40	32.4	35.9	26.3	-6.1	3.7	4.9	5.0	1.4	34
41	30.1	34.5	32.8	2.7	3.4	4.3	5.2	1.8	36
42	28.3	36.0	27.5	-0.8	3.7	4.7	4.9	1.2	32

43	30.9	36.0	32.9	2.0	4.2	4.6	5.4	1.2	29
44	26.5	30.9	28.2	1.7	3.5	3.8	3.9	0.4	30
45	34.1	36.0	36.0	1.9	4.3	5.5	6.2	1.9	36
46	33.3	35.0	34.3	1.0	5.0	5.5	5.7	0.7	36
47	32.0	35.9	36.0	4.0	3.3	5.1	5.6	2.3	36
48	33.3	36.0	36.0	2.7	4.9	6.1	6.4	1.5	36
52	29.5	33.3	34.5	5.0	3.3	4.3	4.7	1.4	-
53	34.8	36.0	36.0	1.2	3.9	5.5	6.4	2.5	36
54	27.2	35.7	32.2	5.0	3.3	4.9	5.5	2.2	34
55	31.8	36.0	36.0	4.2	3.4	5.2	6.4	3.1	36
56	33.0	36.0	36.0	3.0	4.3	5.5	5.5	1.2	36
57	35.3	35.9	36.0	0.7	3.7	4.8	6.1	2.4	36
58	23.9	33.9	30.2	6.3	2.8	4.1	4.3	1.5	33
59	29.2	36.0	36.0	6.8	3.3	5.1	5.5	2.2	36
60	31.1	35.9	29.2	-1.9	3.6	5.1	4.9	1.3	34
61	31.2	36.0	35.2	4.0	3.0	4.8	4.6	1.6	35
62	33.1	35.4	35.8	2.7	3.7	4.7	5.6	1.9	36
63	32.7	36.0	36.0	3.3	3.7	5.3	5.9	2.2	36
Mean	30.3	34.8	29.9	-0.4	3.4	4.7	4.6	1.2	33.5
Max.	35.4	36.0	36.0	8.6	5.0	6.0	6.4	3.1	36
Min.	21.0	17.0	17.2	-15.8	2.3	1.8	2.3	-0.7	22

¹Foliage-retention index is scored 0 to 36 where each of the last four years of foliage is rated on a scale of 0 to 9 where 0 = 0 to 10% foliage present in that year and 9 = 91 to 100% foliage present in that year.

²Mid-crown foliage retention is an ocular estimate from the ground of the number of years of foliage (0 to 8 years).

Table 4. Changes in percentages of occluded stomata (pseudothecial density) for 59 stands sampled for Swiss needle cast in 2001, 2002, 2006, and 2011 in the northern Oregon Cascade foothills. Means usually are from 10 trees per stand except for 2000-01 stomata where 5 trees per stand were sampled and 2004 stomata where 3 trees per stand were sampled.

Stand number	Needle stomata occluded (%)			
	2-yr-old needles Year 2000	1-yr-old needles Year 2001	2-yr-old needles Year 2004	2-yr-old needles Year 2009
1	-	-	43	11.4
2	-	-	0	5.3
3	-	-	10	4.0
4	-	-	29	22.5
5	-	-	4	2.5
6	-	-	3	4.8
7	-	-	18	4.7
8	-	-	0	1.1
9	-	-	40	18.7
10	-	-	17	0.2
11	-	-	-	15.1
12	-	-	20	13.6
13	-	-	35	21.7
14	-	-	16	13.0
15	-	-	1	0.3
16	-	-	12	14.7
17	-	-	22	22.5
18	-	-	1	3.8

19	-	-	43	27.0
20	-	-	9	7.4
21	-	-	36	10.3
22	-	-	37	15.5
23	6	3	10	22.5
24	7	1	39	16.0
25	26	4	25	9.7
27	33	8	12	17.2
28	30	2	20	11.7
29	46	1	49	8.2
30	33	11	43	33.6
31	39	2	34	8.3
32	2	0	4	5.3
33	29	6	24	14.4
34	1	0	3	4.7
35	2	0	2	0.5
36	8	2	4	3.8
37	4	0	17	7.2
38	6	1	6	6.0
39	42	2	22	17.5
40	9	2	6	7.7
41	35	3	5	13.4
42	22	1	11	13.0
43	1	0	0	10.2

44	-	-	14	16.3
45	1	0	1	0.9
46	-	-	15	1.2
47	-	-	1	0.2
48	-	-	1	0.2
52	0	0	1	-
53	1	0	1	0.3
54	5	1	1	2.9
55	0	0	1	1.0
56	1	0	0	0.5
57	1	0	0	1.7
58	25	4	6	1.4
59	1	0	2	1.5
60	12	1	3	2.4
61	0	0	0	0.2
62	1	0	0	0.6
63	9	0	4	1.1
Mean	13.6	1.7	13.3	8.7
Max.	46	11	49	33.6
Min.	0	0	0	0.2

Genetic Selection in Coastal Douglas-fir for Tolerance To Swiss Needle Cast Disease

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Introduction

Swiss needle cast (SNC) of Douglas-fir, caused by the ascomycete fungus *Phaeocryptopus gaeumannii*, is associated with significant volume growth losses (20-50%) along the Oregon Coast. Although the pathogen is endemic, disease symptoms have intensified in coastal forests of Oregon and Washington since the early 1990s, reaching a peak of 177,691 symptomatic hectares detected in the 2011 aerial survey of western Oregon (Figure 1). This symptom expression is the highest in 16 years of survey, despite the conversion of tens of thousands of pure Douglas-fir plantations to mixed or alternate species over that period. Regular surveys have not been done in Washington state in the same way, but in 1999 and 2000 about 75,000 ha. with visible symptoms were detected and the disease continues to affect stands.

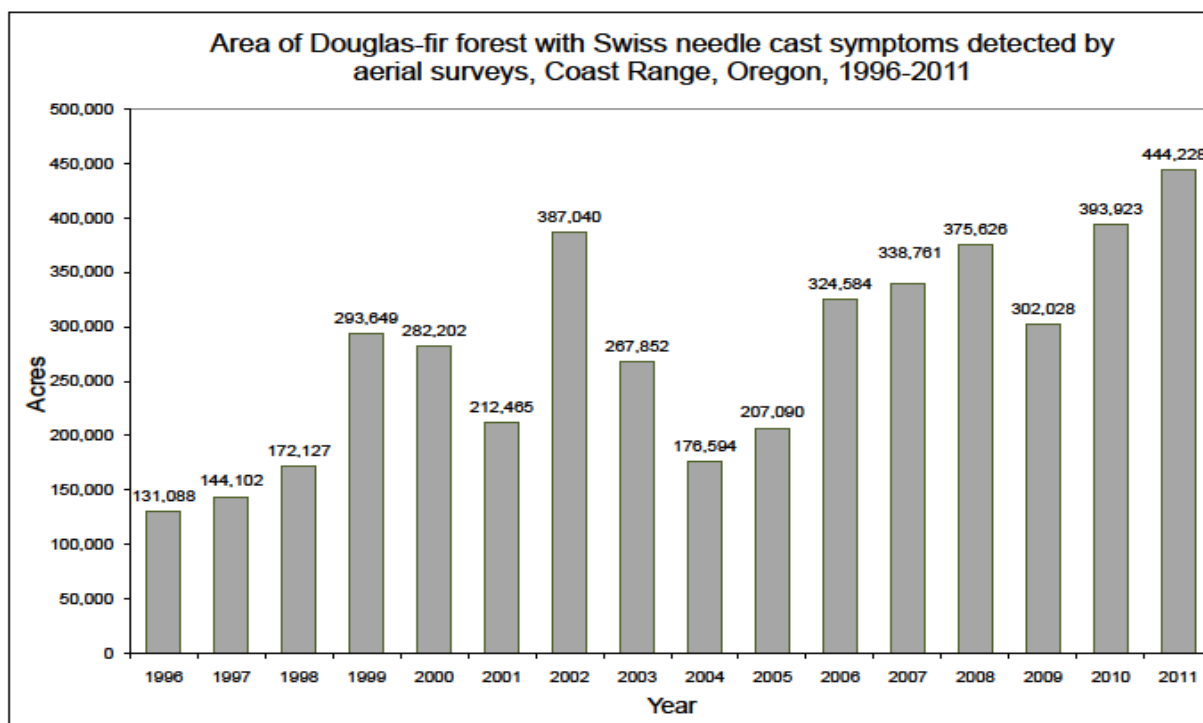


Figure 1. Area of Douglas-fir forest in western Oregon with symptoms of SNC detected during aerial surveys conducted in April-June, 1996-2011. Figure from Alan Kanaskie and Mike McWilliams, Oregon Department of Forestry.

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Coastal Douglas-fir is an enormously important timber species for Oregon; consequently, there has been considerable interest and investment in understanding the disease, quantifying its impact, finding silvicultural and management solutions, and developing seed sources suitable for this zone. The Swiss Needle Cast co-operative (SNCC) based at OSU and several breeding and testing cooperatives (supported by the Northwest Tree Improvement Cooperative also based at OSU) are working toward these goals.

All Douglas-fir everywhere are naturally infected with *P. gaeumannii*, yet the disease only develops in certain geographic settings where *pseudothecia* are produced on 1 and 2 year-old needles. Needle retention (NR) is directly related to tree productivity. Trees with less than 2 years NR are significantly less productive than normal NR (3 years or more). Severely infected trees have <1 year foliage retention. Fungal infection and needle colonization occur passively, through needle stomata and the needle apoplast, respectively, and neither process requires physical or enzymatic penetration of host tissue that might trigger a host defense response. Climatic conditions near the Oregon coast are often conducive to SNC disease development. Mild winter temperatures and spring/ summer leaf wetness are key.

There are no known resistance mechanisms, as all foliage and all trees are susceptible given the right climatic conditions during spore dispersal and colonization. No significant differences were found between families in fungal DNA content (Temel 2002). Nonetheless, tolerance to the disease was documented, with some families continuing to grow well in the presence of SNC, and adequate family-mean narrow-sense heritabilities for foliage traits.

Work in First-Generation Programs

Several studies have centered on the Nehalem progeny trial series of 400 first-generation families established on ten sites in the north Oregon coast range in 1986 and subject to moderate to heavy SNC disease pressure. This series was measured for the fourth time in summer 2010, and age-26 diameter growth from 200 families on five sites were obtained. Data have also been collected from other first-generation programs near the coast. Some key conclusions from Nehalem and other first-generation programs are as follows:

- (1) Foliage traits are heritable (individual $h^2 \approx 0.10$ to 0.23), but less heritable than growth traits ($h^2 \approx 0.3$) (Table 1). This could be from foliage traits being subjectively scored.
- (2) Crown density was seen as a better indicator of genetic tolerance than NR (Johnson 2002), but due to extensive use of NR by the SNCC it has been adopted in the tree improvement programs as well.
- (3) Growth after age-11 was more strongly associated with age-11 tree size (type-B correlations ≈ 0.7) than with foliage traits (type B correlations ≈ 0.2 to 0.5). However, rank changes have taken place for DBH between age-11 and age-26.
- (4) Usable gains for DBH were seen even at age-26. The top 10% of parents for DBH-26 had predicted gains of 18.2% over population mean for DBH-26, and predicted gains of 23.7% over population mean for DBH 18 to 26 increment.
- (5) In areas with > 2 years of foliage, gains from selection for DBH should be adequate to offset volume growth losses from SNC, and keep Douglas-fir as a viable plantation species. This is because predicted gains in volume are typically two or three times as large as predicted gains in DBH.

- (6) Selecting on an index of age-11 crown density + age-11 DBH ($\approx 13.8\%$ gain) was only slightly better than age-11 DBH alone ($\approx 13.4\%$ gain), in improving age-26 DBH.
- (7) Selecting for NR alone, foliage color or crown density at age-11 gave little to modest ($\approx 1\%$, 2.2% and 5.7%) gains in age-26 DBH.

Table 1. Heritabilities obtained from the Nehalem first-generation Douglas-fir program.

Trait	Across sites	
	Individual	Family-Mean
Height 11	0.30	0.81
Volume Index 11	0.29	0.80
Dbh 11	0.27	0.79
Dbh 17/18	0.35	0.82
Dbh 26	0.36	0.70
Dbh Increment (age-11 to 17/18)	0.32	0.80
Needle Retention: 1993 secondary laterals	0.23	0.77
Crown Density	0.18	0.71
Foliage Color	0.11	0.59

Second-cycle Trials

One second-cycle program has been established in Washington (Washington Coast), and four on the Oregon Coast:

- (1) South Central Coast in the South, with the mainline in the core Douglas-fir area, and a smaller satellite program in the zone most affected by SNC.
- (2) Plum Creek's CL98 program adjacent to South Central Coast.
- (3) Trask in the North, with a Coast program (moderately affected by SNC), and an Inland program (little affected by SNC)
- (4) Plum Creek's Toledo program in the same geographic area as Trask Coast.

These five programs have 40 progeny test sites planted between 1997 and 2008. Key points about the second-cycle work to date:

1. Needle retention is being assessed at age-7 and age-12, and DBH is being assessed at age-7 and age-12, so that an age-7 to age-12 DBH increment can be calculated. There may be additional (later) DBH assessments to confirm continued growth in DBH.
2. Ability to maintain height and diameter growth, and needle retention scores, will be the primary selection criteria within these trials.
3. Relative heritability patterns for growth traits vs. NR are similar to the first-generation (NR is less heritable than growth).

4. No molecular marker work has been done to date or currently planned. We speculate that the ability to grow in the presence of SNC is controlled by many small-effect genes.
5. A cloned breeding population might provide additional gains, compared to a seedling breeding population, but due to difficulty of rooting Douglas-fir would be expensive.
6. No early (e.g. age-2) testing has been implemented, research done by Temel et al. (2005) indicated that such testing would provide gains in foliage traits but little in the way of growth gains even at age-10.
7. Tested 2nd-cycle families have shown large realized gains in growth over unimproved Douglas-Fir in the SNC zone. In SCC, the tested families had 39.9% age-7 volume index ($\text{dbh}^2 \times \text{height}$) gains over unimproved controls (on SNC sites) and 2.8% gain for NR. For TRASK, the corresponding number for the top 50 families were 48.2% and 5.7%.

Seed Orchards and Deployment

Orchard blocks (such as Georgia-Pacific's Toledo block, the Forest Service's Hebo block, and the Nehalem block at the Schroeder seed orchard complex near St Paul Oregon) serving the North Oregon coast have been established between the 1970s and 1990s. The Oregon Department of Forestry (ODF) had a strong commitment to growing a proportion of Douglas-fir on the coast, and a large area under timber management. ODF saw tree improvement as the main viable tool to counteract SNC and continue to grow Douglas-fir, and took the lead in developing a "needlecast-tolerant" orchard block around 2002 built around the Nehalem orchard block.

This orchard incorporated elite selections from the Nehalem and other coastal breeding units on the Oregon coast. The orchard is 6 acres in extent, and other cooperators have subsequently joined. Other blocks are being established, and ability to grow in the presence of SNC will remain a priority as selections are added from the 2nd-cycle and beyond. Tree-form wind-pollinated orchards are likely to be the predominant engine for producing tolerant seed. Mixtures of family lots are used. The goal is to develop seed sources capable of acceptable growth rates on sites averaging ≥ 2 years of needle retention.

Alternate Species

In areas with higher disease pressure and foliage retention ≤ 2 years, it may be prudent to use alternate timber species such as western hemlock, western red cedar, red alder, western white pine and Sitka spruce, and many forest owners have been making this switch during the past 10-15 years. Either through complete replacement as described above, or through mixed species plantings with a component of Douglas-fir (in moderate SNC areas), pure Douglas-fir stands are gradually being replaced. One consequence of SNC infection has been strong support for cooperative genetic improvement of western hemlock (Jayawickrama 2003) which is now entering into a third cycle of breeding and testing.

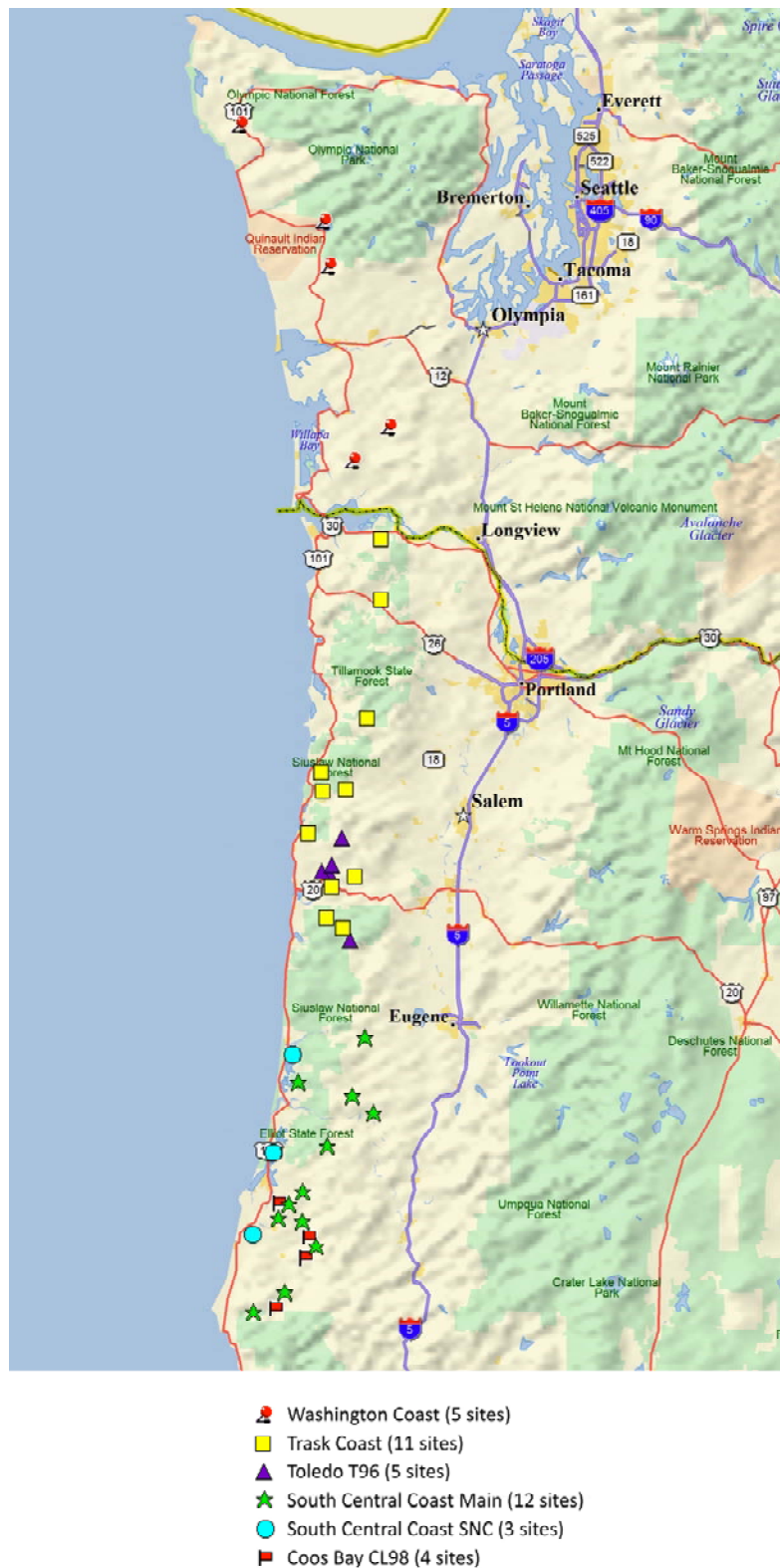


Figure 2. Second-cycle Douglas-fir test sites established on the Oregon and Washington coasts.

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Response of Swiss needle cast-infected Douglas-fir to pre-commercial thinning in northwestern Oregon

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Abstract

Swiss needle cast has intensified in north coastal Oregon over the last 20 years. Thinning has traditionally been a major silvicultural tool for managing Douglas-fir stands in this region under a wide range of management objectives, but concern has arisen about the possible exacerbation of Swiss needle cast by thinning. Twenty three sets of plots (control + thinned) were installed in 5-16 yr old Douglas-fir plantations across a gradient of Swiss needle cast severity in northwestern Oregon to test the effects of pre-commercial thinning on foliage retention and growth response. Average foliage retention increased following thinning, but this increase was limited to the lower crowns of healthy to lightly-infected trees. In the first six years after thinning, there was no evidence that foliage retention increased or decreased within any part of the crown of residual trees in the most severely infected thinned stands (initial foliage retention < 2 yrs). Thinned trees responded positively to thinning, with growth response proportional to initial foliage retention. Periodic annual volume increment per unit foliage in thinned stands was greatest in the most severely infected stands, probably because thinning from below left residual trees that were most tolerant of Swiss Needle Cast. Pre-commercial thinning did not cause any adverse impacts on either Swiss needle cast intensity or residual tree growth.

Introduction

Many Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands in western Oregon are suffering from Swiss needle cast (SNC), a foliage disease caused by the fungus *Phaeocryptopus gaeumannii* (T. Rohde) Petr. (Hansen et al. 2000). In the most severely impacted zones, successful spring colonization of new foliage on expanding Douglas-fir shoots by *Phaeocryptopus* ascospores is evidenced by fruiting bodies (pseudothecia) protruding from stomates by the following spring (Hood and Kershaw 1975). These pseudothecia inhibit normal gas exchange (Manter et al. 2000), and if enough stomates on a needle become plugged, net carbon gain becomes negative and the needle is cast. Although this fungus is endemic throughout the native range of Douglas-fir (Boyce 1940), increases in fungal presence, disease-related defoliation, and associated negative growth impacts have been apparent in coastal Douglas-fir stands since at least the 1990s (Maguire et al. 2002, Maguire et al. 2011). Annual aerial surveys across approximately 3 million acres in Oregon from 1996 to 2010 indicated that the acreage showing disease symptoms has fluctuated annually but remains high, varying from a low of 131,000 acres in 1996 to highs of nearly 400,000 acres both in 2002 and in 2010 (Kanaskie and McWilliams 2010). The extent of the epidemic does not appear to be decreasing, given the thousands of acres of infected

Douglas-fir that have been clearcut and replanted to non-susceptible species during the last 10 years. Of greatest concern to the regional economy is the growth impact on Douglas-fir, the major commercial species in this part of Oregon. In 1996, 14-34-year-old plantations with the most severe SNC were experiencing a volume growth loss of approximately 52%, with a population average loss of 23% during this period (Maguire et al. 2002). Estimates of growth losses from permanent plots measured from 1998 to 2008 were consistent with these estimates for 1996 (Maguire et al. 2011).

After the causal agent and extent of the disease was identified in the mid-1990s, regional land managers recognized that very little was known about either epidemiology of the disease or mitigation strategies for managing the significant inventory of Douglas-fir subject to SNC. This recognition motivated formation of the Swiss Needle Cast Research Cooperative (SNCC) in 1997. At that time, the highest priority was to improve the condition of young Douglas-fir plantations to ensure their survival and growth to merchantable size. Initial objectives of the research effort included identification of silvicultural treatments that could improve foliage retention and growth rates in severely infected young stands, while also addressing the concern that thinning might exacerbate SNC and associated growth decline. Accordingly, a project was launched to investigate the efficacy and risks of pre-commercial thinning in stands with differing levels of initial disease severity.

Reduction of stand density is commonly used in stands where low vigor limits individual tree growth or makes trees susceptible to pests (Mitchell et al. 1983). Results from early research addressing the effect of thinning on relatively young SNC-infected stands in New Zealand were either inconclusive (B. Manley 1985, unpublished data) or indicated that stands could be thinned without a worsening of symptoms (Hood and Sandberg 1979). The potential benefits of thinning SNC-infected stands in northwestern Oregon had been debated vis-a-vis field observations suggesting that thinning was exacerbating symptoms by increasing air flow and tree sway within stands, thereby leading to greater foliar losses.

SNC-induced foliage losses are greatest in the upper crown (Hansen et al. 2000), where physical factors such as wind and rain may accelerate casting of prematurely abscising foliage. Although stands with wider spacing experience greater wind speeds and turbulence (Gardiner et al. 1997), research has shown that SNC-diseased trees carry a greater proportion of their foliage low in the crown, where older needle cohorts are retained longer (Weiskittel et al. 2006). Because density reduction enables crowns to expand and elongate, the rationale behind thinning was an expected increase in crown length, canopy depth, and subsequent foliage area per tree, with corresponding improvement in individual tree growth and increased likelihood that trees would reach merchantable size. Furthermore, because trees show differential levels of SNC disease tolerance (Johnson 2002), thinning from below would presumably remove genotypes that were performing most poorly in the presence of SNC.

The objective of this analysis was to test the following hypotheses: (1) foliage retention on thinned plots did not decline or increase relative to unthinned plots; (2) plot volume growth for a given initial stocking did not differ between thinned and unthinned plots; and (3) plot volume growth for a given initial stocking was unrelated to initial SNC severity.

Methods

Study sites

The study sites were distributed within the Coast Ranges of northwestern Oregon across a gradient of Swiss needle cast (SNC) severity (Fig. 1). Plot locations ranged from 44.54° to 46.22° N latitude, from 123.89° to 123.38° W longitude, and from 58 to 755 m above sea level. Over the last 40 years in this region, the mean January minimum was 0°C and the mean July maximum was 25°C. Total annual precipitation averaged 150-300 cm, with approximately 70% of the total falling between October and March.

Treatments

In the late winter/early spring of 1998, 23 sets of plots were established in 5-16 yr old stands. One of the plots at each site was randomly chosen for pre-commercial thinning, generally to 500 trees per hectare (TPH), while the other was left unthinned (~1000 TPH). Because stand densities were already low on two installations, the thinned plots at these sites were prescribed to a lower target residual density of 250 TPH. Five additional 250 TPH plots were established as a third plot at five of the 21 sites that already included a plot thinned to 500 TPH. On all 21 installations that included a plot thinned to 500 TPH, both the control plots and 500-TPH plots were square and covered 0.08-ha. On the remaining two installations containing a single thinned plot with 250 residual TPH, both the control and thinned plots were twice as large, or 0.16 ha in size. On the five installations that included a third plot thinned to 250 TPH, the 250-TPH plot was also increased to 0.16 ha. All thinnings were implemented before the growing season in 1998, and were based on spacing, so stems were removed proportionally across the diameter distribution.

Measurements

On each measurement plot, all trees were measured for diameter at breast height (dbh; nearest 0.1 cm) prior to thinning. At least 40 residual Douglas-fir trees on each plot were measured for total height (nearest 0.01 m) and height to lowest live branch (nearest 0.01 m). This height subsample included the smallest and largest Douglas-fir trees by dbh, with the remaining sample trees evenly distributed across the diameter distribution. After two, four, six, and ten growing seasons (1998-99, 2000-01, 2002-03, and 2004-07 growth periods), all trees were remeasured for dbh, and all trees from the original height subsample were remeasured for total height and height to crown base. If one of the height trees had died or was top-damaged, a replacement height tree of similar size was chosen to replace it. Missing total heights and heights to crown base for Douglas-fir trees were estimated as a function of dbh by fitting regression models specific to each plot and growth period. Cubic volume of each Douglas-fir was estimated with equations previously developed for second-growth Douglas-fir (Bruce and DeMars 1974).

In April and May of each of the first seven years of the study (1998-2004), ten dominant or co-dominant trees in each plot were assessed for SNC symptoms. From the ground, foliage retention was assessed for each third of the live crown (upper, middle, lower) by visually estimating the average

number of years (nearest 0.1 yrs) of foliage retained. Tree-level foliage retention was calculated as the average of all crown-thirds. Estimates were made on the same trees each year, allowing for damaged trees to be replaced by a tree of similar size. Initial basal areas averaged 6.0, 8.5, and 15.8 m²ha⁻¹ on the 250-TPH, 500-TPH, and control plots, respectively, and initial quadratic mean diameter (after thinning) averaged 17.4, 15.1, and 14.1 cm, respectively (Table 1).

Statistical Analysis

The effect of thinning on foliage retention was analyzed for the crown as a whole, as well as for individual crown-thirds, recognizing the randomized block design of the experiment and repeated measures on individual plots. Comparisons were made among the control, 500 TPH and 250 TPH treatments. Treatment effects were considered significant at $\alpha=0.05$ and marginally significant at $\alpha=0.10$.

Treatment effects on the change in whole crown and individual crown third foliage retention were tested with the following full statistical model:

$$[1] \Delta FR = \alpha_0 + \alpha_1 \cdot FR_0 + \alpha_2 \cdot I_{250} + \alpha_3 \cdot I_{500} + \alpha_4 \cdot FR_0 \cdot I_{250} + \alpha_5 \cdot FR_0 \cdot I_{500} + \delta_1 + \varepsilon_1$$

where ΔFR	=	Periodic annual change in plot-average foliage retention (years)
FR_0	=	Initial foliage retention at start of growth period (years)
I_{250}	=	Indicator variable for thinning to 250 residual trees ha ⁻¹
I_{500}	=	Indicator variable for thinning to 500 residual trees ha ⁻¹
δ_1	=	Random block effect with $\delta_1 \sim N(0, \sigma_\delta^2)$
ε_1	=	Residual error

The residual errors were expected to be correlated among observations within a plot, so four alternative variance-covariance structures were considered for ε_1 : unstructured, Toeplitz, AR(1), and CSH (PROC MIXED in SAS version 9.2). Observations in different plots were assumed uncorrelated, so the full variance-covariance matrix was block-diagonal, with the diagonal containing the estimated variances and off-diagonals containing the estimated covariances among repeated observation within a plot.

Treatment effects on net periodic annual stem volume increment of all Douglas-fir TPH, the largest 500 Douglas-fir TPH, and the largest 250 Douglas-fir TPH were tested with the following full statistical model:

$$[2] \ln(\Delta V_C) = \beta_0 + \beta_1 \cdot \ln(FR_0) + \beta_2 \cdot \ln(BA_{DF}) + \beta_3 \cdot \ln(BA_{ODF}) + \beta_4 \cdot \ln(BA_{OS}) + \beta_5 \cdot I_{250} + \beta_6 \cdot I_{500} + \beta_7 \cdot \ln(FR_0) \cdot I_{250} + \beta_8 \cdot \ln(FR_0) \cdot I_{500} + \beta_9 \cdot \ln(SI) + \delta_2 + \epsilon_2$$

where ΔV_C = Periodic net annual volume increment of Douglas-fir component C, where C=ALL for all Douglas-fir trees ha⁻¹; 500 for the largest 500 trees ha⁻¹; and 250 for the largest 250 trees ha⁻¹ (m³ha⁻¹)

BA_{DF} = Initial Douglas-fir basal area (m²ha⁻¹)

BA_{ODF} = Initial basal area of Douglas-fir not included in component C

BA_{OS} = Initial basal area of other species (m²ha⁻¹)

SI = Bruce's 50 yr SI (based on 2004 height-age pairs) (Bruce 1981)

δ_2 = Random block effect with $\delta_2 \sim N(0, \sigma_\delta^2)$

ϵ_2 = Residual error

and all other variables are defined above

The residual errors were again expected to be correlated among observations within a plot, so four alternative variance-covariance structures were considered for ϵ_2 (PROC MIXED in SAS version 9.2): unstructured, Toeplitz, AR(1), and heterogeneous compound symmetry (Littell et al. 2006). Application of this model to only the largest 250 and 500 Douglas-fir per ha across all treatments was done to test if results would differ when limiting the comparisons to similar stand components.

In order to assess differences among growth periods in thinning effects and their interaction with foliage retention, a reduced model [2] (no covariance among observations) was also applied separately to each growth period.

A full understanding of thinning effects on SNC symptoms required some insight into the variability of foliage retention among crown classes. Data from a related growth impact study implemented by Swiss Needle Cast Cooperative (Maguire et al. 2002) were examined to test the hypothesis that foliage retention declined with lower social status within a stand. Foliage retention values on more than 700 trees from more than 70 plots were available for each of four different measurement periods. Individual-tree foliage retention was regressed on the ratio of individual-tree dbh (D) to plot-level quadratic mean diameter of Douglas-fir (Q), treating plot as a random effect.

Results

Foliage retention

On control plots, average whole crown foliage retention increased between 1998 and 2004, from a low of 2.42 yrs in 1998 to 2.71 yrs in 2004 (Fig.2). During the same period, foliage retention on plots thinned to 500 TPH increased from 2.46 yrs in 1998 to 2.88 yrs in 2004. From 1998 to 2002, there were no statistically significant differences in foliage retention attributable to the 500 TPH thinning treatment. However, treatment differences in foliage retention were apparent starting in 2003, averaging nearly 0.2 yrs during 2003 and 2004 (Fig. 2).

In stands thinned to 250 TPH, average whole crown foliage retention on control plots increased from a low of 2.64 yrs in 1998 to 3.15 yrs in 2004. During the same period, foliage retention on thinned plots increased from 2.80 yrs in 1998 to 3.40 yrs in 2004 (Fig.2). Based on ANOVA, from 1998 to 2004, there were no statistically significant differences in foliage retention attributable to the 250 TPH thinning treatment (marginally greater with thinning in 2004 ($p=0.054$)), though foliage retention was greater in stands thinned to 500 TPH in 2003 ($p=0.047$) and 2004 ($p=0.012$).

After accounting for initial SNC intensity, the annual change in whole crown foliage retention was negatively correlated with foliage retention (Table 2, Fig. 3). On plots retaining foliage less than ~2.7 yrs, foliage retention increased on average, while in healthier stands it decreased. Unthinned stands had a marginally steeper slope on initial foliage retention ($p=0.093$ on α_5 , Fig. 3) than those thinned to 500 TPH. However, stands thinned more heavily to 250 TPH were not significantly different from either the controls or thinning to 500 TPH, perhaps due to the small number of 250 TPH plots and resulting low statistical power. Similar results were obtained when this analysis was applied to foliage retention in each of the crown thirds separately, i.e., the slope of the initial retention effect was marginally steeper in the control plots than in those thinned to 500 TPH ($p=0.075$ on α_5). However, foliage retention increased for all plots but those with the highest initial foliage retention (>3.4 yrs in unthinned controls and >3.7 in plots thinned to 500 TPH; Fig. 3). Initial foliage retention had no significant effects when analyzed by crown thirds in more heavily thinned stands.

The trees selected for SNC severity rating were limited to dominant and co-dominant trees, so the average D/Q was 1.2 with a standard deviation of 0.24. Regardless, foliage retention exhibited a significant increase with increasing D/Q even over this limited diameter range. Trees in a more subordinate position therefore appeared to have significantly lower foliage retention.

Growth

Periodic net annual stem volume increment of Douglas-fir ranged from -5.9 to 28.5 m³/ha/yr in the control plots, from -0.1 to 30.1 m³/ha/yr in the plots thinned to 500 residual TPH, and from 2.8 to 22.9 m³/ha/yr in the plot thinned to 250 residual TPH (Table 1).

In the final model describing net periodic annual increment of thinned and control plots, the lowest AIC was associated with the model assuming an autoregressive covariance structure. Periodic

annual increment was positively correlated with initial foliage retention (Table 3). For a given level of initial Douglas-fir basal area, periodic annual increment was significantly greater on plots thinned to 500 TPH than on control plots, with the thinning response greater at lower levels of initial foliage retention (Table 3 and Fig. 4). For healthy stands with foliage retention of 4.0 yrs, thinning to 500 TPH was implied to increase PAI by 4.9%, for a given level of initial basal area in Douglas-fir and in other species. For stands with a foliage retention of 1.1 yrs, this increase was implied to be 58.5% (Table 3 and Fig. 4). There were no significant differences between the response of control plots and those thinned to 250 TPH.

When the analysis was limited to the largest 500 TPH, the lowest AIC was associated with the model assuming a heterogeneous compound symmetric covariance structure. Net PAI of the largest 500 TPH in the 500 TPH thinning exceeded that of the control plot regardless of foliage retention (Fig. 5). The largest 500 TPH in stands with a foliage retention of 1.1 yrs were implied to produce 81.9% more volume for a given level of initial basal area, while those in stands with a foliage retention of 4.0 yrs produced only 17.8% more volume (Table 3, Fig. 5).

When the analysis was limited to the largest 250 TPH, the lowest AIC was associated with the model assuming a heterogeneous compound symmetric covariance structure. Net PAI of the largest 250 TPH in the 500 TPH thinning exceeded that of the same component within the control plot regardless of foliage retention (Fig. 6). There were no significant differences between the response of the 250 largest TPH on the control plots and the same stand component on plots thinned to 250 TPH. The largest 250 TPH in stands thinned to 500 TPH and with a foliage retention of 1.1 yrs were implied to produce 90.2% more volume than those in control plots for a given level of basal area, while those in stands with a foliage retention of 4.0 yrs produced only 17.3% more volume (Table 3, Fig. 6).

When growth periods were analyzed separately, no response to thinning was apparent in the first two years following treatment at either level of thinning. In subsequent periods, the thinning response in plots with maximal foliage retention and thinned to 500 TPH was significant and positive, ranging from 13% in the second growth period (3-4 years after thinning) to 20% in the fourth growth period (7-10 years after thinning) (Table 4, Fig. 7). During the same periods, response to thinning to 500 TPH in the most severely infected stands (1.1 yrs foliage retention) ranged from 90 to 123% (Fig. 7). Douglas-fir net PAI also responded significantly to the 250 TPH thinning, although the interaction between foliage retention and thinning was marginally significant ($p=0.076$) in the third growth period (5-6 years) after thinning. During the second (years 3-4) and fourth growth periods (years 7-10) after thinning, the interaction between foliage retention and thinning to 250 TPH was non-significant ($p\sim 0.14$; Table 4), however, as stated above, the combined main effect of thinnings and their interaction effects with foliage retention led to a significantly positive net effect of thinning in the second through fourth growth periods, regardless of initial foliage retention (Fig. 7).

Discussion

Contrary to concerns about adverse effects of thinning in the presence of Swiss needle cast, there was no evidence of any significant decline in foliage retention induced by thinning, even in the

most severely infected stands. Although foliage retention increased in the lower crowns of all but the most healthy trees following treatment, the increase was less in plots thinned to 500 TPH than in unthinned plots. This damped increase in foliage retention after thinning may result from enhanced conditions for successful infection of *P. gaumannii* or some other factors such as the increase in wind turbulence and physical battering that occurs after thinning (Zhu et al. 2001). It has also been shown that growth acceleration (e.g., after fertilization; Balster and Marshall 2000) leads to a decline in foliage retention due to: 1) greater annual shoot lengths; and 2) constant foliated length on branches. Therefore, the slower increase in foliage retention at the base of the crown may indicate release of the lower branches by thinning or densification of the lower crown (Brix 1981).

Pseudothecial abundance is greatest and foliage retention poorest in the upper crowns of trees, which suggests that conditions in the tree tops are more conducive to spore interception, spore germination, or pseudothecial development (Hansen et al. 2000). Both epidemiological research and climate modeling have identified spring leaf wetness and winter temperatures as being directly related to successful *Phaeocryptopus* germination and growth, and subsequent needle loss (Capitano 1999, Stone et al. 2007, Zhao et al. 2011). Although leaf wetness is likely to be greater and more sustained in the lower canopy where wind speeds are lower and atmospheric drying is less effective, springtime humidity along the US Pacific coast is generally high. Temperatures conducive to fungal development can be also expected to be greater at the tops of trees than at the base of the crown (Zweifel et al. 2002). Whether there are differences in *Phaeocryptopus* ascospore deposition within the crown is unknown—while interception of ascospores by upper branches might result in decreased penetration of spores to lower branches, it is unknown what role throughfall precipitation and successive dripping of intercepted precipitation from upper to lower foliage play in dispersal and deposition. Other research has linked excess foliar nitrogen and associated free amino acid (FAA) concentrations with increased levels of *Phaeocryptopus* (El Hajj et al. 2004). Although the nutritional requirements of *Phaeocryptopus* remain poorly understood, this proposed link, in concert with an observed increase in N concentration with increased canopy light exposure (Brooks et al. 1996, Schoettle and Smith 1998), could partly explain the decreasing gradient in SNC severity with depth into crown.

Numerous changes occur within newly thinned stands that affect the environment vis-à-vis SNC. The fact that foliage retention within the lower crown of healthy thinned stands was greater than in unthinned stands suggests that in the absence of SNC or loosely held needles, increased wind speeds do not by themselves cause a net loss of needles. At the same time, increased wind speeds in the lower canopy would presumably result in lower humidity and more effective drying of needles, thus negatively impacting fungal germination and needle colonization. Although it has been hypothesized that high FAA concentrations resulting from surplus foliar N could provide substrate for fungal growth, N concentration tends to be lower in foliage near the base of the crown in closed stands. However, residual trees in thinned stands have been shown to exhibit greater nitrogen allocation to RuBisCo in lower foliage and to increase total foliar N (Han et al. 2006), as a means of responding to the increased light levels (Brix 1993). Temperature or enhanced longitudinal growth may be more likely drivers of reduced increase in foliage retention in the lower crown immediately after thinning (Fig. 3). Thinning can

increase temperatures in the lower canopy (Rambo and North 2009), resulting in more rapid psuedothecial development (Capitano 1999) of older, previously infected needles.

The extent to which an increase or decrease in stand-level foliage retention could be an artifact of thinning from below is unknown; i.e., the relationship between average tree-level foliage retention and relative height or crown class is largely unknown. In the current analysis, stand level foliage retention was entirely based on estimates from dominant trees; therefore, if foliage retention was lower or higher on smaller trees that were removed during thinning, the immediate effect of thinning would be to decrease or increase, respectively, the average stand foliage retention. The increase in foliage retention with tree size shown above, even over the very limited range in diameters of the SNC-rated trees from the SNCC growth impact study (Maguire et al. 2002), suggests that this type of artificial thinning effect would be possible. However, the trees scored for SNC in the pre-commercial thinning study were constant throughout the 10-year period, except for occasional replacement of damaged trees. Furthermore, because the thinning was proportional, the stand component from which trees rated for foliage retention were chosen was present in all plots regardless of treatment.

Because pre-commercial thinning in young Douglas-fir stands is generally performed from below, a question remains as to how well the results from this study apply after such a treatment. To the extent that differences in relative height are related to resistance to or tolerance of SNC, thinning from below could be viewed as a process of selecting genetically more desirable trees from the standpoint of growth in the presence of SNC. However, within-crown SNC symptoms did little to improve the predictability of SNC tolerance over use of DBH alone in Douglas-fir progeny tests (Johnson 2002). In progeny tests subject to SNC, therefore, the larger and better-growing trees may not necessarily exhibit better foliage retention. These results suggest that smaller trees within a stand may be smaller only in part due to greater genetic susceptibility, and that their growth rate per se may render them less able to resist the disease. On the stand level, the presence of these smaller trees would tend to lower the growth rate for a given initial basal area, as illustrated by the stand-level thinning response of all trees relative to the thinning response of only the largest 500 Douglas-fir TPH (Figs. 4 vs. 5).

Another reason for the improvement in volume growth per unit initial basal area within the thinned Douglas-fir stands can be inferred from stand dynamics within SNC-infected control plots, where species other than Douglas-fir tend to be common. These other species originated from natural regeneration, and in the control plots foliage retention was negatively correlated with basal area in other species. The vast majority of the non-Douglas-fir basal area was made up of western hemlock, red alder, or bitter cherry. Of these three species, alder and cherry have faster juvenile height growth than Douglas-fir (Harrington 1990, Rose and Rosner 2005), so can overtop it if they regenerated at approximately the same age (Oliver and Larson 1996). Western hemlock is most prevalent in the coastal areas where SNC severity is greatest, and although western hemlock generally has slower juvenile height growth than Douglas-fir, its shade tolerance allows it to persist; therefore, because severe SNC can slow the height growth of Douglas-fir (Maguire et al. 2002), hemlock may be in a good position to exploit the decline in Douglas-fir. Because the pre-commercial thinning treatment for this study preferentially removed both subordinate Douglas-fir and other species that were highly competitive with Douglas-fir,

residual trees in several impacted plots benefitted. The decision to favor Douglas-fir over other species in severely SNC-impacted stands depends primarily on economics, including both relative value and relative growth rate.

It is well known that thinning increases the amount of light available to residual trees (Pothier and Margolis, 1991, Brix 1993). Thinning is also known to increase leaf area throughout the crown, but especially in the lower crown (Brix 1981, Yu et al. 2003). Because SNC-infected trees carry relatively large amounts of their foliage mass in the lower portions of the crown, even before thinning, and because illumination increases dramatically in those crown portions following thinning (Han 2006), it can be inferred that residual trees in an infected stand experience a larger relative increase in light capture.

Other studies investigating the effects of pre-commercial thinning on periodic annual volume growth per unit basal area in Douglas-fir stands have generally found an immediate benefit to density reduction (Brix 1993, Li et al. 2007). At the same time, previous research has found that newly thinned SNC-infected stands generally respond more slowly to newly available growing space (Mainwaring et al. 2005), due perhaps to slower rates of crown expansion (Weiskittel 2003, Weiskittel et al. 2007) or to competition from a greater quantity of understory vegetation surviving under the low LAIs resulting from SNC (Weiskittel and Maguire 2007). Of the seven sites where the effect of the 250 TPH thinning could be tested, five of the sites demonstrated an immediate increase in PAI per unit basal area, while the other two (disease-free sites) exhibited only small differences until the final period. These two healthy sites were the youngest stands in the study, with an average breast height age of 8 yrs (v. 12.5 yrs for other five sites) and an average height of 8.3 m (v. 13.9 m for other five sites). Although these younger stands can be expected to respond quickly to new growing space and resource availability, control plots of this age necessarily had lower levels of site occupancy, so were experiencing slower rates of crown recession than older stands. Furthermore, the effect of thinning on growth depends upon the degree of density reduction. Although this study was imposed on operational plantations which met the study criteria, initial tree density on control plots at the two slow-responding sites was the lowest of the seven sites receiving the 250 TPH treatment. The effect of all these factors on relative crown lengths of thinned vs. unthinned trees explains the difference between those sites that responded to density reduction immediately and those that lagged (Fig. 8). If stand canopies are not closed at time of thinning, growth response per unit initial basal area will probably be delayed until crown recession begins in the unthinned stand.

Previous studies have generally found greater volume production per unit basal area with greater density reduction (Brix 1993, Li et al. 2007). The fact that the 500 TPH treatment has generally outproduced the heavier thinning over a ten year period can be partially explained by the similarity of residual trees. Although the 500 TPH treatment had a slightly higher height to crown base during each measurement period (Fig. 9), the difference in 2004 was still limited to only about 0.5 m. Thinning in young stands can result in a reinvigoration of understory vegetation, the potential influence of which is greater with more intense density reduction and smaller residual tree size. Sparser crowns of trees severely impacted by SNC would make understory survival and reinitiation potentially more influential than where crowns retain normal density, so the potentially greater release effect of the heavier thinning on competing vegetation may have dampened the response.

Analysis of the largest 500 or 250 TPH in each stand revealed a notable difference in the performance of the 500 and 250 TPH thinning treatments. Periodic annual increment of the largest trees (250 or 500 TPH) improved after thinning to 500 TPH, but didn't differ significantly from the control when thinned to 250 TPH. At nearly all sites, the largest 250 or 500 TPH were smaller in the thinned stands, with quadratic mean diameter being an average of 13 and 16% smaller in the 250 and 500 TPH treatments, respectively, than in the control stands. This is because during the thinning treatments, spacing was given precedence over tree quality (Kanaskie et al. 2002). The heavier thinning may also have resulted in greater thinning shock (Harrington and Reukema 1983) than the light thinning. The small number of sites (7) thinned to 250 TPH did not include severely infected stands, which exhibited the greatest response to thinning in this study. The lowest average 1998-2004 foliage retention among the seven plots thinned to 250 TPH was 2.36 yrs, suggesting stand-level growth losses of only about 20% (Maguire et al. 2011). Given the small number of 250 TPH treatments, and their non-representation in severely impacted stands, conclusions about net PAI of stands with low initial foliage retention and thinned to 250 TPH require further testing.

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Tables and Figures

Table 1. Initial attributes (1998, after thinning) of Douglas-fir plots included in the SNCC pre-commercial thinning study.

Variable	Units	Control mean (stdev)	500 TPH mean (stdev)	250 TPH mean (stdev)
Douglas-fir tree density	trees ha ⁻¹	1020.8 (313.3)	472.4 (36.0)	242.6 (15.8)
Douglas-fir basal area	m ² ha ⁻¹	15.76 (6.32)	8.51 (2.89)	5.99 (2.51)
Douglas-fir breast height age	yrs	10.9 (2.4)	10.6 (2.3)	11.1 (3.1)
Douglas-fir QMD	cm	14.1 (3.1)	15.1 (3.0)	17.4 (4.6)
Douglas-fir top height	m	11.66 (2.06)	11.49 (1.95)	12.28 (2.84)
Douglas-fir site index	m at 50 yrs	43.0 (6.7)	43.4 (6.3)	44.4 (4.0)
Basal area of other conifers	m ² ha ⁻¹	1.75 (6.14)	0	0
Basal area of broadleaved species	m ² ha ⁻¹	1.21 (1.14)	0	0
Total tree density	trees ha ⁻¹	1496.6 (950.2)	491.5 (50.0)	247.0 (20.2)
Total plot basal area	m ² ha ⁻¹	18.72 (8.79)	8.51 (2.89)	5.99 (2.51)
Total basal area removed	m ² ha ⁻²	0	10.50 (7.29)	12.23 (7.40)
Foliage retention	years	2.43 (0.52)	2.46 (0.62)	2.80 (0.30)
Periodic annual increment	m ³ ha ⁻¹ yr ⁻¹	17.26 (6.84)	15.08 (6.78)	12.29 (4.96)

Table 2: Parameter estimates and standard errors for model describing annual change in Douglas-fir foliage retention (equation [1])

Parameter	Variable	Whole crown		Lowest crown third	
		Estimate	SE	Estimate	SE
α_0	intercept	1.0747	0.1342	1.4001	0.1694
α_1	FR ₀	-0.3982	0.04409	-0.411	0.04604
α_2	I ₂₅₀	-0.1223	0.1903	-0.21	0.2607
α_3	I ₅₀₀	-0.09758	0.08981	-0.1534	0.1323
α_4	FR ₀ · I ₂₅₀	0.05889	0.05982	0.07854	0.06799
α_5	FR ₀ · I ₅₀₀	0.05425	0.0322	0.06896	0.03854

Table 3: Parameter estimates and standard errors for model describing net periodic annual volume growth of Douglas-fir after precommercial thinning (equation [2]).

Parameter	Variable	All trees		Largest 500 TPH		Largest 250 TPH	
		Estimate	SE	Estimate	SE	Estimate	SE
β_0	intercept	-4.1087	0.12362	-3.5544	1.2796	-3.8987	0.9558
β_1	$\ln(\text{FR}_0)$	0.5604	0.1061	0.5965	0.1174	0.5606	0.09286
β_2	$\ln(\text{BA}_{\text{DF}})$	0.6331	0.04291	0.6836	0.05272	0.7660	0.04497
β_3	$\ln(\text{BA}_{\text{ODF}})$			0.000338	0.004003	-0.00324	0.005491
β_4	$\ln(\text{BA}_{\text{OS}})$	0.00419	0.00313	0.006856	0.003567	0.004597	0.002350
β_5	I_{250}	0.2704	0.2163			0.3323	0.2650
β_6	I_{500}	0.4912	0.09236	0.6302	0.1179	0.6785	0.0797
β_7	$\ln(\text{FR}_0) \cdot I_{250}$	-0.2580	0.1871			-0.08211	0.1846
β_8	$\ln(\text{FR}_0) \cdot I_{500}$	-0.3196	0.08481	-0.3367	0.09250	-0.3745	0.07216
β_9	$\ln(\text{SI})$			0.9839	0.3536	0.9951	0.2658

Table 4: Estimates of selected parameters for specific periods in model for describing periodic annual volume increment of Douglas-fir after precommercial thinning (equation [2] with zero covariance among observations).

	Period 1		Period 2		Period 3		Period 4	
	Parameter estimate	Standard error	Parameter estimate	Standard error	Parameter estimate	Standard error	Parameter estimate	Standard error
β_5	0.1917	0.6887	0.7618	0.2956	0.8066	0.2738	0.9742	0.3925
β_6	0.09229	0.3946	0.6019	0.1548	0.7389	0.1485	0.7168	0.1595
β_7	-0.4388	0.6107	-0.4528	0.2638	-0.4871	0.232	-0.561	0.3189
β_8	-0.3137	0.2087	-0.3358	0.1271	-0.3878	0.1215	-0.3549	0.141

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Fig. 1



Fig. 2

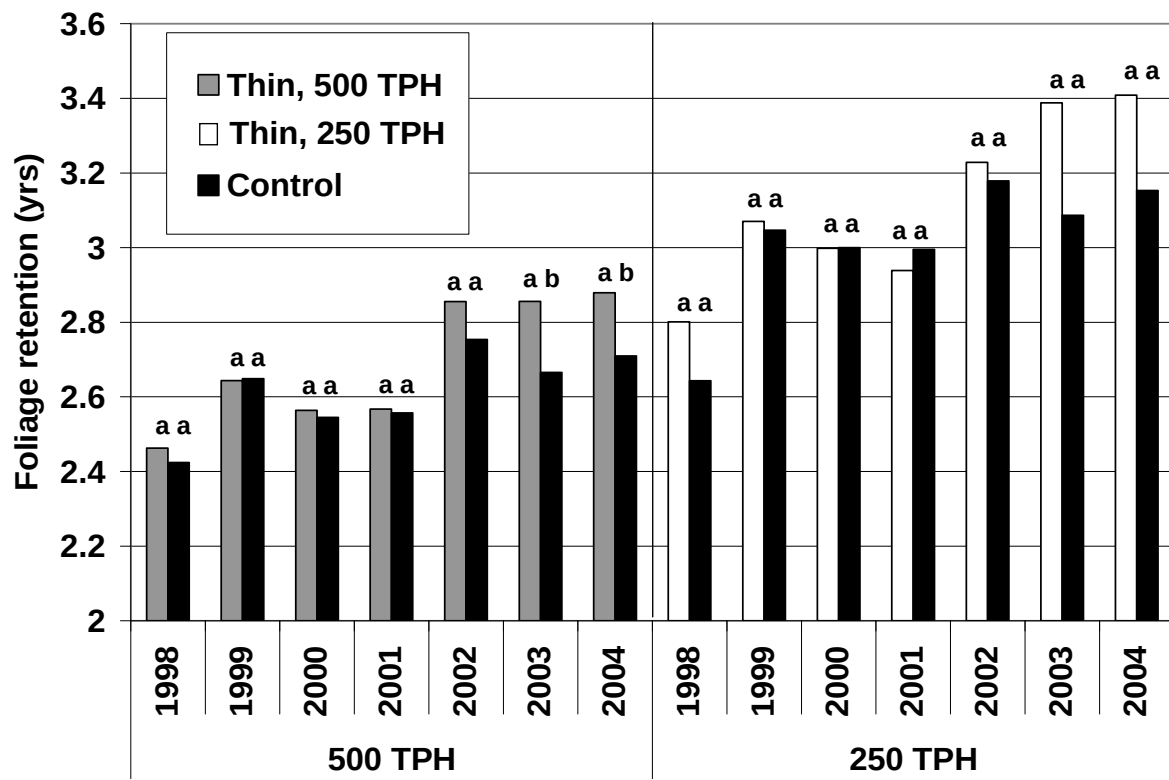


Fig. 3

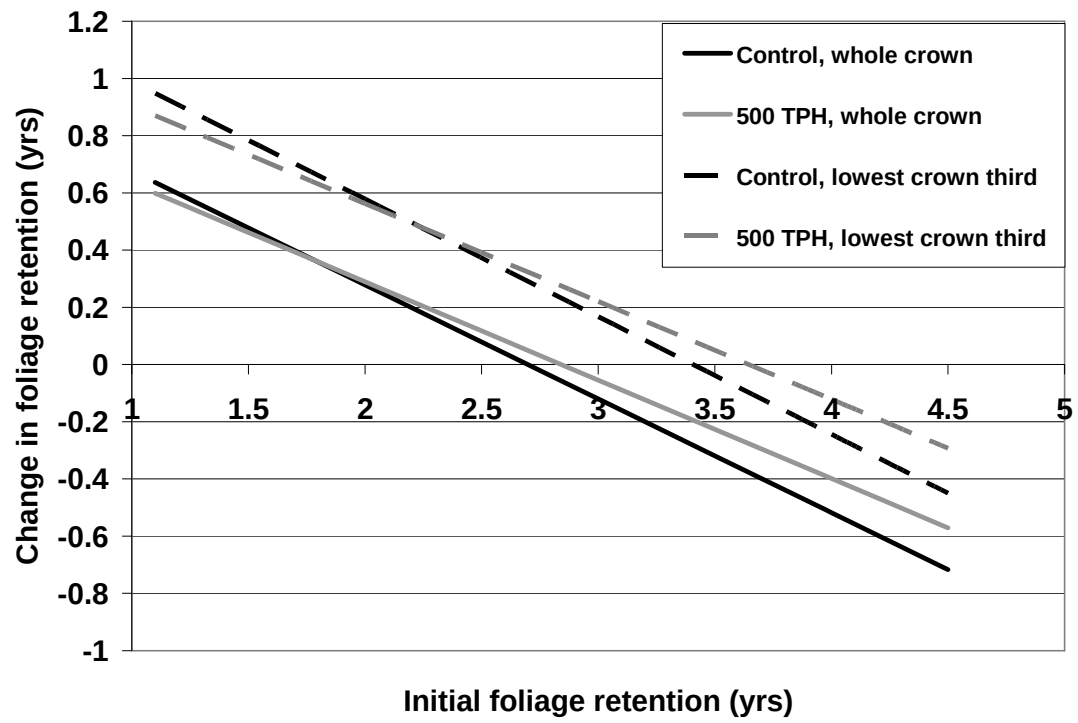


Fig. 4

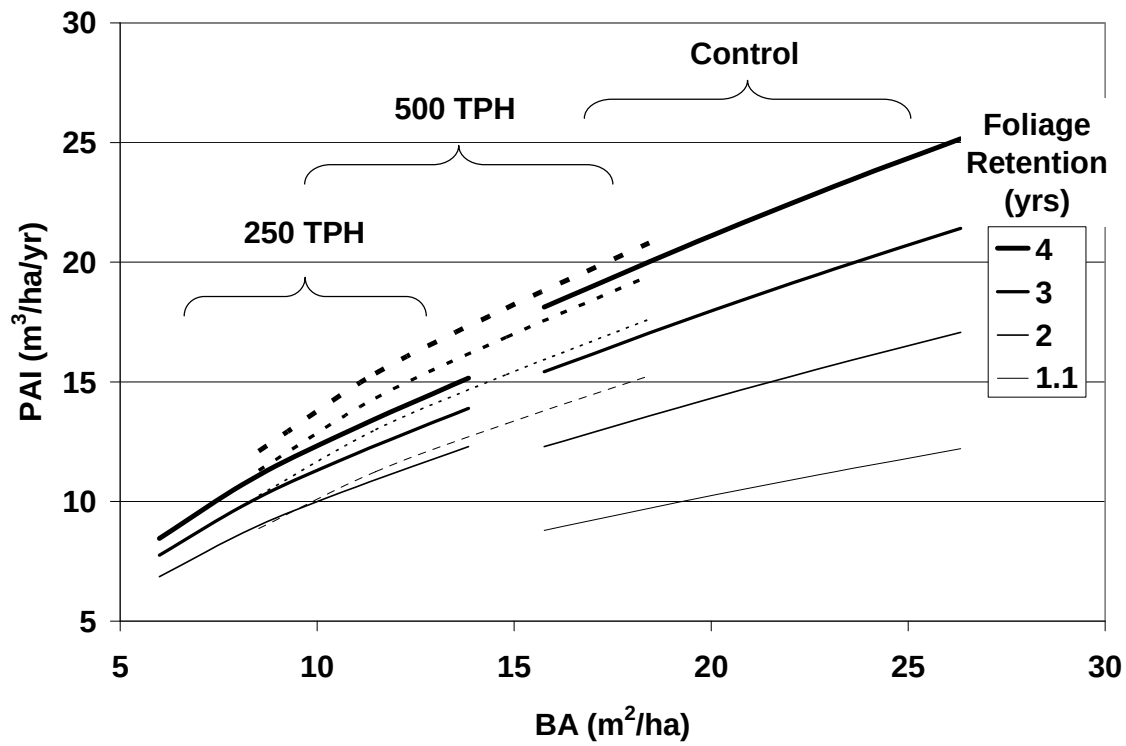


Fig. 5

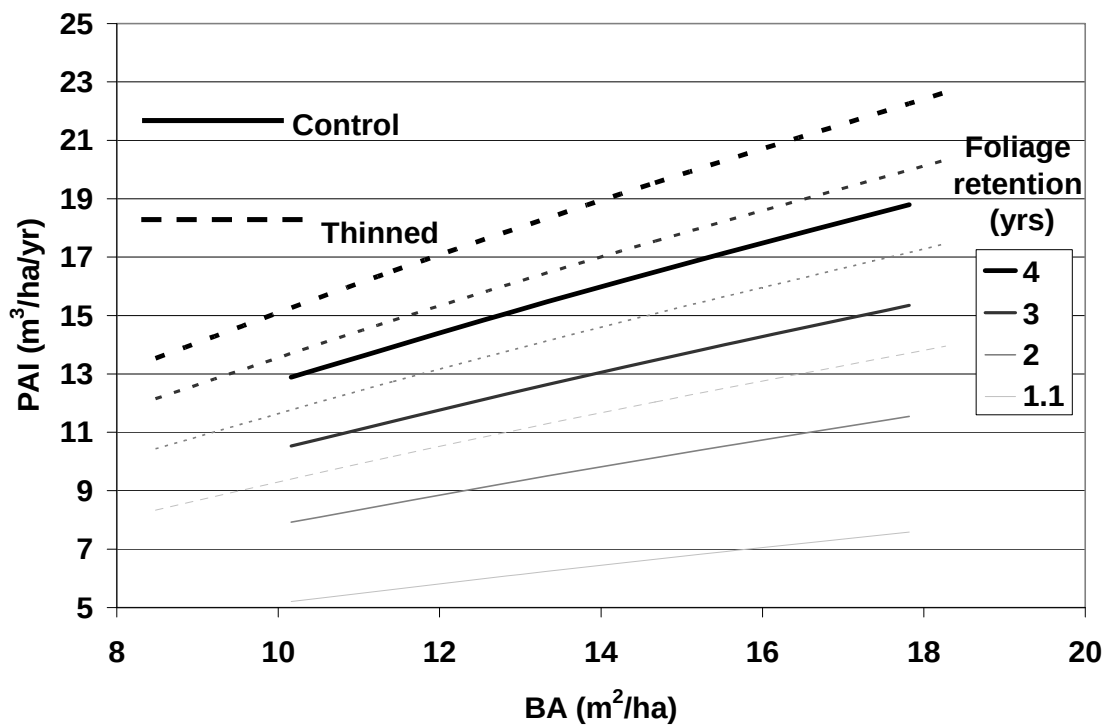


Fig. 6

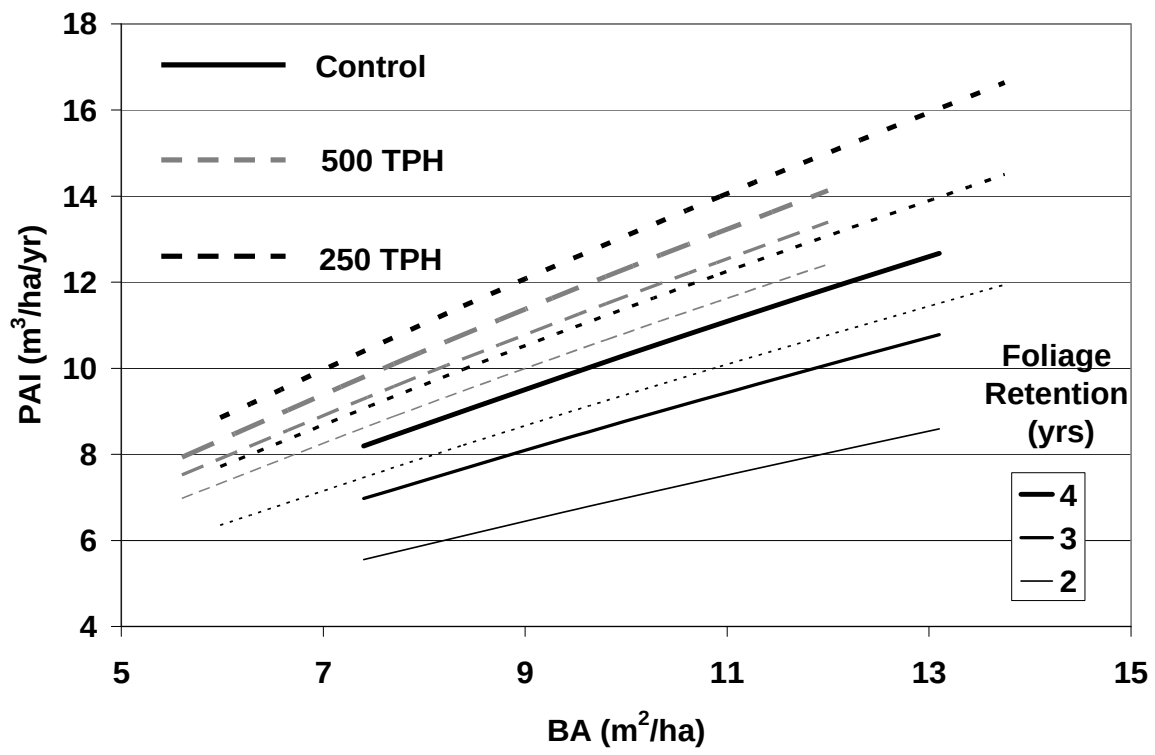


Fig. 7

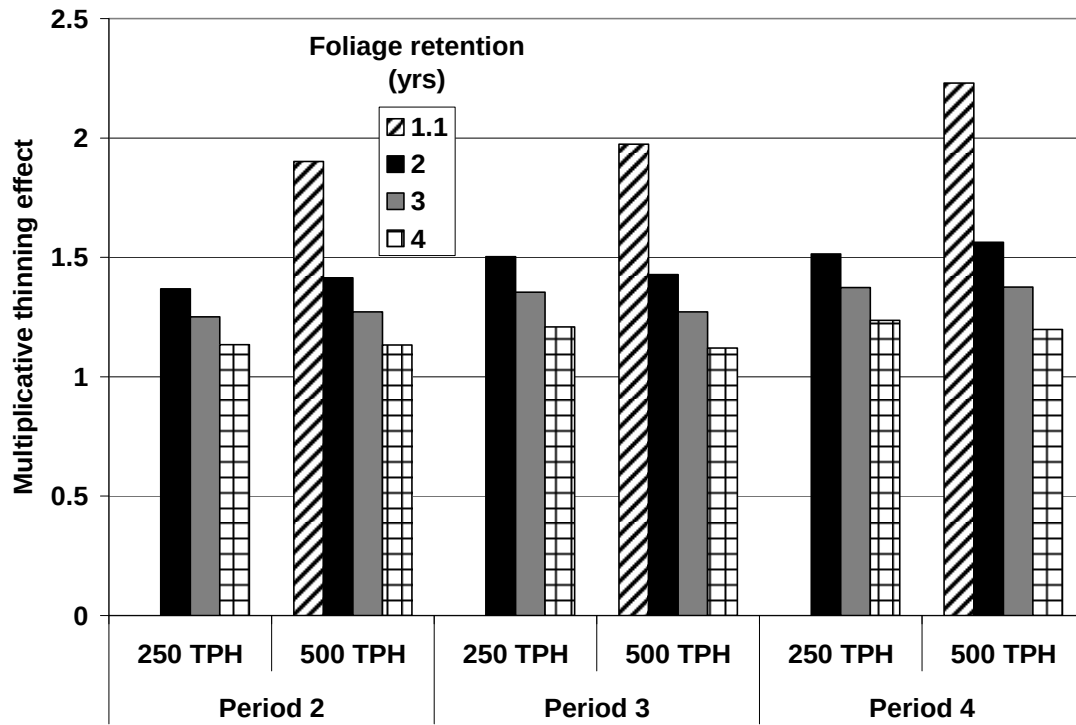


Fig. 8

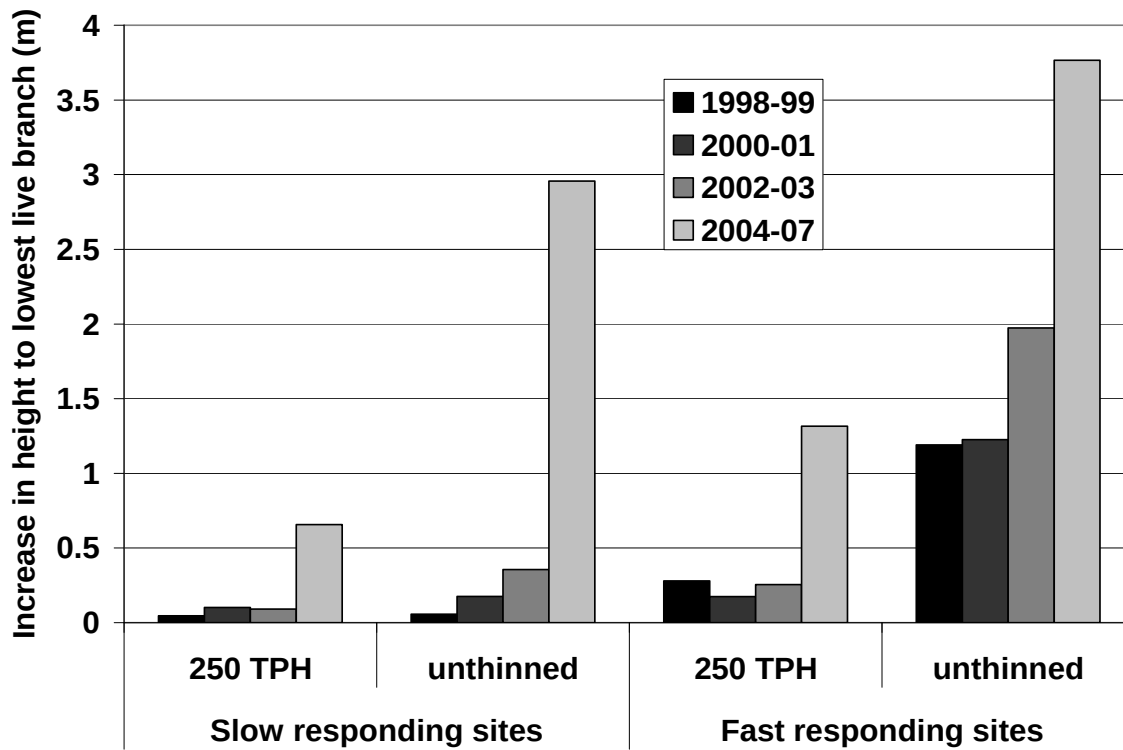
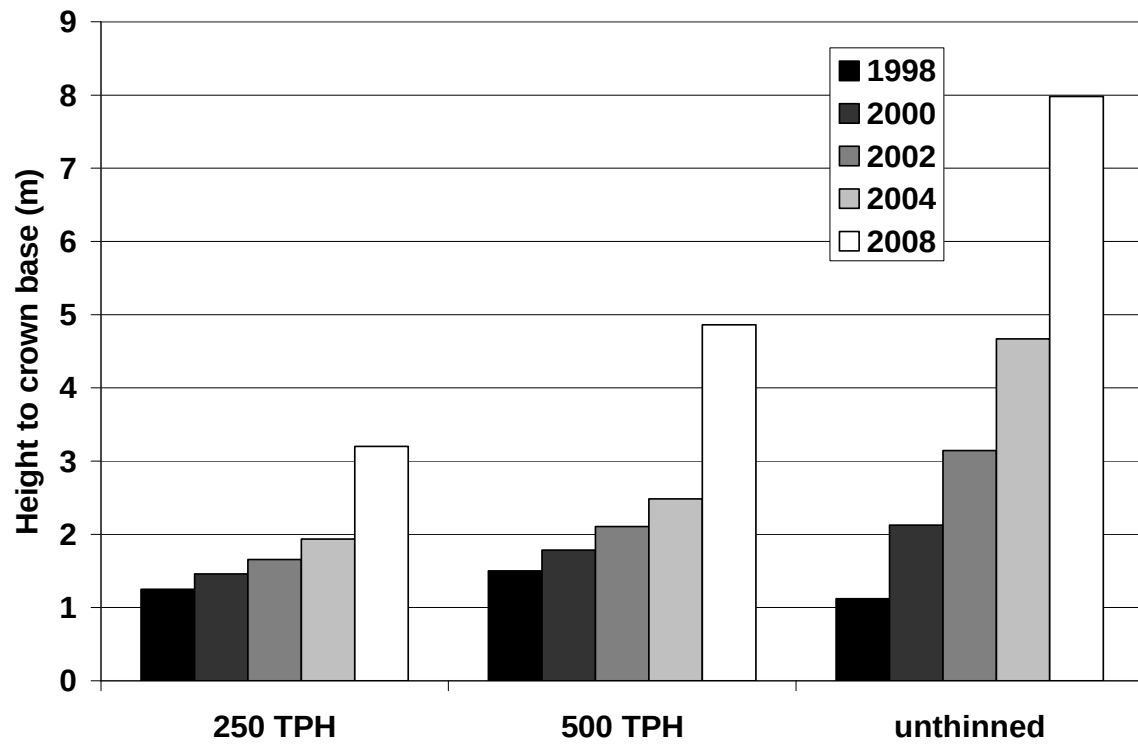


Fig. 9



Fertilization impacts on Swiss needle cast disease severity in western Oregon

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Summary

The influence of fertilization on disease severity is unknown in most forest pathosystems. Fertilization treatments were randomly applied to 0.01 ha plots centered on individual dominant or co-dominant Douglas-fir trees in ten Douglas-fir stands from coastal Oregon to the foothills of the Oregon Cascade Range. This region is affected by Swiss needle cast, caused by the fungal pathogen *Phaeocryptopus gaeumannii*. Selected stands represented a range of Swiss needle cast disease severity, and ten replications of each fertilization treatment were applied in each stand. The six treatments included nitrogen (urea), calcium carbonate (lime), calcium (calcium chloride), phosphorus (monosodium phosphate), a site-specific blend (Kinsey) and an unfertilized control. Fertilization took place from February to April 2007, and single branches were collected from treated trees for disease severity assessment of foliage in May 2010. Disease severity of one- and two-yr-old needles was evaluated by counting the frequency of infected needles and the density of *P. gaeumannii* fruiting bodies (pseudothecia) on a random subset of needles from each tree and needle age class. Mixed effects analysis was used to assess fertilization treatment effects on infection index (mean fruiting body density) after accounting for site as a blocking factor. ANOVA was used to assess differences in infection index between treatments at each of the ten study locations. Across and within sites, fertilization treatment did not significantly affect infection index of one- or two-year old needles ($p > 0.05$). Small differences in mean fruiting body density ($\leq 3\%$) between fertilization and control treatments across sites were not statistically significant, nor are they believed to be biologically or economically significant. Decisions regarding fertilization should be based on site-specific attributes, such as soil chemistry. There is no evidence that fertilization directly impacts Swiss needle cast severity in western Oregon.

1 Introduction

Swiss needle cast (SNC) is a foliage disease of Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) caused by the ascomycete fungus *Phaeocryptopus gaeumannii* (Rhode) Petrak. Fungal fruiting bodies (pseudothecia) occlude needle stomata, which impairs gas exchange and leads to needle carbon starvation and abscission at high infection levels (MANTER et al. 2000; MANTER et al. 2003). Disease symptoms include premature needle shed, chlorotic needles and tree crowns, and reduced height and diameter growth (HANSEN et al. 2000; MAGUIRE et al.

2002). Although the fungus is native to the range of Douglas-fir in western North America and was once considered innocuous in this region, a foliage epidemic affecting hundreds of thousands of acres has occurred in the Coast Range of Oregon and Washington since the 1990s (SHAW et al. 2011). This experimental field study was designed to investigate the relationship between specific operational fertilization treatments and SNC severity and Douglas-fir tree growth in western Oregon.

Several climate factors are correlated with moderate and severe disease. These include abundant leaf wetness from fog and precipitation during the sporulation period (May to July), and mild temperatures during the winter, which are believed to allow for more rapid needle colonization (ROSSO and HANSEN 2003; MANTER et al. 2005; STONE et al. 2008a). Climate conditions conducive to disease development are generally found at low elevations within 20-30 miles (30-50 km) of the coast, on sites that were historically dominated by Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*) and red alder (*Alnus rubra*) (HANSEN et al. 2000). In western Oregon (USA), distance-from-coast and elevation consistently emerge as strong predictive variables in disease severity distribution models (HANSEN et al. 2000; ROSSO and HANSEN 2003; MANTER et al. 2005). While distance-from-coast and elevation are not mechanistic explanatory variables, they act as surrogates for climate and site variables that change along these gradients and have a significant impact on disease development. Soil N concentration is negatively correlated with distance-from-coast (PERAKIS et al. 2005), and there has been growing interest in the potential effect of N levels and nutrient imbalance on disease development and severity (EL-HAJJ et al. 2004). In addition, managers are interested in implementing fertilization regimes that may ameliorate or offset growth losses from SNC, and, conversely, avoiding regimes that may exacerbate disease and growth loss.

In several agricultural pathosystems, N, Ca, P and other fertilizer treatments have been shown to directly impact disease severity, but the direction of impact is often dependent on the pathosystem, the specific application materials (e.g. ammonium, nitrate or nitrite), the timing of application, and other factors (DATNOFF et al. 2007; ENGELHARD 1989). Nutrient manipulation may reduce disease by bolstering plant resistance or tolerance through enhancing the production of compounds and signaling molecules associated with chemical or physical defense; for example, soluble and cell wall-bound phenolics, monoterpenes, lignin and ‘second messengers’ (BONELLO et al. 1993). Conversely, nutrient manipulation may increase disease by improving pathogen access to nutriment through its host or by negatively impacting the production or distribution of host defense compounds in plant tissue. Sugimoto et al. (2010) demonstrated that soil Ca applications to soybean crops improved resistance to the stem rot pathogen, *Phytophthora sojae*. Accumulation of Ca crystals around the cambium and xylem elements of treated plants indicated that Ca served as a barrier to vascular tissue penetration. Fertilization treatments, such as lime, may also alter soil pH, thereby affecting the availability and uptake of other charged soil nutrients (e.g. P), not only the nutrients directly applied (HAYNES 1982; PUNJA 1989). Changes in soil acidity may alter the composition of soil microbial communities, and in some cases, may affect population levels of microorganisms antagonistic to soilborne pathogens, thereby influencing disease levels (PUNJA 1989).

Comparatively fewer studies have been conducted on the influence of fertilization or nutrient levels on pathogens of forest trees, at least in part due to the long-lived nature of trees and the complexity of nutrient cycling in forest systems. In addition, observational studies on the relationship between mineral nutrition and disease do not allow causal inferences to be drawn, as nutrient impacts cannot be distinguished from the impacts of other environmental factors. A field

experiment conducted by Blogett et al. (2005) found that N fertilization decreased resistance of red pine (*Pinus resinosa*) to the fungal shoot blight and canker pathogen, *Diplodia pinea* (syn. *Sphaeropsis sapinea*). Although it is generally believed that stressed trees are predisposed to disease in this pathosystem, and fertilization is often recommended to increase tree vigor, significantly lower lignin concentrations were detected in fertilized trees compared to controls. Wallis et al. (2011) investigated the influence of N fertilization of Austrian pine (*Pinus nigra*) inoculated with *Diplodia pinea*, and found that lesion size was negatively correlated with levels of soluble phenolics and monoterpenes, and that significantly higher levels of these compounds were present at high and low N fertilization levels compared with the intermediate level. An observational study conducted by Stanosz et al. (2004) on the influence of paper mill waste treatment on the *Diplodia pinea*-red pine pathosystem detected significantly higher incidence of infected trees and shoots in treated stands. It was suggested that nutrient imbalance (high N relative to essential micronutrients) may have increased disease severity in treated stands by intensifying the effects of moisture stress, because latent infection can develop into severe infection under drought conditions.

In the *P. gaeumannii*-Douglas-fir pathosystem, nearly all infection occurs in current-year foliage during shoot elongation. Fungal biomass increases in needles as they age and is positively correlated with fruiting body density, resulting in greater density of occluded stomata over time (STONE et al. 2008b). Manter et al. (2003) demonstrated that deleterious effects (reduced carbon assimilation) of fungal infection and colonization were only observed after fungal fruiting bodies developed in needle stomata, and that fungal-mediated reduced carbon uptake is the primary disease mechanism. *Phaeocryptopus gaeumannii* can grow within needles without causing symptom development or measureable growth loss as long as the photosynthetic

capacity of efficient, young (1- to 2-yr-old) needles is not compromised by stomatal occlusion (HOOD 1982). Premature abscission of relatively young needles must then be attributable to high levels of successful initial infection, accelerated colonization and fruiting body development within needles under certain environmental or host nutritional conditions, or both (Manter et al. 2005).

P. gaeumannii infects Douglas-fir through needle stomata, and does not rely on physical or enzymatic penetration of host cells. Similarly, needle colonization occurs in the intercellular region of host needles. *P. gaeumannii* hyphae have been observed pressed closely against mesophyll and palisade cells walls, but there is no evidence that fungal haustoria penetrate host cells to access the nutrition within (STONE et al. 2008b). Therefore, this system contrasts with others in which nutrients have been shown to directly impact the host-pathogen relationship, in that the fungus does not disrupt cellular structure by destroying or penetrating cells, and there are no known host defense mechanisms (i.e. structural and biochemical defenses, such as abscission layers or programmed cell death). In addition, no pathogen-produced toxins or changes in chlorophyll fluorescence have been documented in association with SNC symptoms (MANTER et al. 2000; CRANE 2002).

It has been proposed that nutrient imbalance compromises the integrity of foliar cell membranes, causing increased nutriment leakage into the apoplast, where it can be accessed by *P. gaeumannii* and contribute to its proliferation. Some have speculated that high levels of N relative to other macro and micronutrients may have facilitated the current SNC epidemic along portions of the Pacific Northwest coast, where foliar N levels often exceed the established 1.4% threshold for N-limitation in coastal Oregon Douglas-fir (EL-HAJJ et al. 2004; PERAKIS et al. 2005). El-Hajj et al. (2004) fertilized Douglas-fir trees with two levels of N (urea) in Idaho and

documented 2.2- to 3.6-times greater pseudothecia density on 2-yr-old needles of treated trees. However, the small sample size (5 trees/treatment), the study location in the intermountain west, and the *P. menziesii* ssp. *glauca* seed source present problems in extending these findings to forest plantations in coastal Oregon and Washington. In the north-central Oregon Coast Range, Perakis et al. (2005) measured soil and foliar nutrition in 22 stands across a gradient of SNC. Douglas-fir foliar N levels ranged from 0.85 to 1.74%, and were positively correlated with soil N levels, which ranged from 0.15 to 1.05%. The results suggested that nitrate-leaching of Ca on N-rich sites, combined with low rates of atmospheric Ca deposition relative to tree demands, contributed to Ca depletion and N oversaturation on coastal sites, possibly contributing to low needle retention. It is difficult to interpret the relationship between foliar and soil Ca and N levels and SNC severity, as these factors covary with distance-from-coast along with climate variables that are known to strongly influence abundance of the causal fungus (MANTER et al. 2005; STONE et al. 2008).

N fertilization (as urea) has been a common management practice used to increase tree growth and yield, and timber producers in coastal Oregon and Washington are concerned that N fertilization may worsen SNC symptom severity (FILIP et al. 2000). Plantations are traditionally fertilized with urea at the time of pre-commercial thinning (8- to 15-yrs-old) or commercial thinning (20- to 25-yrs-old), and may be fertilized at regular intervals (e.g. every 5 yrs) until harvest (Pers. Comm. M. Gourley, Starker Forests, Inc., Corvallis, OR, USA, Jan 2011). Influenced by theories regarding nutrient imbalance and SNC, some managers are using Ca fertilization (as lime) to ameliorate growth loss from disease by rebalancing the ratio of N to other essential nutrients by adding Ca and raising soil pH. Ca and alternative or site-specific

fertilization treatments can be costly, and their benefits, in terms of tree growth and disease impacts, have not been empirically tested in the region of the current SNC epidemic.

The primary objective of this study was to evaluate differences in disease severity between trees treated with specific nutritional amendments across a range of SNC disease severity in western Oregon. This was accomplished through application of fertilization treatments at 16 study locations chosen to represent a range of disease severity (MAINWARING et al. 2009; MAINWARING and MAGUIRE 2010). Treatments included nitrogen (urea), calcium carbonate (lime), calcium chloride, phosphorous (monosodium phosphate), a site-specific blend (Kinsey) and an unfertilized control. Analysis of growth response to fertilization across a range of SNC severity has been reported separately (MAINWARING et al. 2009; MAINWARING and MAGUIRE 2010).

2 Material and Methods

2.1 Study Site Descriptions

Sites were distributed across a range in elevation, aspect and SNC severity from the Oregon and southwest Washington Coast Range to the foothills of the Cascade Range (Table 1; Fig. 1). Target stands were 20 (+/- 10) years old, contained 300 (+/- 100) trees per acre and had not been previously thinned or fertilized. Privately-owned stands that met these criteria and were broadly distributed through the region of interest were selected for the study. Sites were chosen to avoid prior fertilization; consequently, site productivity was generally high. Tree and stand attributes, and mineral soil and foliar chemistry were assessed in all stands before treatment in fall 2006, and one and three growing seasons after treatment (MAINWARING et al. 2009; MAINWARING and MAGUIRE 2010).

Table 1. Name and site information for 10 study sites in western Oregon. Distance is km from the Pacific Ocean. Mean foliage retention (Fol. Ret.) provided for 2006 (pre-treatment), with standard deviation in parentheses.

Site	Location	Landowner (at start of study ¹)	Location	Elevation (m)	Distance (km)	Slope (%)	Aspect	Fol. Ret.
GDH	Hemlock	Stimson (Green Diamond ¹)	T3S, R9W, S8	122	11.6	10	S	1.62 (0.45)
MNS	Menasha-south	Cambell (Menasha ¹)	T26S, R13W, S10	61	11.6	30	E	2.66 (0.71)
ODF	Elk City	Oregon Dept. Forestry	T11S, R10W, S1	152	17.7	30	N	2.34 (0.63)
HAGR	Grand Ronde	Hampton	T5S, R8W, S6	366	20.1	35	NE	2.22 (0.67)
MNN	Menasha-north	Cambell (Menasha ¹)	T26S, R11W, S6	244	20.9	10	S	2.22 (0.57)
HAK	Knappa	Hampton	T8N, R7W, S29	183	28.2	10	N	2.36 (0.72)
STR	Burnt Woods	Starker	T11S, R7W, S30	305	38.6	10	N	2.71 (0.69)
OSU	McDonald Forest	Oregon State University	T9S, R5W, S4	91	59.5	0	—	3.32 (0.51)
GPH	Pleasant Hill	Giustina L&T	T19S, R2W, S24	305	102.2	10	N	3.64 (0.38)
CTC	Sweethome	Cascade Timber	T12S, R1E, S28	442	111	15	S	3.38 (0.83)

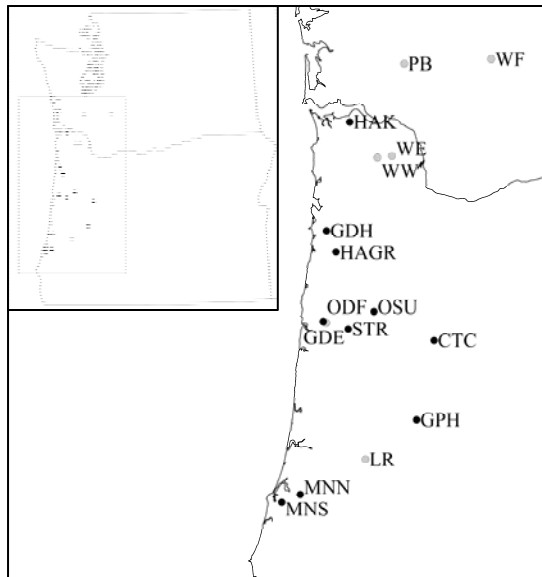


Fig 1. Study locations in the Oregon and Washington Coast Range and the foothills of the Cascade Range, USA. Black circles represent stands that were sampled for disease severity assessment; grey circles represent stands that were not.

Studied stands ranged from the coastal *Picea sitchensis* (Sitka spruce) vegetation zone inland to the *Tsuga heterophylla* (western hemlock) zone, which spans much of western Oregon

and Washington. The *Picea sitchensis* vegetation zone is generally found within a few kilometers of the coast below 150 m in elevation, but extends farther inland along river drainages. This zone tends to have the highest SNC severity, and is characterized by a consistently wet and mild climate, with minimal moisture stress and frequent fog and low cloud in summer. Soils in this zone are deep, rich and fine-textured, and surface soils tend to have high organic and total N content, and low pH (4.5 to 5.5) and base-cation saturation. Sitka spruce, western hemlock, western red cedar, Douglas-fir and red alder dominate this highly productive region (FRANKLIN and DYRNESS 1973).

The more extensive *Tsuga heterophylla* zone tends to experience relatively greater temperature and moisture extremes than the *Picea sitchensis* zone, and there is substantial climatic variation associated with the wide range of elevation, latitude, longitude and regional topography. Most precipitation occurs during winter, while summer receives less than ten percent of the annual total. Soils tend to be moderately deep and somewhat acidic, and, in the Coast Range, organic matter is high. Dominant tree species include Douglas-fir and climax western hemlock and western red cedar (FRANKLIN and DYRNESS 1973).

2.2 Fertilization Regimes & Soil Collection

Ten of the 16 study locations were selected for foliage collection and disease severity assessment, with preference given to sites that were located in Oregon, received all six fertilization treatments and provided a range of SNC disease severity. Of these ten study sites, nine received the six main fertilization treatments, while one (GPH) received all treatments but the site-specific Kinsey blend (Table 2). One site (OSU) also received a N: P treatment (448 kg N: 112 kg P) as urea and monoammonium phosphate. The Kinsey treatment targeted specific

base-cation saturation ratios (McLEAN et al. 1983), and was based on analysis of soil samples collected beneath treatment trees and pooled within treatments at each site (Oregon State University Central Analytical Laboratory, Corvallis, OR, USA). Two mineral soil core samples were collected (12.5-cm depth), 1.5 m from opposite sides of each treatment tree, perpendicular to the slope. Trees assigned to the Kinsey treatment were sampled twice, once as described, and once including the duff layer. The Kinsey treatment called for the addition of Cu, S and Ca (as lime) to all sites, N, P and K to all but one of the nine sites (STR), as well as various combinations of dolomitic lime and other micronutrients (Table 3).

Table 2. Application rates and materials of fertilization treatments applied to 0.01-ha plots centered on dominant or co-dominant Douglas-fir trees at 10 sites in western Oregon. Kinsey treatment applications rates are displayed in Table 3.

Treatment	Material	Chemical formula	Material appl. rate (kg/ha)	Elemental appl. rate (kg/ha)	Expected outcome
Control	-	-	-	-	-
N	urea	(NH ₂) ₂ CO	493	225	increased N
Ca	lime (calcium carbonate)	CaCO ₃	2915	1020	increased Ca & soil pH
Ca	calcium chloride	CaCl ₂	291	105	increased Ca w/o pH change
P	monosodium phosphate	NaH ₂ PO ₄	2240	580	increased P & soil pH

Table 3. Kinsey fertilization treatment application rates and materials applied to 0.01-ha plots centered on dominant or co-dominant Douglas-fir trees at 9 sites in western Oregon. Sites ordered by increasing distance from coast.

Material	GDH	MNS	ODF	HAGR	MNN	HAK	STR	OSU	CTC
Fertilizer application rates (kg/ha)									
NH ₄ H ₂ POH	255	255	255	255	255	255	—	255	255
K ₂ SO ₄	127	—	—	127	—	—	—	433	509
S ₈	97	97	92	92	87	81	97	97	107
Borate-46	—	5	10	15	—	7	15	15	15
ZnSO ₄	20	—	20	20	20	—	20	10	—
CuSO ₄	20	25	25	10	25	25	20	20	10
FeSO ₄	—	407	407	331	407	407	—	433	407
K ₂ Mg ₂ (SO ₄) ₃	305	407	407	305	330	407	—	—	—
MnSO ₄	102	—	—	—	—	—	—	—	—
CaCO ₃	1222	2291	2291	1935	967	1527	2851	2138	4939
CaMg(CO ₃) ₂	3157	1731	2189	2749	3259	2138	2546	—	4226
Elemental application rates (kg/ha)									
N	31	31	31	31	31	31	—	31	31
P	69	69	69	69	69	69	—	69	69
K	113	74	74	113	60	74	—	194	228
S	209	269	269	250	247	255	97	265	279

Ca	464	871	871	735	367	580	1083	812	1877
Mg	444	270	329	391	460	323	331	—	549
Mn	29	—	—	—	—	—	—	—	—
B	—	1	1	2	—	1	2	2	2
Zn	7	—	7	7	7	—	7	4	—
Cu	5	6	6	2	6	6	5	5	2
Fe	—	85	85	70	85	85	—	91	85

Treatments were ground-applied and randomly assigned to circular 0.01 ha (5.67 m radius) fixed-area plots, with each plot centered on an undamaged dominant or co-dominant measurement tree. Trees were considered damaged if they were leaning or had broken tops, forked tops or bole wounds. Potential plot center trees were selected on a 20-m grid, and grid points were skipped if no suitable plot center trees were available. At each site, fertilization treatments were replicated ten times, and treatments were applied Feb- Apr 2007 (Fig. 2). For the Kinsey treatment, attaining the specified ratio of base cations required fertilizer application across two years. Non-lime materials were applied concurrent with other fertilization treatments and lime was applied during the winter of 2007-08. Mineral soil samples were also collected one and three growing seasons post-treatment for assessment of fertilization impacts on soil chemistry.

Yr.	2006												2007												2008												2009												2010				
Mo.	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5																					
	Foliar & soil nutrients assessed (pre-trt.)			Trt. applied (all)			Growing season 1			Foliar & soil nutrients assessed (1 season post-trt.)			Kinsey trt. applied (2nd)			Growing season 2			Growing season 3			Foliar & soil nutrients assessed (3 seasons post-trt.)			Foliage collected for disease assessment																												
	2-Yr needles																														1-Yr needles																						

Fig. 2. Project timeline. Trt= treatment.

Materials were chosen to allow for investigation of the impacts of N and other soil nutrient amendments at rates commonly used in Douglas-fir plantations in the study region. To

examine the effects of specific nutrient additions on tree growth and disease severity, most of the treatments altered the level of one or few elements, as opposed to complex combinations of elements, in an attempt to isolate their effects. The site-specific Kinsey blend was an exception to this strategy, but was implemented because it has been suggested that rebalancing nutrients may reduce disease impacts. Two Ca treatments were applied to distinguish between the impacts of Ca accompanied by increased soil pH (calcium carbonate, lime) and the impacts of Ca in the absence of significant pH change (calcium chloride). Industrial rates were used for the selected materials to represent “real-world” plantation scenarios, and were not intended to elevate soil or foliar nutrient levels in excess of what would be expected under standard plantation management.

2.3 Foliage Collection for Disease Assessment & Foliar Chemistry

1- and 2-yr-old foliage was collected from treatment trees in May 2010 for disease severity assessment (Fig. 2). Tree climbers removed the largest 4-yr old lateral branch from the southernmost branch of the fifth whorl from the top of the each treatment tree (MAGUIRE and KANASKIE 2002; MAGUIRE et al. 2002). Approximately half of the needles were removed from the primary branch axis of the selected 4-yr old lateral branch, and half were removed from the smaller branches growing off of this branch. 1- and 2-yr-old needle cohorts from each tree were stored separately in labeled polyethylene bags for disease severity assessment. At least 30 needle samples from 25 trees could not be collected because no new growth was present or insufficient 1- or 2-yr-old needles remained on the collected branch. There were never fewer than seven of the ten expected samples per treatment, needle age class and site, and 1120 samples from 565 trees were processed for disease severity.

Branches were also collected pre-treatment (Oct-Dec 2006), one growing season post-treatment (Oct-Dec 2007) and three growing seasons post-treatment (Oct-Dec 2009) for foliar chemistry assessment (Fig. 2). 1-yr-old needles from trees in the same treatment group at each site were pooled and mixed, and approximately 1 g of dried foliage per sample was submitted for analysis (Oregon State University Central Analytical Laboratory, Corvallis, OR, USA). Foliage was collected for nutrient analysis in autumn, when nutrient levels are believed to stabilize after the growing season. 1-yr-old needles collected in Oct-Dec 2009 for nutrient analysis were from the same cohort as the 1-yr-old needles collected in May 2010 for disease severity assessment, as both of these collections were made prior to the 2010 growing season. Foliar nutrients were assessed as percent or parts-per-million (ppm) dry weight.

2.4 Foliage Processing & Disease Severity Assessment

Foliage was processed for disease severity using methods developed by Hansen et al. (2000), with minor modifications. For each tree and needle class, 50 needles were randomly selected and attached to a 3 x 5 index card with double-sided tape, such that abaxial needle surfaces faced upward. Stereo dissecting microscopes (40X magnification) were used to determine the proportion of needles on which *P. gaeumannii* fruiting bodies (pseudothecia) were present (infection incidence).

The first ten needles on which the fungus was present were marked from one to ten, and pseudothecia density on each of these needles was examined at approximately 210x magnification with digital microscopes (Dino-Lite Pro AM413ZT- Polarizing) using compatible DinoCapture 2.0 software (AnMo Electronics Co., Torrance, CA). Counts of the proportion of stomata occluded by pseudothecia (pseudothecia density) were conducted at three distinct

locations along the needle, with the needle divided into three sections of equal length (base, middle, and tip) given the total length of the needle. In each needle-third, a random starting point for the count was selected, and 100 total stomata were examined (50 on either side of the needle mid-rib). Stomata were examined consecutively, moving perpendicular to the midrib, and the number of stomata occluded by pseudothecia (out of 100 stomata examined) in each needle-third was recorded.

Damage or other species of foliar fungi (e.g. *Stomiopeltis*, *Rasutoria psuedotsugae*, etc.) occasionally obstructed the visibility of needle stomata. When this occurred, damaged regions were bypassed until the count could be resumed. Pseudothecia density was then averaged by needle, and across needles from the same tree and cohort, to provide an estimate of mean pseudothecia density for each tree/needle-cohort sample. Infection index, the product of mean pseudothecia density and infection incidence (MANTER et al. 2005), was then calculated for each tree/needle-cohort sample to provide an overall estimate of mean pseudothecia density that accounted for the fact that not all needles were infected.

2.5 Statistical Analyses

Needle age classes were analyzed separately. Mixed effects analysis was used to assess fertilization treatment effect on infection index (average pseudothecia density) after accounting for site as a blocking factor (Insightful Corp., S-PLUS, 2007). One-way ANOVA was used to assess differences in infection index between treatments at each of the ten study locations (Insightful Corp., S-PLUS, 2007). Simple linear regression was used to evaluate the relationship between foliar nutrient levels and infection index at the site-level (Insightful Corp., S-PLUS, 2007).

Standard methods were used to verify that data met the assumptions of employed statistical tests. Graphical representations of infection index across sites, and of infection index within sites across treatments, were used to assess distribution shape and variance. Boxplot midlines represent the median, top and bottom box limits represent the 75th and 25th quartile range, and whiskers span 1.5 times the inter-quartile range. Sites and needle age classes with minimal disease had low variance in infection index and right skew compared to sites with moderate or severe disease. Inclusion of data from low-severity sites did not alter statistical conclusions; therefore, these data were retained in the mixed effects analyses. Statistical tests were performed on untransformed data. The arcsine square root transformation was considered, but use of the transformation did not alter statistical conclusions nor did it uniformly improve distributions across the dataset. Although treatments were randomly applied, allowing for causal inferences regarding treatment effect, non-random site selection limits the scope of inference to the particular stands studied.

3 Results

3.1 Soil Chemistry

Soil nutrient levels and pH were correlated with distance-from-coast, consistent with the trends observed by Perakis et al. (2005). In general, soil pH, Ca, K, Mg and P increased with distance-from-coast, while C, N and Na decreased (Table 4). Comparisons of soil chemistry pre- and post-treatment revealed that most treatments caused expected changes in soil pH, P, Ca and N (Table 5).

Table 4. Average pre-treatment soil chemistry by site (ordered by increasing distance from coast). Standard deviation in parentheses.

Site	pH	C (%)	Ca (ppm)	K (ppm)	Mg (ppm)	N (%)	Na (ppm)	P (ppm)
GDH	4.7 (0.1)	11.4 (0.8)	107 (16)	126 (13)	64 (10)	0.59 (0.03)	54 (12)	0.3 (0.3)

MNS	5.2 (0.1)	8.8 (1.0)	529 (72)	276 (23)	180 (13)	0.46 (0.05)	56 (2)	1.9 (0.1)
ODF	4.9 (0.1)	9.3 (0.8)	343 (108)	265 (34)	175 (43)	0.49 (0.05)	46 (2)	2.5 (1.4)
HAGR	5.0 (0.1)	9.3 (1.4)	550 (95)	258 (40)	230 (36)	0.49 (0.08)	63 (13)	1.1 (0.3)
MNN	4.6 (0.4)	12.4 (1.9)	155 (36)	231 (14)	65 (14)	0.80 (0.10)	56 (13)	2.0 (0.4)
HAK	5.1 (0.1)	11.2 (1.0)	260 (31)	155 (13)	84 (11)	0.55 (0.04)	65 (17)	5.5 (1.1)
STR	5.4 (0.1)	5.0 (0.3)	1216 (130)	399 (20)	344 (37)	0.28 (0.01)	42 (1)	15.9 (2.0)
OSU	6.3 (0.2)	3.1 (0.2)	2651 (354)	445 (55)	300 (42)	0.21 (0.01)	33 (6)	22.0 (5.2)
GPH	5.9 (0.1)	4.2 (0.3)	1782 (242)	347 (37)	264 (34)	0.19 (0.01)	27 (1)	13.8 (4.0)
CTC	5.4 (0.1)	6.6 (0.3)	3400 (288)	523 (46)	660 (29)	0.32 (0.01)	41 (1)	0.9 (0.3)

Table 5. Average arithmetic change (Yr3- Pre) and average proportional change ((Yr3- Pre)/Pre) in soil chemistry by treatment (trt) across sites 3 yrs post-treatment vs. pre-treatment. Standard deviation in parentheses. Treatment N: P only applied at site OSU. Bold indicates nutrient changes targeted or affected by treatments. Yr3= nutrient level 3 yrs post-trt; Pre= nutrient level pre-trt. N (%), Ca (ppm) and P (ppm) calculated from dried weight.

	pH	Ca		N		P	
Trt	Yr3-Pre	Yr3-Pre	(Yr3-Pre)/ Pre	Yr3-Pre	(Yr3-Pre)/ Pre	Yr3-Pre	(Yr3-Pre)/ Pre
Control	-0.09 (0.31)	-96 (177)	0.03 (0.27)	0.04 (0.05)	0.07 (0.10)	2 (2)	1.64 (2.48)
N	-0.04 (0.07)	-134 (193)	-0.10 (0.13)	0.01 (0.06)	0.03 (0.10)	2 (3)	2.20 (3.92)
Lime	0.25 (0.08)	456 (228)	1.63 (2.01)	0.04 (0.05)	0.07 (0.11)	2 (4)	1.79 (2.09)
CaCl ₂	0.01 (0.08)	-35 (337)	0.25 (0.45)	0.04 (0.05)	0.08 (0.11)	2 (1)	1.04 (1.41)
P	0.27 (0.10)	-78 (162)	0.06 (0.35)	0.02 (0.03)	0.03 (0.07)	48 (31)	28.79 (39.29)
Kinsey	0.13 (0.09)	292 (181)	1.26 (1.70)	0.02 (0.04)	0.02 (0.08)	4 (2)	3.16 (3.47)
N : P	-0.08	-10	0	0	0	20	0.93

Three years post-treatment, the P, lime and Kinsey treatments uniformly increased soil pH, with the most pronounced increases for the P and lime treatments (Table 5). In contrast, CaCl₂ did not alter soil pH. The N treatment lowered soil pH at all but one site (HAK). The magnitude and durability of soil Ca increases were greater for the lime treatment compared to the CaCl₂ treatment, and this supports the idea that pH change is critical to facilitating and/or maintaining increases in soil Ca on sites with low initial soil pH.

Dramatic average increases in P were observed for the P treatment and the N: P treatment (Table 5). P treatment caused the largest relative increases in P on sites closest to the coast that had lower initial levels of soil P (data not shown).

Lime and Kinsey treatments were associated with an increase in soil Ca (Table 5). The greatest increases occurred close to the coast on sites with low initial levels of soil Ca. Despite the mean decrease in Ca associated with CaCl_2 treatment, this treatment increased soil Ca at seven of ten sites by an average of 40%, and caused little change at two sites (data not shown). For the P and control treatments, Ca tended to increase at sites closest to the coast with low initial soil Ca levels and decrease at sites farthest from the coast (data not shown). The N treatment decreased soil Ca at most sites, and this may have been associated with increased cation leaching from this treatments influence on soil pH.

The N and N: P treatments were not correlated with a notable or consistent increase in soil N. Instead, soil N tended to increase moderately at sites closest to the coast with P and Ca applications (data not shown). However, the increase in soil N for the control treatment at several sites, particularly those close to the coast, confounded interpretation of changes in soil N.

3.2 Foliar Chemistry

Like soil nutrients, levels of several foliar nutrients were correlated with distance-from-coast. In general, Ca, K, Mg, P, B and Mn increased with distance-from-coast, and N and N: Ca decreased (Table 6).

Table 6. Mean foliar nutrient levels by site pre-treatment. Sites ordered by distance from coast. Treatment-pooled nutrient values averaged at each site.

Site	N : Ca	Ca (%)	K (%)	Mg (%)	N (%)	P (%)	B (ppm)	Mn (ppm)	Zn (ppm)
GDH	8.89 (1.14)	0.17 (0.02)	0.63 (0.03)	0.10 (0.00)	1.49 (0.06)	0.12 (0.01)	13 (1)	75 (8)	10 (1)
MNS	4.94 (0.40)	0.29 (0.03)	0.68 (0.05)	0.09 (0.01)	1.44 (0.04)	0.11 (0.01)	15 (1)	62 (4)	12 (1)
ODF	5.09 (0.80)	0.30 (0.05)	0.76 (0.04)	0.15 (0.02)	1.52 (0.05)	0.14 (0.01)	17 (3)	76 (8)	12 (1)
HAGR	5.03 (0.45)	0.32 (0.02)	0.76 (0.05)	0.13 (0.01)	1.60 (0.13)	0.14 (0.01)	15 (2)	73 (4)	12 (1)
MNN	6.90 (0.45)	0.21 (0.02)	0.58 (0.02)	0.09 (0.00)	1.42 (0.08)	0.11 (0.01)	16 (1)	68 (5)	9 (0)
HAK	4.94 (0.63)	0.27 (0.04)	0.69 (0.03)	0.12 (0.00)	1.29 (0.03)	0.14 (0.01)	17 (1)	70 (11)	13 (1)
STR	2.53 (0.19)	0.52 (0.06)	0.78 (0.03)	0.13 (0.00)	1.31 (0.06)	0.17 (0.01)	19 (1)	87 (20)	13 (1)
OSU	2.05 (0.22)	0.64 (0.05)	0.79 (0.05)	0.14 (0.01)	1.30 (0.05)	0.18 (0.01)	26 (2)	115 (14)	10 (1)
GPH	2.45 (0.14)	0.52 (0.02)	0.85 (0.04)	0.13 (0.01)	1.27 (0.03)	0.15 (0.01)	20 (1)	163 (60)	11 (1)

CTC	2.47 (0.15)	0.55 (0.04)	0.77 (0.04)	0.15 (0.01)	1.36 (0.08)	0.15 (0.01)	24 (3)	156 (56)	19 (4)
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Levels of foliar nutrients changed over the three-year study, but treatment effects were sometimes confounded by changes in foliar nutrient levels in the control treatment (Table 7). After three years, the P treatment was consistently associated with the largest increases in foliar P relative to initial levels (average increase 20%). In contrast, the N treatment was associated with a decrease in P, which was more pronounced one year post-treatment compared to three years post-treatment. The N: P treatment was also associated with a decrease in foliar P three years after treatment.

Treatment effects on foliar Ca were difficult to interpret due to changes in foliar Ca in the control treatment at many sites, and inconsistent treatment effects on Ca levels. However, three years after treatment, lime was associated with a slight average increase in foliar Ca. The N: P treatment was associated with the largest increase in foliar Ca, but was based on the pooled foliage sample from just one site (OSU) where this treatment was applied. Although the Kinsey and CaCl_2 treatments increased soil Ca, average increases in foliar Ca were not observed for these treatments.

One year after fertilization, N treatment increased foliar N by an average of 0.14%, representing an 11% increase from initial levels. The N: P treatment applied at OSU was associated with a 0.98% increase in foliar N, representing a 71% increase from initial levels. Average increases in foliar N were less pronounced three years after treatment, but were still elevated compared to the control treatment and to the cross-treatment average. Increases in foliar N for the N treatment were most pronounced on the most inland sites (data not shown), which had relatively lower initial levels of foliar N.

Large changes in some foliar micronutrient levels were observed during the study, and the direction of change (increase or decrease) was often similar across sites and treatments, including the control (data not shown). However, the Kinsey blend was associated with a pulse in foliar micronutrient levels, especially B, at some sites. One year after treatment, Kinsey was the only treatment to increase foliar B at six sites, increasing B by as much as 72% compared to initial values (at site HAK). This effect was less pronounced three years after treatment.

Table 7. Average arithmetic and proportional change in foliar nutrient levels by treatment (trt). Pre-trt values (Pre) compared to values one (Yr1) and three yrs (Yr3) post-trt. Standard deviation in parentheses. Trt N: P only applied at site OSU. Bold indicates nutrient changes that were targeted or affected by trts.

Yr 1 vs. Pre-trt						
Trt	Ca (%)		N (%)		P (%)	
	Yr1-Pre	(Yr1-Pre)/Pre	Yr1-Pre	(Yr1-Pre)/Pre	Yr1-Pre	(Yr1-Pre)/Pre
Control	-0.07 (0.04)	-0.18 (0.12)	-0.10 (0.16)	-0.07 (0.11)	-0.01 (0.01)	-0.09 (0.08)
N	-0.05 (0.06)	-0.12 (0.13)	0.14 (0.23)	0.11 (0.17)	-0.03 (0.01)	-0.19 (0.08)
lime	-0.05 (0.04)	-0.15 (0.10)	-0.11 (0.13)	-0.07 (0.09)	-0.01 (0.01)	-0.10 (0.09)
CaCl2	-0.04 (0.06)	-0.09 (0.13)	-0.09 (0.11)	-0.06 (0.08)	-0.01 (0.01)	-0.07 (0.08)
P	-0.06 (0.05)	-0.16 (0.11)	-0.14 (0.16)	-0.09 (0.09)	0.00 (0.02)	0.03 (0.15)
Kinsey	-0.03 (0.07)	-0.08 (0.15)	-0.15 (0.16)	-0.10 (0.10)	-0.01 (0.02)	-0.07 (0.12)
N: P	-0.05	-0.07	0.98	0.71	-0.01	-0.07
Average	-0.05 (0.05)	-0.13 (0.12)	-0.06 (0.23)	-0.03 (0.16)	-0.01 (0.02)	-0.08 (0.12)
Yr 3 vs. Pre-trt						
Trt	Ca (%)		N (%)		P (%)	
	Yr3-Pre	(Yr3-Pre)/Pre	Yr3-Pre	(Yr3-Pre)/Pre	Yr3-Pre	(Yr3-Pre)/Pre
Control	0.00 (0.04)	-0.04 (0.12)	0.05 (0.09)	0.04 (0.07)	0.01 (0.02)	0.08 (0.10)
N	0.00 (0.04)	-0.02 (0.13)	0.07 (0.15)	0.05 (0.11)	-0.01 (0.02)	-0.05 (0.12)
lime	0.02 (0.04)	0.04 (0.12)	0.05 (0.13)	0.04 (0.10)	0.01 (0.01)	0.08 (0.08)
CaCl2	-0.02 (0.05)	-0.04 (0.09)	0.00 (0.13)	0.01 (0.09)	0.01 (0.01)	0.11 (0.09)
P	-0.03 (0.06)	-0.09 (0.14)	-0.02 (0.18)	0.00 (0.12)	0.03	0.20 (0.09)
Kinsey	-0.02 (0.05)	-0.04 (0.16)	-0.03 (0.17)	-0.01 (0.12)	0.01 (0.02)	0.08 (0.13)
N: P	0.15	0.24	0.28	0.2	-0.04	-0.21
Average	-0.01 (0.05)	-0.03 (0.13)	0.03 (0.15)	0.03 (0.10)	0.01 (0.02)	0.08 (0.13)

3.3 Infection levels by site

Infection index varied across sites, and differences in infection index were most pronounced for 2-yr-old needles (Fig. 3). Negligible disease was detected for both needle age classes at three sites (CTC, GPH and OSU), while moderate to severe disease levels were

detected at the remaining sites. The most severely impacted site (GDH) had a high infection index for both needle age classes, whereas all other sites had relatively low levels of infection (median infection index <5%) on 1-yr-old needles.

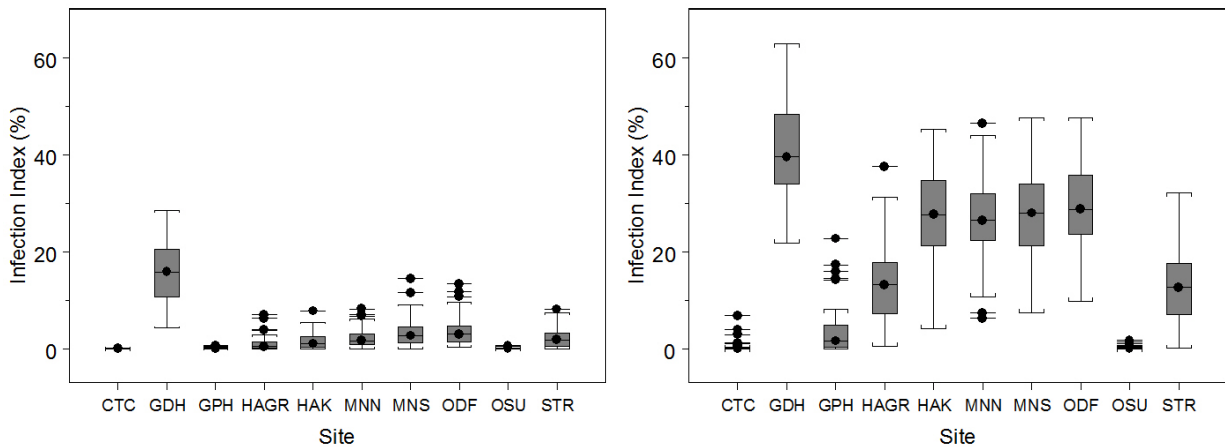


Fig. 3. Infection index by site for 1-yr-old needles (left) and 2-yr-old needles (right).

3.4 Linear Mixed Effects Analyses: differences in infection index by treatment across sites

Across sites, there was no evidence of treatment effect on infection index for 1- or 2-yr-old needles after accounting for site (p-values 0.47 and 0.14, respectively; bottom row Table 8). Significant differences (p-values < 0.05) in infection index were detected in direct comparisons between the control treatment, which was associated with the highest infection index for both needle age classes, and some individual fertilization treatments (indicated by asterisks [*] in the bottom row Table 8). However, across all sites, differences in estimated mean infection index between the highest- and lowest-ranked treatments was 0.6 for 1-yr-old needles and 3.2 for 2-yr-old needles, representing negligible differences in infection index between treatments (bottom row Table 8).

Table 8. Infection index by site and needle age. Sites ordered by infection index (highest to lowest). Infection index is the product of percent infection incidence and percent mean pseudothecia density (15.7 indicates that, on average, 15.7% of stomates were occluded). Min and max are mean infection index values associated with the best- and worst-ranked treatments (trts). ANOVA p-values for treatment effects are given. Treatments: (1) control, (2) N, (3) lime, (4) CaCl₂, (5) P, (6) Kinsey, and (7) N: P. In the bottom row, overall p-values for treatment effect and treatment ranks (treatments 1-6) come from linear mixed effects analysis with site as a blocking factor (asterisk [*] indicates a significant difference in infection index between individual treatments and the control at p<0.05).

Site	Needle Age	Mean	Median	Std. Dev.	Min (Trt μ)	Max (Trt μ)	n	p-value	Order of trts (infection, low to high)
GDH	1	15.7	15.8	6.7	11.8	19.1	58	0.11	1,4,5,2,6,3
	2	40.6	39.3	9.3	35.6	49.0	51	0.09	4,1,2,6,5,3
ODF	1	3.8	3.0	3.0	2.5	5.7	56	0.24	5,4,2,3,1,6
	2	29.4	28.7	8.4	25.7	31.3	56	0.78	4,1,2,3,5,6
MNS	1	3.4	2.7	2.9	2.0	5.4	56	0.11	1,5,4,2,6,3
	2	27.3	28.0	9.2	20.1	30.7	54	0.49	1,2,6,4,3,5
MNN	1	2.4	1.7	2.0	1.6	3.5	57	0.37	2,1,3,6,5,4
	2	27.1	26.4	9.0	22.1	32.2	56	0.27	2,1,4,3,5,6
HAK	1	1.6	1.1	1.6	0.9	2.6	55	0.13	6,3,4,1,2,5
	2	27.5	27.6	9.6	24.6	35	55	0.13	6,1,4,5,3,2
STR	1	2.1	1.8	1.9	1.2	2.9	54	0.48	2,3,5,6,4,1
	2	13.0	12.7	7.5	10.8	15.7	55	0.67	2,1,6,4,3,5
HAGR	1	1.1	0.4	1.4	0.5	1.8	59	0.36	6,1,4,5,2,3
	2	13.6	13.2	7.8	10.9	17.7	60	0.49	1,6,3,2,5,4
GPH	1	0.1	0	0.2	<0.1	0.1	46	0.37	5,3,2,4,1
	2	3.7	1.6	5.2	2.8	5.1	46	0.91	1,4,5,3,2
CTC	1	<0.1	0	0.1	0	0.1	57	0.19	6,2,4,5,3,1
	2	0.6	<0.1	2.1	<0.1	2.4	56	0.14	6,2,5,1,4,3
OSU	1	<0.1	0	0.1	0	0.1	67	0.55	5,2,3,7,1,4,6
	2	0.1	0	0.3	<0.1	0.2	66	0.21	7,5,4,1,2,3,6
Overall	1	3	0.9	5.2	2.7	3.3	565	0.47	1,5,4,2,6,3
Overall	2	18	17.5	15.2	16.7	19.9	555	0.14	1,2,6,4*,3*,5*

3.5 One-Way ANOVA: differences in infection index by treatment within sites

No significant treatment effect on infection index was detected within individual study sites (ANOVA p-values > 0.05; Table 8). Differences in infection index between treatments, within sites, were generally small in magnitude, and ranking fertilization treatment from highest to lowest infection index (according to one-way ANOVA beta coefficient estimates) revealed no consistent trends in treatment-rank across sites or needle age classes (Table 8). Differences in

treatment-rank were observed between needle age classes from the same site, which originated from the same treatment trees and branches. When the average rank for each treatment was compared across sites and needle age classes, some treatments performed slightly better or worse than expected in the absence of treatment effect (Table 9).

Although there was no evidence of treatment effect on disease severity, differences in mean infection index between the best- and worst-ranked treatments at individual sites were greatest for 2-yr-old needles and on sites with high disease pressure that experienced relatively higher variance in infection index (Table 8). The most severely impacted site (GDH) displayed the greatest difference in mean infection index between the best- and worst-ranked treatments (13.4), which corresponded to lime and CaCl_2 , respectively. When sites were grouped by relative disease severity level (low, moderate and high), graphical representations of infection index by treatment also supported a lack of treatment effect (Fig. 4).

Table 9. Average treatment rank (1-6) by needle age. Standard deviation of rank in parentheses. Rank of ‘1’ indicates that treatment was associated with lowest mean infection index according to ANOVA beta coefficient estimates. Treatments ranked < 3.5 performed better than expected, and treatments > 3.5 performed worse than expected given the statistically supported assumption of no treatment effect. Asterisk [*] indicates that 3.5 was outside the interval of mean and standard deviation.

Treatment	Yr 1 Needles	Yr 2 Needles	Yr 1 & 2 combined
Control	3.3 (2.0)	5.0 (0.9)*	4.1 (1.8)
N	4.0 (1.5)	3.8 (1.8)	3.9 (1.6)
Lime	3.1 (1.7)	2.2 (0.9)*	2.7 (1.4)
CaCl_2	3.3 (1.4)	3.9 (1.6)	3.6 (1.5)
P	4.0 (1.8)	2.7 (1.5)	3.3 (1.7)
Kinsey	3.3 (2.1)	3.4 (2.1)	3.4 (2.0)

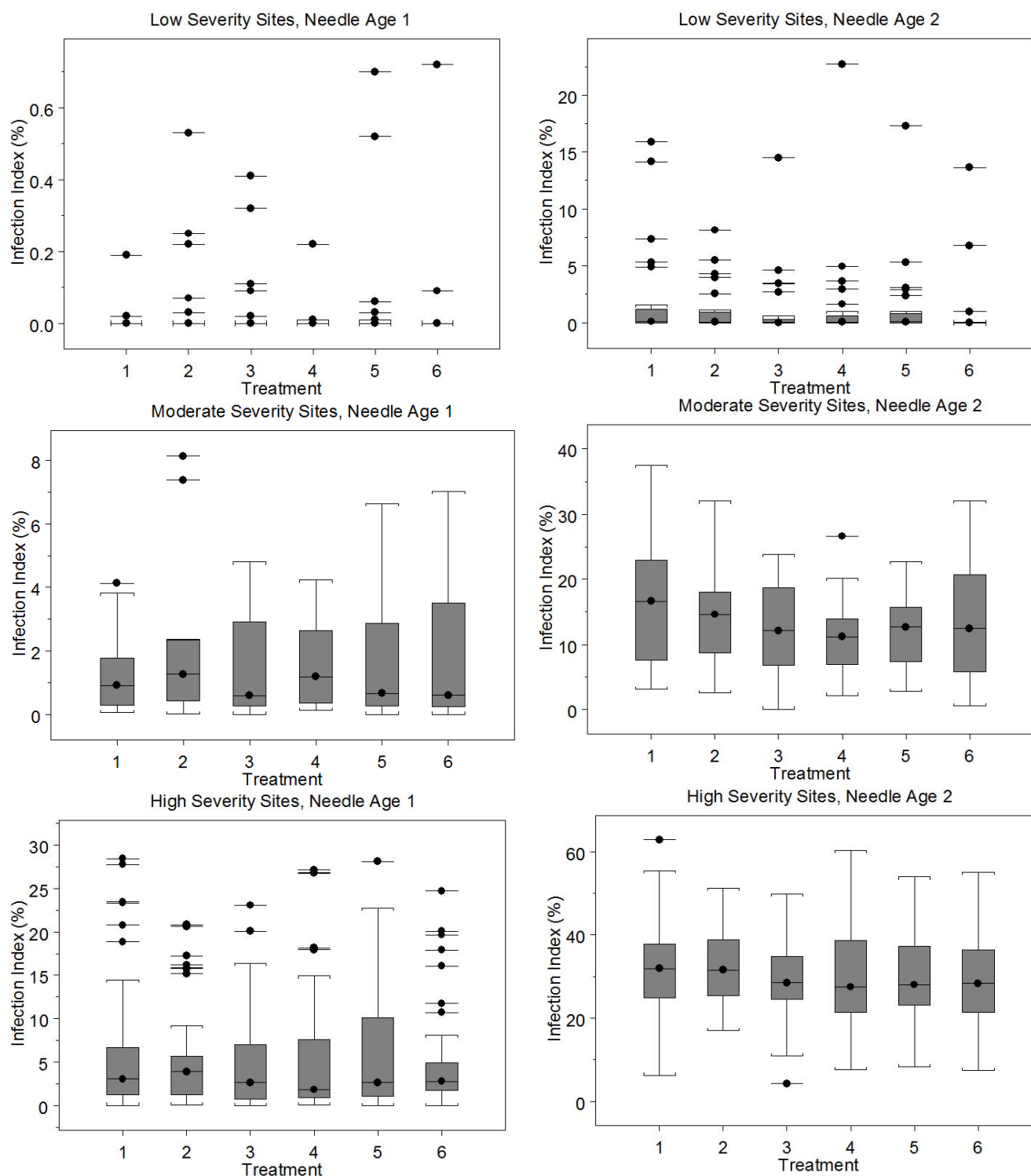


Fig. 4. Infection index by treatment for each needle age class and disease severity levels (low, moderate, high). Low severity sites = OSU, CTC, GPH; moderate severity sites = STR, HAGR, and high severity sites = GDH, HAK, MNN, MNS, ODF. Each graph depicts infection indices for approximately 10 trees/trt/site for 1-yr-old and 2-yr-old needles. Treatments: (1) control, (2) N, (3) lime, (4) CaCl₂, (5) P, and (6) Kinsey.

3.6 Simple Linear Regression: correlation between site-level infection and nutrient levels

Exploring relationships between infection index of 2-yr-old needles and foliar nutrient levels (pre-treatment and 1 and 3 years post-treatment) using simple linear regression analysis provided strong evidence of a negative relationship between infection index and Ca, K, P, B, and Mn (Table 10). Scatter plots revealed autocorrelation between these factors and distance-from-coast (not shown). Infection index of 2-yr-old needles was used for this analysis because, across sites, 2-yr-old needles displayed greater variation in disease severity than 1-yr-old needles. Changes in the strength of the relationship between infection index and foliar nutrient levels over time, particularly one year post-treatment, are potentially related to fluctuation in nutrient levels associated with fertilization treatment. There was no evidence of a linear relationship between disease severity and foliar N and N: Ca. Nutrient levels of 1-yr-old needles were not assessed in 2008, which would have directly corresponded to 2-yr-old needles assessed for disease severity in May 2010. However, it is assumed that the average infection index at each site remains relatively stable over time, allowing for these site-level comparisons of infection index and nutrient levels.

Table 10. Linear relationships between infection index of 2-yr-old needles (collected May 2010) and foliar nutrient levels pre- and post-treatment. Nutrients for which simple linear regression analysis revealed a significant linear relationship with infection index are in bold (at $\alpha = 0.05$).

Nutrient		Pre-treatment (2006)	Post-treatment (2007)	Post-treatment (2009)
N:Ca	p-value	0.00	0.00	0.00
	non-0 slope	0.16	0.08	0.12
	R ²	0.81	0.84	0.87
%Ca	p-value	0.00	0.00	0.00
	non-0 slope	0.00	0.00	0.00
	R²	0.86	0.77	0.89
%N	p-value	0.22	0.82	0.15
	non-0 slope	0.31	0.89	0.25
	R ²	0.18	0.01	0.24
%K	p-value	0.01	0.00	0.00
	non-0 slope	0.00	0.00	0.00
	R²	0.58	0.77	0.65
%Mg	p-value	0.05	0.06	0.01

	non-0 slope R²	0.01 0.39	0.02 0.37	0.00 0.58
%P	p-value non-0 slope R²	0.02 0.00 0.53	0.00 0.00 0.68	0.01 0.00 0.56
B (ppm)	p-value non-0 slope R²	0.00 0.00 0.73	0.59 0.28 0.04	0.02 0.00 0.51
Mn (ppm)	p-value non-0 slope R²	0.01 0.00 0.63	0.00 0.00 0.68	0.00 0.00 0.83

4 Discussion

The potential for fertilization treatment to affect SNC severity in western Oregon is of great interest to Douglas-fir timberland managers throughout the region. This study found no evidence that fertilization treatments applied at operational levels significantly altered SNC severity, as measured by the abundance of fruiting bodies on needles. Disease severity did not differ between treatments within or among the ten stands examined, which covered a range of disease severity levels, soil composition and other site attributes. The hypotheses that N fertilization increases susceptibility to SNC and that Ca and alternative fertilization regimes decrease susceptibility were not supported.

In this foliar pathosystem, ground-applied mineral nutrition must be available in the soil, absorbed by the roots, and transported to the foliage before the pathogen is likely to be directly affected. Soil and foliar chemistry assessments provided evidence that soil and foliar nutrient levels were altered by fertilization treatment. The magnitude and durability of the effect on soil nutrients was site and treatment dependent; treatment effects were generally greatest where applied nutrients were initially low and presumably limiting. Fertilization effects on foliar chemistry also differed by site, and were most pronounced for the P and N treatments.

There was no significant difference in infection index between treatments within sites. When data from all sites were considered, there was no evidence that infection index differed

between treatments. Although some differences in infection index were detected when individual treatments were directly compared to the control treatment, the magnitude of these differences were negligible and are not believed to be biologically or economically significant. In contrast, there were large differences in mean infection levels between sites. At the highest severity site, approximately 40% of stomata of 2-yr-old needles were occluded by pseudothecia, compared to 0.1% at the lowest severity site.

The lack of fertilization treatment effect was also supported by the inconsistent rank of treatments by infection index across sites, even sites with similar levels of infection, and by differences in treatment rank within sites, between needle age classes. Some treatments were associated with better or worse treatment ranks than expected under the assumption of no treatment effect. Interestingly, the control treatment was associated with the highest infection index for both needle age classes when all sites were pooled, providing evidence that fertilizer treatments applied in this study did not increase susceptibility of Douglas-fir to *P. gaeumannii* infection and colonization relative to the control treatment.

The lack of treatment effect on SNC infection index in this study made it inappropriate to pool infection levels by treatment to directly analyze the relationship between nutrient levels and disease severity, except at the site-level. Site-level comparisons supported previously observed correlations between disease severity and levels of several foliar nutrients (e.g. Ca) (Perakis et al. 2005). However, this analysis did not support a strong relationship between infection levels and foliar N or N: Ca.

Perakis et al. (2005) observed foliar N levels from 0.85-1.74% in Douglas-fir stands of the Oregon Coast Range. A similar range was observed in this study before fertilization treatment (1.21-1.81%), and the highest level of foliar N achieved through fertilization was

2.36% (N: P treatment). In contrast to our findings, the study conducted by El Hajj et al. (2004) reported significantly increased (2.2- to 3.6-times higher) pseudothecia density on 2-yr-old needles of urea-treated trees compared to controls. Urea fertilization had resulted in foliar N levels of 1.0-1.30%, compared to 0.9-1.0% for the control treatment. This study was conducted on 10-yr-old Douglas-fir trees that were part of a progeny test of low-elevation open-pollinated seed sources at an experimental forest in Priest River, ID (700 m elevation) and had an average needle retention of 2.7 yrs (El-Hajj et al. 2004). It is unclear why this study obtained markedly different results than our own, particularly because increases in foliar N were not dramatic and apparently did not exceed the threshold for N-limitation. There are several reasons that the results of this study should not be extended to coastal Douglas-fir stands of western Oregon, including the small sample size (5 trees/ treatment); the lack of replication across stands; the younger age and interior form of the trees (*P. menziesii* ssp. *glauca*); the repeated and intensive fertilization required to raise foliar N; and the inland and high-elevation location of the study.

While operational fertilization did not affect disease severity in our study, fertilization treatment directly affected tree growth on sites affected by SNC, independent of disease (MAINWARING et al. 2009; MAINWARING and MAGUIRE 2010). After accounting for site and tree covariates, N and lime fertilization resulted in marginally greater volume production (~3.4%) compared to the control treatments across sites. The relative benefits of fertilization varied by site, with the largest positive growth responses detected on sites on which the applied nutrients were limiting. For example, significant growth responses to N treatment occurred on sites with relatively lower site indices and higher soil pH. Site indices less than 33.5 m (110 ft; high site III) or 36.6 m (120 ft; low site II) at age 50 are considered low for Douglas-fir in the Coast Range (KING 1966). It is recommended that managers assess soil chemistry in their stands

in order to select the most appropriate fertilization regimes and to avoid the expense of fertilizer applications that are unlikely to result in increased volume growth given the initial site conditions. While fertilization treatments have the potential to positively or negatively affect Douglas-fir volume growth in stands impacted by Swiss needle cast, impacts on growth are apparently unrelated to fertilization effects on the host-pathogen interaction.

Studies that have been conducted in the Pacific Northwest and New Zealand on the influence of silvicultural strategies (commercial and pre-commercial thinning and vegetation management) on volume growth and SNC severity in affected stands have also found no direct interaction between silvicultural strategies and disease severity (HOOD and SANDBERG 1979; MAINWARING et al. 2005; SHAW et al. 2011). In other words, various silvicultural strategies did not directly affect the host-pathogen interaction, but conferred the same relative benefits as in the absence of disease. This may be due to the specific mechanisms of infection and colonization in this pathosystem, which do not appear to be significantly affected by changes in host resource availability, vigor or nutritional status that might be expected under operational silvicultural treatments. There is no evidence that inducible or constitutive host defense responses play a role in this pathosystem, which, if present, might provide a logical means for altered host nutritional status to directly affect host susceptibility, as has been observed in other agricultural and forest pathosystems (e.g. *Diplodia pinea*) (STANOSZ et al. 2004; BLOGETT et al. 2005; WALLIS et al. 2011).

Thinning and other silvicultural activities also have the potential to impact moisture, temperature and light conditions around host tree foliage, thereby influencing the infection environment. However, on sites close to the coast with high levels of disease, it is believed that prolonged leaf wetness during the infection period in spring and summer exceeds a threshold

beyond which thinning practices have little impact on the infection environment. In Christmas-tree plantations, in which cultural practices may promote high infection levels, thinning and pruning activities have been shown to effectively reduce disease levels (CHASTAGNER 1997). Protectant fungicidal treatments that contain chlorothalonil or sulfur-based compounds significantly reduce fungal infection and symptom development, but fungicides are not a durable or economical means of SNC disease control in plantation forests (CRANE 2002; STONE et al. 2007).

An improvement on our study design would be to measure nutrient levels individually for all trees (not pooled by treatment), which would provide a more robust sample size and make it possible to conduct regression analysis for all sample trees with infection index as the response variable and nutrient levels or ratios as explanatory variables. However, the goal of this study was to determine if and how operational fertilization applications, not foliar or soil nutrient levels per se, impact disease severity and tree growth, and the study design accomplished this objective. Fertilization treatments applied at standard industrial rates did not affect the density of fungal fruiting bodies on the foliage of Douglas-fir trees.

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Regional and annual trends in Douglas-fir foliage retention: Correlations with climatic variables

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ABSTRACT

Swiss needle cast imposes strong geographical patterns in Douglas-fir needle retention throughout the Coast Ranges of Oregon and southwestern Washington. These geographical patterns in foliage retention have been related to the spatial variability in average climatic conditions, with climate presumed a major causal factor in the spread and intensification of the fungus that causes Swiss needle cast. Annual fluctuations in foliage retention have likewise been hypothesized to follow fluctuations in annual climatic conditions. The objective of this analysis was to test a full suite of climatic variables for their ability to predict regional and annual patterns in Douglas-fir foliage retention on 296 permanent sample plots comprising six different Swiss needle cast studies. Foliage retention was estimated annually from 1996 to 2009 and climatic data were generated from the PRISM website through ClimateWNA (Wang et al., 2006). Among the 85 annual, seasonal, and monthly climate variables explored, average foliage retention was predicted most consistently by a temperature-based continentality index, mean annual precipitation, winter temperature, summer temperature, and spring or summer precipitation. The same 85 variables were tested for predicting annual fluctuations in foliage retention, allowing for lagged effects of climatic conditions 1–4 years prior to each year of observation. The annual foliage retention models had climate variables similar to the periodic average foliage retention models, but with a variety of lagged effects. The periodic average foliage retention model suggested that under future climate scenarios foliage retention would increase.

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1. Introduction

Swiss Needle Cast (SNC) has become a major foliar disease of Douglas-fir (*Pseudotsuga menziesii*) in coastal areas of Oregon and Washington (Hansen et al., 2000). The causal fungus, *Phaeocryptopus gaumannii* (T. Rohde) Petr., occludes the stomates with fruiting bodies, or pseudothecia, resulting in carbon starvation and premature foliage loss (Manter et al., 2003). Since 1990, SNC has intensified dramatically in coastal Oregon. The area of Douglas-fir forest with SNC symptoms detectable by aerial survey in the Coast Ranges of Oregon increased from 53,072 ha in 1996 to 159,483 ha in 2010 (Kanaskie and McWilliam, 2010). SNC had previously been a serious concern only where Douglas-fir was cultivated outside of its native range in western North America (Boyce, 1940). The influence of climatic factors on infection indices (Manter et al., 2005) has suggested that recent changes in local climatic conditions have facilitated emergence of the disease or that sus-

ceptible genotypes of Douglas-fir have been planted on coastal sites where climatic conditions are more favorable to the disease.

The reduction in needle retention symptomatic of SNC causes significant Douglas-fir growth losses (Maguire et al., 2002). Foliage retention has been routinely applied as an index of disease severity, and has been applied to estimate growth losses at the stand level. Individual-tree diameter and height growth predictions can also be modified by plot-level foliage retention in ORGANON, a growth model that can simulate growth of intensively managed Douglas-fir stands (Hann, 2006; Garber et al., 2007). In other species and regions of the world, needle retention has been correlated with a range of site factors, including inherent productivity (Pensa and Jalkanen, 2005), elevation (Reich et al., 1995), and various climatic factors correlated with elevation and latitude (Reich et al., 1995; Xiao, 2003); however, the proposed mechanisms have not included indirect effects through pathogens. Mild winter temperatures have been hypothesized to favor the development of fungal mycelia within the needles of infected Douglas-fir (Manter et al., 2005), and abundant spring moisture has been hypothesized to facilitate germination of spores on the surfaces of needles and allow hyphae to grow across the needle surface until they can enter a stomate.

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Analyses to date have investigated the correlation between stand foliage retention averaged over a period of time and average climatic conditions for the same period and site. If the climate characterizing a site is driving part of the spatial variation in foliage retention, observed annual fluctuations in foliage retention should likewise be correlated with annual variation of the same climatic factors. These spatial and temporal relationships with climate have been verified for *P. gaumannii* infection index (frequency of stomates occluded by pseudothecia; Manter et al., 2005). Spatial variability has been investigated for foliage retention, primarily because foliage retention has been regarded as the operational link to geographic risk rating systems. In contrast, annual climatic influences on epidemiology are better understood by directly observing annual responses of the pathogen itself. However, continuous monitoring of foliage retention on plots established by the Swiss Needle Cast Cooperative (SNCC; <http://sncc.forestry.oregonstate.edu/>) has provided a broader geographic scope and extended time series of observations than are currently available for pseudothecia counts. This database allowed extensive testing of the effects of both average climate characterizing a site and annual variation in climatic variables on foliage retention as the primary symptom of SNC. The objectives of this paper were to: (1) test a large set of site-specific climatic variables for their ability to predict geographic variation in plot average foliage retention over the period of observation; (2) test a large set of site-specific climatic variables for their ability to predict annual fluctuations in foliage retention, including lagged effects of climatic conditions; and (3) apply resulting models to forecast foliage retention under future climate scenarios at each plot. Identification of factors controlling geographic variation in average foliage retention have previously facilitated development of geographic risk-rating systems for SNC (Rosso and Hansen, 2003; Coop and Stone, 2007; Latta et al., 2009). Identification of lagged climatic variables that explain the largest possible proportion of variation in annual fluctuations in foliage retention should improve our understanding of climatic effects on SNC intensification, including the degree to which recent intensification can be attributed to corresponding trends in climate.

2. Material and methods

2.1. Field work

Plots were distributed across a range of SNC severity, stand density, aspect, and slope (Fig. 1). The study sites extended from 42.13°N to 46.65°N latitude and from 122.00°W to 124.35°W longitude. Elevation ranged from 9 to 1280 m above sea level. Over the last 40 years, the mean January minimum temperature for this region was 1.5 °C and the mean July maximum temperature was 22.8 °C. Total annual precipitation averaged approximately 240 cm, with approximately 80% of the total falling from October to March.

Data for all studies were collected by field crews trained by the Oregon Department of Forestry to ensure consistency and repeatability of measurements. 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 near the center of each third, and average number of needle age classes present at time of sampling was estimated to the nearest 0.5 year (Maguire et al., 2002). The needle retention of the tree was then estimated by averaging these values across the crown thirds (Fig. 2).

The Growth Impact Study (GIS) plots were established to monitor SNC symptoms and tree growth in 10–30 year-old Douglas-fir

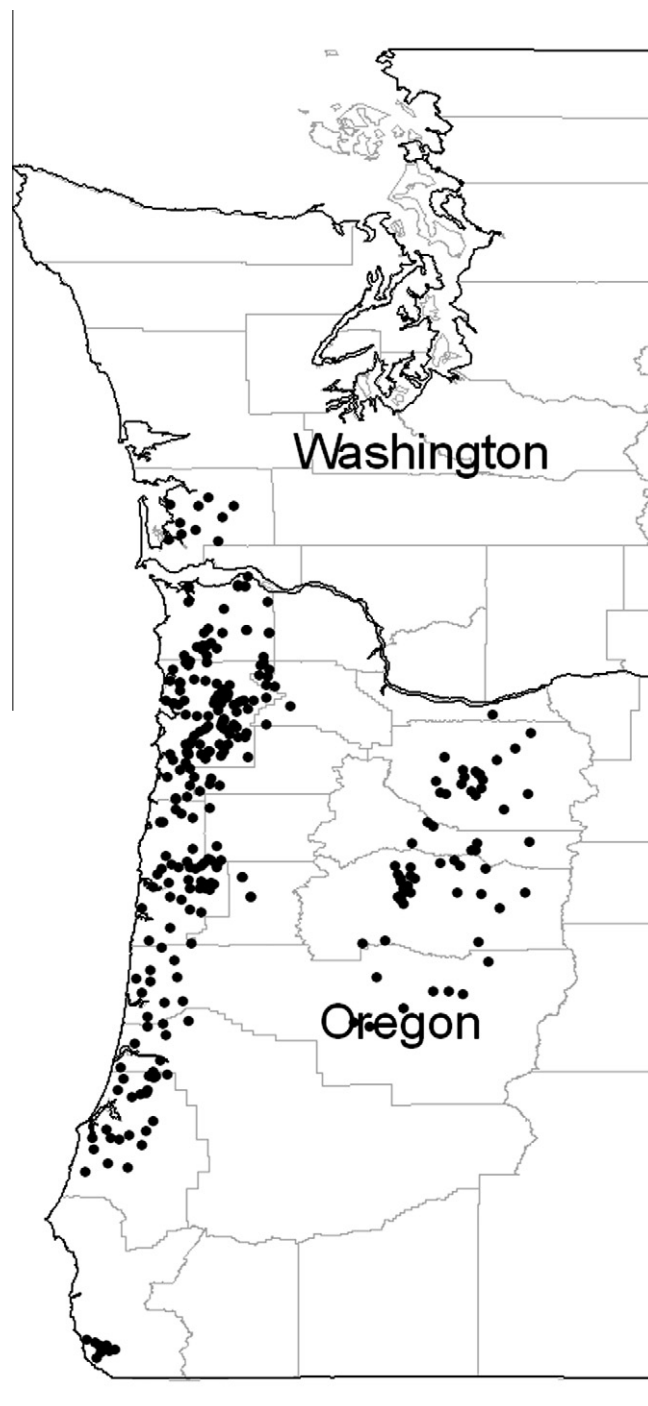


Fig. 1. Geographic distribution of plots and transects scored for Douglas-fir foliage retention.

plantations between Astoria and Newport and within 18 miles of the Pacific Coast (Maguire et al., 2002, Maguire et al., submitted for publication). Needle retention was estimated on ten dominant trees per plot. Foliage retention was estimated at plot establishment in 1998, and annually just prior to bud break from 1999 to 2004. Plot-level foliage retention was computed as the average of the ten sample trees per plot.

The PCT study was designed to test the effect of thinning and initial SNC severity on symptom development and growth response (Maguire et al., in press). The treated plots were thinned before the growing season started in 1998. Spring (April–May)

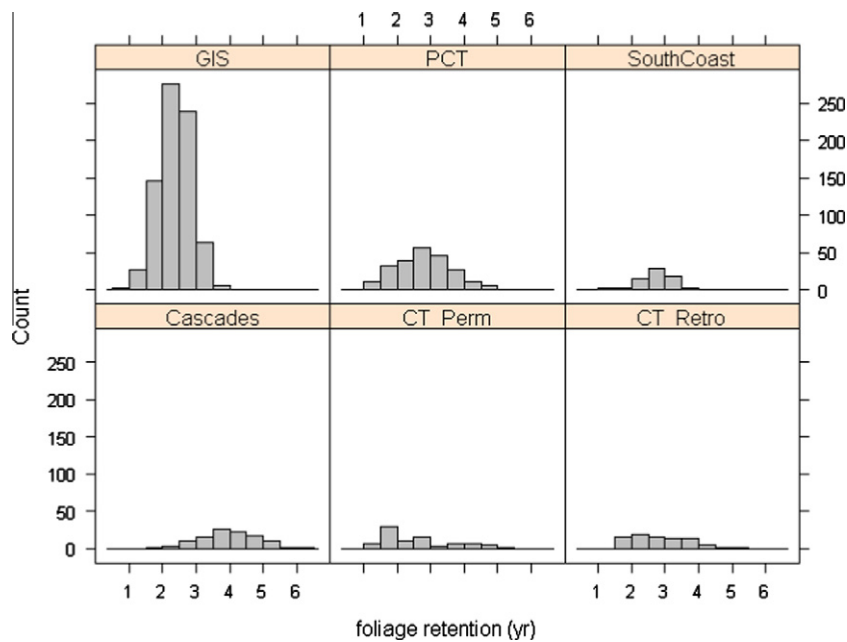


Fig. 2. Frequency histograms of foliage retention for six Swiss needle cast studies used in development of foliage retention models.

Table 1
Number of plots measured for Douglas-fir foliage retention by study and year of observation.

Plots type	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2009	Grand total
Cascades						55					55			110
CT_Perm							15	14	15	14	15	14		87
CT_Retro							24	20			23	17		84
GIS	77	77	77	77	76	76	76	76	72	72				756
PCT_Control			28	28	28	28	28	28	28	28				224
South coast									1				62	63
Grand total	77	77	105	105	104	159	143	138	116	114	93	31	62	1324

foliage retention was estimated annually at each of these study sites from 1998 to 2005 (Table 1) applying the same protocol as on the GIS plots.

Cascades growth impact study was installed in 2001 and remeasured in 2006 (Filip et al., 2006). Foliage retention was estimated by crown thirds as described above, but the ten sample trees were distributed along a randomly located 75-m transect within sample stands. Two dominant or codominant trees nearest to five equidistant points along the transect were scored for foliage retention. The same ten dominant or codominant trees were scored for foliage retention again in 2006, allowing for replacement with the nearest dominant or codominant tree if an original sample tree had died.

South coast foliage retention data were collected in 2009 on supplementary transects installed in randomly selected 10–30 year-old stands in the central and southern Oregon Coast Ranges and in the southern Washington Coast Ranges. The objective for measuring foliage retention in these stands was to extend the geographic and climatic range of previous SNCC work. The protocol for estimating foliage retention was identical to the protocol described above for the Cascades growth impact study.

CT_Perm and CT_Retro plots were established to investigate the interaction of thinning and SNC severity on growth of older stands ranging between 20 and 60 years of age (Table 1). All plots contained at least 75% Douglas-fir by basal area. The CT_Perm plots were unthinned control plots and CT_Retro plots had undergone commercial thinning 4–10 years prior to establishment (Mainwaring et al., 2005, Mainwaring and Maguire, 2008). Because these trees were

much taller than those in other studies, foliage retention for each of ten trees per plot was estimated from secondary or lateral branches on a primary branch near the middle of the crown only (Table 2).

2.2. Climate data

Climate data for each plot and each year from 1992 to 2009 were calculated with ClimateWNA v4.62 (Tables 3 and 4). ClimateWNA extracts and downscales PRISM (Daly et al., 2002) monthly data (2.5 × 2.5 arcmin) for the reference period (1961–1990), and calculates seasonal and annual climate variables for specific locations in western North America based on latitude, longitude and elevation (optional). This software also downscales and integrates historical (1901–2009) (Mitchell and Jones, 2005; Mbogga et al., 2009) and future climate datasets generated by various global circulation models (GCM). Three future periods were explored, here referred to as 2020 (30 year average of 2010–2039), 2050 (30 year average of 2040–2069) and 2080 (30 year average of 2070–2099). The output included both measurable climate variables and derived climatic indices (Hamann and Wang, 2005).

GCM projections for future periods in ClimateWNA were obtained from the TYN SC 2.0 dataset (Mitchell et al., 2004) and from Pacific Climate Impact Consortium. These GCM predictions were obtained from the Intergovernmental Panel on Climate Change (IPCC) Fourth assessment (AR4) (IPCC, 2007). ClimateWNA used various combinations of ten GCMs and three emission scenarios

Table 2

Number of plots, average foliage retention (FR), slope, latitude, longitude, and elevation (elev) for plots in the six different SNC studies.

Region	N obs.	Variable	Mean	Std. dev.	Minimum	Maximum
CT_Perm	29	FR	2.60	1.02	1.26	4.78
		Slope	12.13	6.84	0.00	25.36
		Lat.	45.24	0.71	43.58	46.17
		Long.	−123.57	0.37	−123.99	−122.29
		Elev.	394.10	196.15	61.00	1024.00
CT_Retro	44	FR	2.85	0.80	1.65	4.58
		Slope	10.26	8.22	0.00	30.03
		Lat.	45.25	0.71	43.50	46.17
		Long.	−123.52	0.40	−124.06	−122.31
		Elev.	492.77	190.16	45.00	875.00
Cascades	55	FR	4.03	0.55	2.45	5.50
		Slope	10.58	8.06	0.00	34.88
		Lat.	44.72	0.42	43.85	45.50
		Long.	−122.45	0.25	−122.94	−122.00
		Elev.	652.64	312.93	152.00	1280.00
GIS	77	FR	2.38	0.42	1.26	3.35
		Slope	16.00	12.61	0.00	44.60
		Lat.	45.25	0.42	44.58	46.09
		Long.	−123.78	0.09	−123.99	−123.61
		Elev.	245.09	156.58	61.00	914.00
PCT	28	FR	2.79	0.78	1.28	4.43
		Slope	11.60	12.31	0.00	38.10
		Lat.	45.44	0.56	44.54	46.22
		Long.	−123.58	0.14	−123.89	−123.38
		Elev.	238.29	158.45	48.00	766.00
SouthCoast	63	FR	2.76	0.43	1.48	3.77
		Slope	7.83	7.06	0.00	22.05
		Lat.	43.98	1.32	42.10	46.64
		Long.	−124.02	0.19	−124.35	−123.57
		Elev.	227.08	139.61	9.00	609.00

(A1B, A2, and B1) to generate 13 sets of future climatic conditions for each period described above as 2020, 2050, and 2080.

2.3. Statistical analysis

All subsets regression and a mixed modelling approach were used to develop models for predicting foliage retention from climatic variables using PROC REG and PROC MIXED in SAS version 9.2. Both periodic average foliage retention and annual fluctuation in foliage retention were modeled, the former to understand fundamental site differences as determined by long-term climatic averages, and the latter to understand how annual fluctuations in the same or similar climatic variables caused the range and average of foliage retention to vary from year to year. For both periodic average and annual foliage retention models, 2/3 of all plots were used for model development and 1/3 was used for validation. Maximum acceptable variance inflation factor (VIF) was set at 10 to minimize the impact of collinearity among the variables. The best models were selected by optimal combinations of high R^2 , low AIC, and low MSE.

2.3.1. Average periodic foliage retention

Periodic average foliage retention was modeled as a function of climatic variables averaged over the same period of observation plus the four-year period immediately preceding the first observation for a given dataset. Separate models were developed for annual, seasonal, and monthly weather variables. Models based on a mix of climate variables at different temporal resolutions were avoided to simplify interpretation of the results and to facilitate their application to climate data that are restricted to a specific resolution. Each observation of periodic average foliage retention was weighted by the length of the observation period. An all-subsets regression approach helped identify sets of models with strong

statistical properties, and then specific models were selected based on their consistency with known aspects of SNC disease epidemiology and presumed causal factors. To facilitate comparison to previous work, the models developed by Coop and Stone (2007) and Latta et al. (2009) were also fitted to the comprehensive dataset.

Selected models were applied to the validation dataset and assessed by plotting predicted on observed foliage retention and computing the following validation statistics:

$$D = \text{Mean difference} = \Sigma d / n_v$$

$$\text{MAD} = \text{Mean absolute difference} = \Sigma |d| / n_v$$

where d is difference (observed retention – predicted retention), and n_v is number of observations in validation dataset.

The model selected as best using annual climatic variables was applied to the 13 future climate scenarios described above for 2020, 2050, and 2080. The average of the 13 predictions for each plot was then computed to generate frequency distributions across SNC severity for these three future periods.

2.3.2. Trends in annual foliage retention

Foliage retention in any single year was expected to have been influenced by climatic variables up to approximately 4 years prior to observation, because maximum needle longevity averaged slightly less than 4 years. Therefore, climate variables for foliage retention observed in any given year included seasonal or monthly variables in the current year up through May (month of observation), as well as climate variables from each of the previous 4 years to account for lagged and cumulative effects. Initial annual foliage retention models were developed by applying all-subsets regression to identify the best models based on annual, seasonal, and monthly variables separately. As was the case for periodic average retention, models based on a mix of climate variables at different

Table 3

Climatic variables tested as predictors of foliage retention in Douglas-fir.

Group	Predictor	Definition
Annual variables	<i>Direct variables</i>	
	MAT	Mean annual temperature (°C)
	MWMT	Mean warmest month temperature (°C)
	MCMT	Mean coldest month temperature (°C)
	TD	Temperature difference between MWMT and MCMT, or continentality (°C)
	MAP	Mean annual precipitation (mm)
	MSP	Mean annual summer (May to September) precipitation (mm)
	AHM	Annual heat:moisture index $((MAT+10)/(MAP/1000))$
	SHM	Summer heat:moisture index $((MWMT)/(MSP/1000))$
<i>Derived variables</i>	DD0	Degree-days below 0 °C, chilling degree-days
	DD5	Degree-days above 5 °C, growing degree-days
	DDu18	Degree-days below 18 °C, heating degree-days
	DDa18	Degree-days above 18 °C, cooling degree-days
	NFFD	The number of frost-free days
	FFP	Frost-free period
	bFFP	The Julian date on which FFP begins
	eFFP	The Julian date on which FFP ends
	PAS	Precipitation as snow (mm) between August in previous year and July in current year
	EMT	Extreme minimum temperature over 30 years
	Eref	Hargreaves reference evaporation, calculated with the Hargreaves equation (EHar) with a latitude correction applied, i.e., $Eref = EHar(1.18 - 0.0067latitude)$, $n = 56$, $R^2 = 0.734$, $sexy = 0.039EHar$ and the latitude is in degrees.
	CMD	Hargreaves climatic moisture deficit, sum of the monthly difference between a reference evaporation (Eref) and precipitation.
Seasonal variables	Tave_wt, Tave_sp, Tave_sm, Tave_at	Mean temperature (°C) of winter (Dec.(previous year)–February), spring (March–May), summer (June–August), and autumn (September–November)
	Tmax_wt, Tmax_sp, Tmax_sm, Tmax_at	Mean maximum temperature (°C) of winter, spring, summer, and autumn
	Tmin_wt, Tmin_sp, Tmin_sm, Tmin_at	Mean minimum temperature (°C) of winter, spring, summer, and autumn
	PPT_wt, PPT_sp, PPT_sm, PPT_at	Precipitation (mm) of winter, spring, summer, and autumn
Monthly variables	Tave01–Tave12	January–December mean temperatures (°C)
	Tmax01–Tmax12	January–December maximum mean temperatures (°C)
	Tmin01–Tmin12	January–December minimum mean temperatures (°C)
	PPT01–PPT12	January–December precipitation (mm)

temporal resolutions were avoided to simplify interpretation of the results and to facilitate their application to climate data that are restricted to a specific resolution. Candidate models for annual foliage retention were restricted to those with parameter estimates that were all significant at $\alpha = 0.05$ and predictor variables with $VIF < 10$. Models with 2–4 variables for each of the three temporal resolutions were selected based on R^2 and MSE. The selected annual foliage retention models were required to have a combination of fewest predictors and high precision, but also contain predictors that were most consistent with known aspects of SNC epidemiology. Because foliage retention was measured repeatedly on plots, the independence of observations assumed in ordinary least squares was clearly violated. Mixed-effect models eliminated some of the autocorrelation by introducing plot as a random effect. The efficacy of random plot effects for addressing autocorrelation was further assessed by reductions in AIC obtained by modeling the variance-covariance structure of the residual errors directly.

3. Results

3.1. Average foliage retention model

Annual, seasonal, and monthly climatic variables all had reasonably strong predictive ability in the selected models ($R^2 \geq 0.62$; Table 5). Annual and monthly variables explained a greater proportion of the variation than seasonal variables, with R^2 ranging from 0.67 to 0.68, 0.62 to 0.66, and 0.65 to 0.72 for annual, monthly and seasonal variables, respectively (Table 5). Approximately 6% and 10% more of the variation in foliage retention was explained by these models relative to the models presented by Coop and Stone (2010) and Latta et al. (2009), respectively. The selected model from each of the annual, seasonal, and monthly sets (models

2, 4, and 7 in Tables 5 and 6) suggested that the geographic variation in periodic average foliage retention was driven by a variable representing winter temperature (Tave_{wt}, Tmin12), a variable representing summer temperature (Tmax_{sm}, Tave08), or a variable representing a combination of both (TD). All three models also included a variable representing precipitation (MAP in model 2), particularly precipitation received in the spring or early summer (PPTsp in model 4, PPT07 in model 7). In general, foliage retention at a given location increased with increasing summer temperature, decreasing winter temperature, or increasing difference between winter and summer temperatures (Fig. 3). Likewise, foliage retention decreased with greater precipitation, with spring and early summer precipitation imposing greatest influence (Table 6).

Validation statistics indicated that models with annual climate variables had relatively large differences between observed and predicted retention ($D = -0.06$ to -0.05), and low MAD (0.35–0.37). In contrast, models with seasonal climate variables had low D (-0.01 to 0.04), and high MAD (0.38–0.47). Between these extremes were models based on monthly climate variables, with intermediate values of D (-0.07 to 0.04), and MAD (0.35–0.46). Performance of the three selected models (2, 4, and 7 in Table 6) on the validation dataset suggested no serious problems in model behavior (Fig. 4).

3.2. Forecasts with the average foliage retention model

Under each of the 13 future climate scenarios, average foliage retention predicted for 2020, 2050, and 2080 differed among the annual, seasonal and monthly models (models 2, 4, and 7, respectively; the models selected as best among those based on annual, seasonal, and monthly climate predictors). Average foliage retention across all plots was predicted by the annual model (model 2) to increase gradually from 3.0 to 3.1 to 3.3 years in 2020,

Table 4

Averages, minima, and maxima for key climatic variables for predicting foliage retention in coastal Douglas-fir stands. Variables and their units are defined in Table 3.

Variable	Mean	Std. dev.	Minimum	Maximum
TD	12.42	1.62	8.21	15.92
AHM	9.51	2.56	4.07	16.65
MAP	2371.38	629.53	1348.00	4825.00
DD0	20.42	20.76	3.00	148.00
Tmax_sp	14.54	1.41	9.39	17.16
Tave_sm	16.17	0.91	13.81	18.62
Tmax_sm	22.27	1.47	18.44	26.23
Tmin_wt	1.81	1.35	−2.80	5.66
Tave_wt	5.57	1.48	0.57	8.84
PPT_sp	557.84	120.65	331.80	983.07
PPT_at	613.16	161.62	276.80	1243.56
Tmax06	19.87	1.24	15.17	22.82
Tave07	17.01	1.10	14.55	20.26
Tave08	17.26	0.91	14.46	19.86
Tmin12	1.75	1.36	−3.06	5.64
Tave12	5.04	1.45	0.16	8.10
PPT06	76.30	20.32	33.40	122.70
PPT07	20.69	10.34	3.80	41.80
PPT08	34.92	12.78	10.20	65.89
PPT09	63.92	22.98	22.40	129.22

2050, and 2080, respectively. In contrast, the seasonal model (model 4) predicted a gradual decline in foliage retention from 3.0 in 2020 to 2.9 in 2050 and 2.8 years in 2080. The monthly model predicted a trend in foliage retention similar to the annual model, with a gradual increase from 2.9 to 3.0 to 3.2 years. Consistent with these results, the frequency distributions for foliage retention in 2020, 2050, and 2080 indicated that in the future fewer plots would have foliage retention ≤ 2 years, and more plots would also have foliage retention > 5 years according to the annual and monthly models, but the reverse was true for the seasonal model (Fig. 5). Foliage retention on the majority of study plots was predicted to increase by about half a year from the current range of 2–3 years to a future range of 2.5–3.5 years in 2080 based on the annual and monthly models (Fig. 5). Predicted trends in specific climatic variables lend insight into predicted changes in foliage retention. The GCMs generally predicted a gradual increase in continentality index (TD), a slight increase in mean annual precipitation (MAP), and a marked decline in chilling degree days (DD0) (Fig. 6). With respect to seasonal climate conditions, GCMs predicted a gradual increase in maximum summer temperature (Tmax_sm) and average winter temperature (Tave_wt), and a slight decrease in spring precipitation (PPT_sp). At the monthly resolution, GCMs predicted a future increase in August temperature (Tave08), a decrease in July precipitation (PPT07), and a marked increase in December temperature (Tmin12).

Table 5

Selected models for predicting periodic average foliage retention from annual, seasonal, and monthly climate variables averaged over the period of observation. All predictors are significant at $\alpha = 0.05$; bold type indicates variables with a positive effect on foliage retention; regular type indicates a negative effect.

Model authors or resolution	Model number	Number of predictors	Model statistics		Predictor variables	Validation statistics	
			R ²	MSE		D	MAD
Coop and Stone (2007)		3	0.56	1.09	RH7 DDS asp	0.01	0.50
Latta et al. (2009)		2	0.52	1.20	Tm1 CMI7	−0.09	0.56
Annual	1	2	0.67	0.83	TD MAP	−0.05	0.37
	2	3	0.68	0.80	TD MAP DD0	−0.06	0.35
Seasonal	3	2	0.62	0.94	Tmin_wt, Tave_sm	0.04	0.47
	4	3	0.65	0.87	Tmax_sm , Tave_wt, PPT_sp	0.02	0.42
	5	4	0.66	0.86	Tmax_sp, Tmax_sm , Tave_wt, PPT_sp	−0.01	0.38
Monthly	6	2	0.65	0.88	Tave08 , Tmin12	0.04	0.46
	7	3	0.68	0.80	Tave08 , Tmin12, PPT07	−0.01	0.39
	8	4	0.72	0.72	Tave08 , Tmax06, Tmin12, PPT08	−0.07	0.35

Table 6

Parameter estimates and their standard errors for models predicting periodic average foliage retention from climatic variables.

Model	Parameter estimates and standard errors
Coop and Stone (2007)	FR = 7.6 − 0.0585RH7 − 0.142DDS − 0.000830asp (0.562) (0.00855) (0.0150) (0.000314)
Latta et al. (2009)	FR = 3.7 − 0.397Tm1 − 0.102CMI7 (0.275) (0.0277) (0.0204)
Annual	
1	FR = −1.0 + 0.372TD − 0.000292MAP (0.275) (0.0194) (0.0000541)
2	FR = −0.4 + 0.312TD − 0.000311MAP + 0.00855DD0 (0.335) (0.0270) (0.0000534) (0.00273)
Seasonal	
3	FR = −3.0 − 0.453Tmin_wt + 0.415Tave_sm (0.665) (0.0269) (0.0417)
4	FR = 2.2 + 0.175Tmax_sm − 0.394Tave_wt − 0.00188PPT_sp (0.663) (0.0241) (0.0251) (0.000302)
5	FR = 2.5 − 0.127Tmax_sp + 0.223Tmax_sm − 0.298Tave_wt − 0.00191PPT_sp (0.675) (0.0646) (0.0342) (0.0546) (0.000300)
Seasonal	
6	FR = −3.6 + 0.418Tave08 − 0.427Tmin12 (0.671) (0.0390) (0.0259)
7	FR = −1.8 + 0.330Tave08 − 0.388Tmin12 − 0.0162PPT07 (0.754) (0.0418) (0.0261) (0.00351)
8	FR = −2.2 + 0.666Tave08 − 0.259Tmax06 − 0.379Tmin12 − 0.0157PPT08 (0.701) (0.0820) (0.0585) (0.0244) (0.00287)

3.3. Annual foliage retention model

Fit statistics from both ordinary least squares (all-subsets) and mixed-effects models showed that the best annual, seasonal, and monthly models demonstrated comparable performance, with lowest AICs reaching 849 for the best seasonal model, 861 for the best monthly model and 885 for the best annual model (Table 7). A wide variety of alternative variance-covariance structures for the residual errors achieved no significant improvement in AIC. The best was the AR(1) model, but it reduced AIC by less than 2%. All three of the selected models (models 10, 12, and 15) suggested that foliage retention in any given year increased with increasing summer temperature (Tmax_sm2, Tmax081) and with either decreasing winter temperature (Tave_wt2, Tave123) or increasing difference between summer and winter temperature (TD2) (Tables 7 and 8). In addition to these temperature effects, greater spring precipitation (PPT_sp1, PPT064) was associated with lower foliage retention in the seasonal and monthly models, and mean annual precipitation (MAP) was likewise negatively correlated with foliage retention. In general, the best models contained

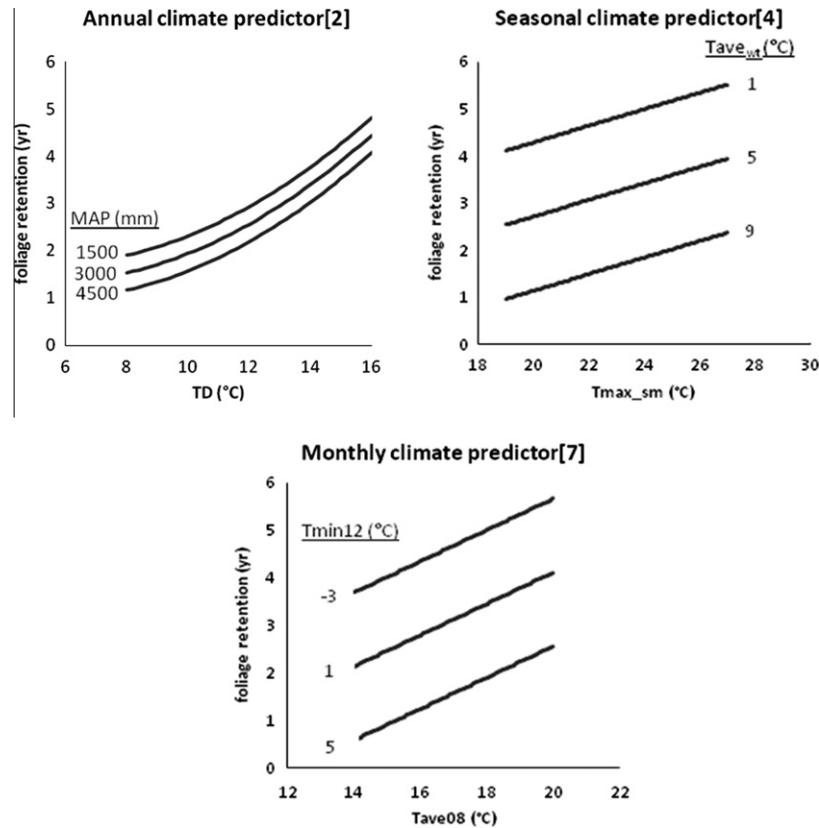


Fig. 3. Foliage retention predicted from three best periodic average retention models (model 2, 4, and 7). For model 2, DD0 was represented by its relationship to TD and MAP ($DD0 = 371.7 - 69.5 \cdot TD + 3.15 \cdot TD^2 + 0.00756 \cdot MAP$); for model 4, PPT_sp was set to the average of 557 mm; and for model 7, PPT07 was set to the average of 20 mm.

climate variables with lag times of 2 or 3 years. Comparison of predicted annual fluctuations in foliage retention to observed fluctuations for three randomly selected plots (one each with light, moderate, and severe SNC) suggested that the selected models tracked foliage retention best on the most severely impacted plots (Fig. 8).

Random effects for the plots in the validation dataset are unknown, so they cannot be accounted for when predicting foliage retention on the validation plots. As a result, the validation statistics were expected to indicate performance similar to fixed-effects models (Table 7). Validation statistics for the mixed-effects models showed that annual foliage retention models yielded a negative D (−0.16 to 0.00), indicating a slight underestimate of foliage retention in any given year. The annual, seasonal, and monthly models performed equally well on the validation dataset, although models based on annual climate variables yielded slightly better validation statistics, with D ranging from −0.04 to 0.00 and MAD ranging from 0.41 to 0.44). Performance of the three selected models (10, 12, and 15) on the validation dataset suggested no serious problems in model behavior (Fig. 7).

4. Discussion

The comprehensive screening of 85 climate variables in the present study was intended to measure the amount of predictive power that would potentially be sacrificed by a priori selection of climatic variables that are consistent with the working hypothesis for climatic drivers of SNC. The first phase of the analysis was intended to confirm previous work that established risk-rating systems based on geographic variation in needle retention and corresponding long-term climatic conditions at permanent plots. The second phase involved assessment of annual fluctuations in

foliage retention to further confirm the influence of climatic drivers on fungal development and SNC severity. Results were generally consistent with the expectation that mild winter temperatures and greater late spring/early summer precipitation would be associated with greater Swiss needle cast severity and lower foliage retention. However, other variables like late summer temperature were consistently influential as well, and predictive ability was comparable among many alternative models based on annual, seasonal, or monthly climatic variables.

4.1. Climate data

ClimateWNA provided 85 climatic variables for the reference period 1961–1990 and for any location in western North America described by its longitude, latitude, and elevation. The earlier version of ClimateWNA, ClimateBC was widely applied as a tool for natural resource management, forest genecology and studies related to climate change (Spittlehouse, 2006). Variables from ClimateWNA performed well for predicting geographic variation in foliage retention, and helped make a convincing case for a link between Douglas-fir foliage retention and local climate. Preliminary analyses with climatic variables interpolated from PRISM data by geographically weighted regression (Latta et al., 2009) performed almost as well as ClimateWNA; however, the proportion of explained variation was consistently greater with climatic predictors from ClimateWNA.

4.2. Average foliage retention model

Previous research has supported the hypothesis that winter temperature and/or spring moisture are driving factors for the epidemiology of *P. gaeumannii* and Swiss needle cast intensity in

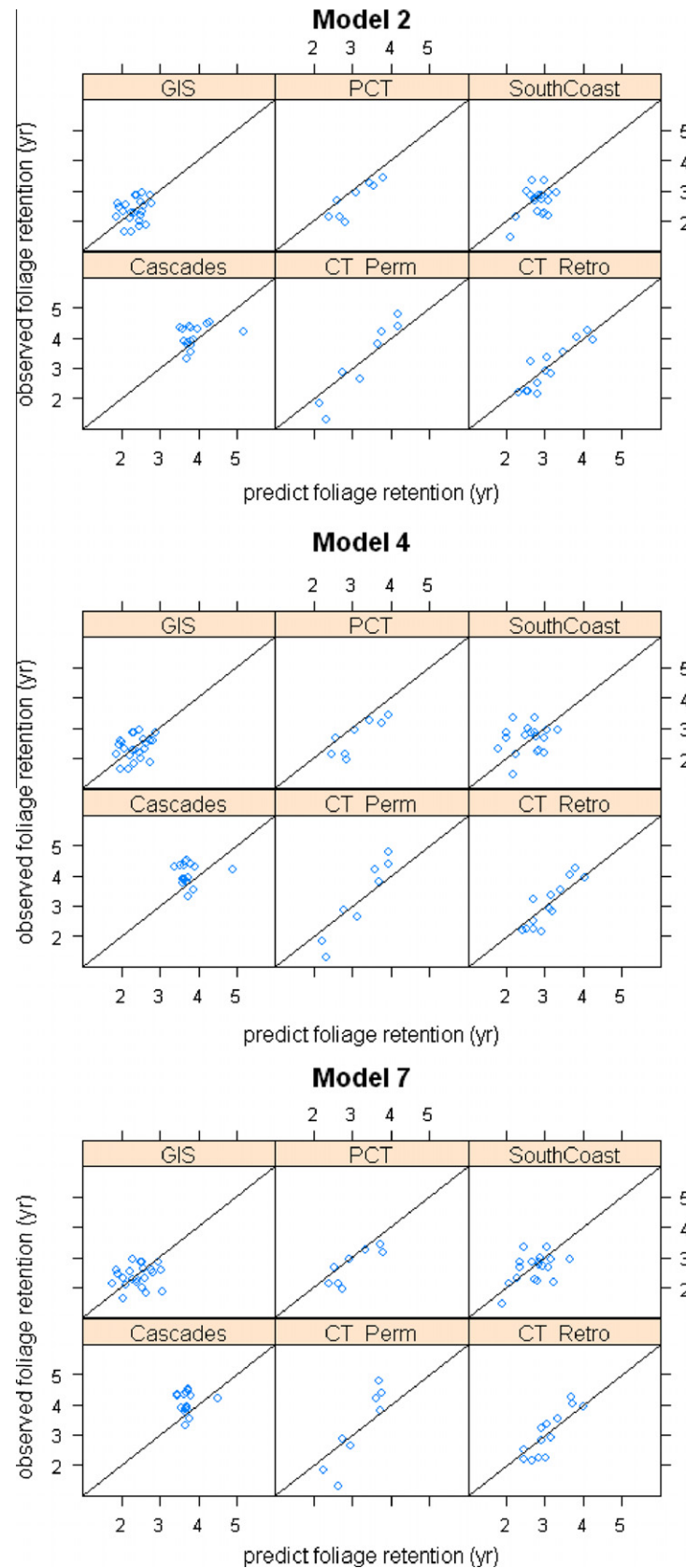


Fig. 4. Periodic average foliage retention predicted from selected models based on annual (model 2), seasonal (model 4), or monthly climatic variables (model 7) relative to observed retention for the validation dataset.

western Oregon (Rosso and Hansen, 2003; Manter et al., 2005; Stone and Coop, 2006). Coop and Stone (2007) developed a foliage

retention model that predicted average foliage retention over a 12-year period from winter degree days, relative humidity in July,

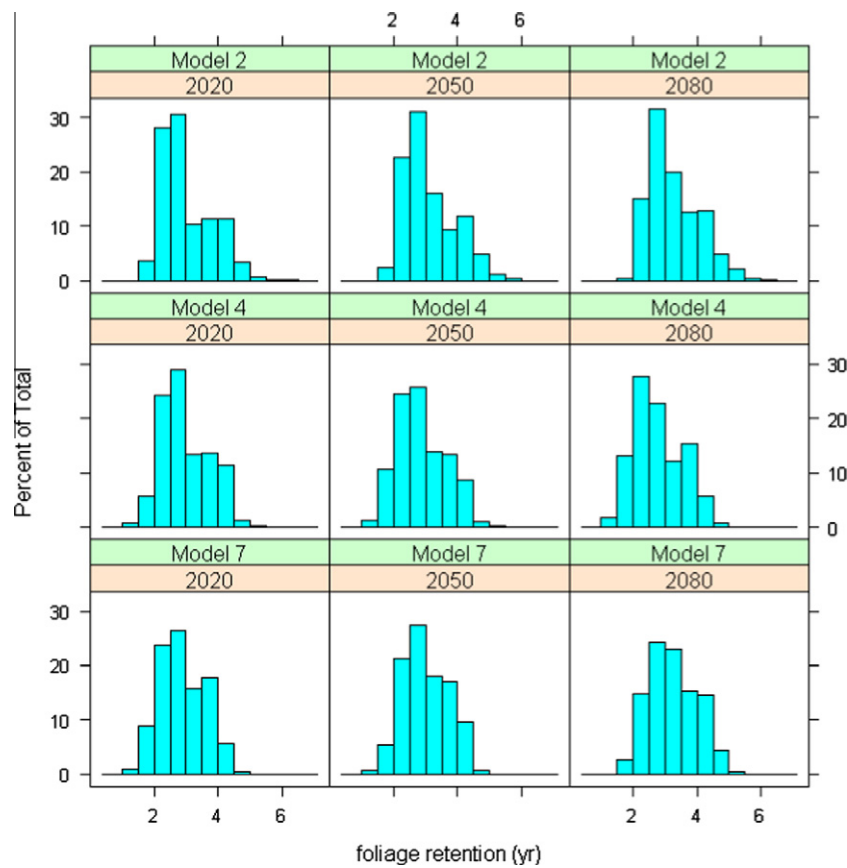


Fig. 5. Frequency distribution of future (predicted) foliage retention. Predicted retentions are based on climatic variables forecasted with ClimateWNA for 2020, 2050, and 2080.

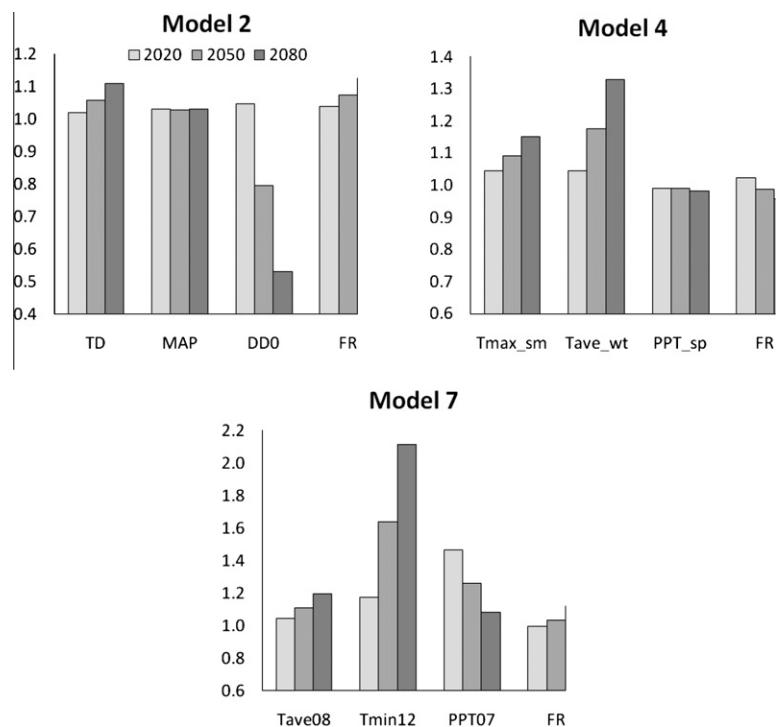


Fig. 6. The ratio of predicted to current average values of foliage retention and climatic variables from model 2, 4, and 7 for the 13 future climate scenarios predicted by ClimateWNA.

Table 7

Selected mixed-effects models for predicting foliage retention in any given year from annual, seasonal, and monthly climate variables. The numbers at the end of the symbols for annual and seasonal variables indicate the number of years the variable was lagged. The first two numbers of monthly variables indicate month, and the last number indicates the number of years the variable was lagged. All predictors are significant at $\alpha = 0.05$; bold type indicates variables with a positive effect on foliage retention; regular type indicates a negative effect.

Resolution	Model number	Number of predictors	Model statistics			Predictor variables	Validation statistics	
			R^2	MSE	AIC		D	MAD
Annual	9	2	0.56	0.29	946	MAP1, TD2	−0.04	0.44
	10	3	0.60	0.26	885	MAP1, TD2 , DD04	0.00	0.41
Seasonal	11	2	0.55	0.29	919	Tmin_wt2, Tave_sm2	−0.06	0.48
	12	3	0.59	0.27	895	PPT_sp1, Tmax_sm2 , Tave_wt2	−0.04	0.46
	13	4	0.59	0.27	849	Tave_wt0, Tmax_sp3, Tmax_sm3 , PPT_sp4	−0.04	0.43
Monthly	14	2	0.51	0.32	1016	Tmax081 , Tave122	−0.16	0.52
	15	3	0.57	0.28	992	Tave081 , Tave123, PPT064	−0.15	0.47
	16	4	0.61	0.25	861	Tmax043, Tmax073 , Tmin013, PPT043	−0.04	0.41

Table 8

Parameter estimates and their standard errors for mixed-effects models predicting foliage retention in any given year from climatic variables.

Model	Parameter estimates and standard errors
<i>Annual</i>	
9	FR = 0.2 − 0.000113MAP1 + 0.231TD2 (0.1644) (0.0000239) (0.0116)
10	FR = −0.0 − 0.000146MAP1 + 0.246TD2 + 0.00735DD04 (0.159) (0.0000233) (0.0111) (0.000821)
<i>Seasonal</i>	
11	FR = −3.2 − 0.311Tmin_wt2 + 0.408Tave_sm2 (0.313) (0.0169) (0.0204)
12	FR = 0.5 − 0.000764PPT_sp1 + 0.218Tmax_sm2 − 0.361Tave_wt2 (0.218) (0.0000938) (0.0110) (0.0172)
13	FR = 3.0 − 0.123Tave_wt0 − 0.227Tmax_sp3 + 0.182Tmax_sm3 − 0.000527PPT_sp4 (0.258) (0.0173) (0.0147) (0.0113) (0.0000851)
<i>Monthly</i>	
14	FR = 0.4 + 0.158Tmax081 − 0.230Tave122 (0.239) (0.0107) (0.0155)
15	FR = −0.2 + 0.291Tave081 − 0.288Tave123 − 0.00485PPT064 (0.275) (0.0183) (0.0178) (0.000340)
16	FR = 2.0 − 0.204Tmax043 + 0.194Tmax073 − 0.144Tmin013 − 0.00205PPT043 (0.216) (0.0114) (0.00912) (0.00939) (0.000173)

and aspect. Latta et al. (2009) developed a similar model for average foliage retention based on mean temperature in January and a Climate Moisture Index (calculated from precipitation and evaporation) in July. Although the working hypothesis in these analyses was that foliage retention in Douglas-fir is controlled completely or predominantly by *P. gaeumannii*, other climate and site variables with less obvious connection to development of foliar fungi have been found to explain geographic variation in conifer foliage retention (Xiao, 2003; Pouttu and Dobbartin, 2000). Characterization of prevailing climatic conditions at specific sites has been a useful approach for establishing risk-rating systems for growing Douglas-fir in north coastal Oregon (Rosso and Hansen, 2003; Coop and Stone, 2007), and application of climatic conditions as driving variables follow logically from observations about where the disease has become a problem both within and outside the native range of Douglas-fir (Boyce, 1940; Hood, 1982; Hansen et al., 2000). However, climatic conditions are spatially confounded with other environmental variables, and the significant marginal effects of additional variables such as aspect on disease severity (Rosso and Hansen, 2003; Coop and Stone, 2007) suggest a number of shortcomings that may include the following: (1) available climatic variables lack sufficient resolution; (2) the salient climatic variables are not available; (3) the functional integration of available climatic variables and their effects on the host and pathogen are not achieved by multiple regression; and (4) environmental factors other than climate are also influential. Like other analyses, ours has attempted to identify that portion of variation in foliage retention that is cor-

related with both spatial and temporal variation in climatic conditions.

Among the eight average foliage retention models presented (Table 5), the most common annual climate predictor was a continentality index computed as the temperature difference (TD) between mean warmest month temperature (MWMT) and mean coldest month temperature (MCMT). The two most common seasonal climate predictors were summer temperature (Tmax_sm) and winter temperature (Tave_wt or Tmin_wt), and the most common monthly predictors were temperature in December (Tmin12) and temperature in August (Tave08). Climatic predictors at all three temporal resolutions therefore reflected similar climatic effects; i.e., larger differences in temperature between the warmest and coldest month corresponded with greater foliage retention. Although the mechanisms by which these variables influence foliage retention can only be speculated on, some of our results confirm past work on SNC development, but some appear contradictory as described below.

Manter et al. (2005) defined three key seasons for *Phaeocryptopus* infection and development: May–June as the period of spore dispersion, deposition, germination and initial infection; August–October as the period of fungal development within infected needles; and December–February as the period critical to the rate of pseudothecia development. More severe SNC symptoms have been consistently observed on southerly aspects (Rosso and Hansen, 2003; Coop and Stone, 2007), and green house experiments have verified that, after initial field inoculation, pseudothecia proliferate

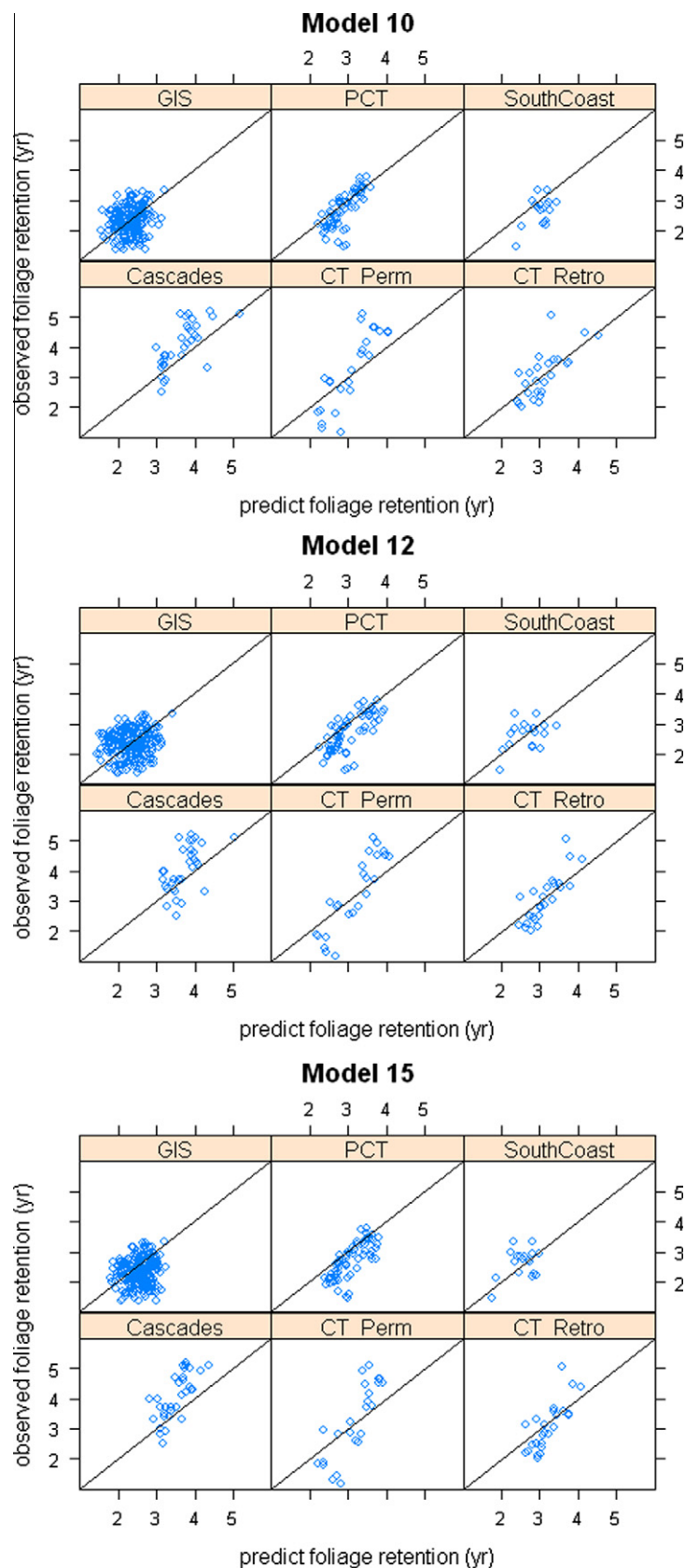


Fig. 7. Time series of foliage retention from 1995 to 2005 predicted from three selected annual retention models (models 10, 12, and 15) for three plots representing low, moderate, and severe Swiss needle cast (plots 37, 93, and 92, respectively).

best under full sun (vs. shading) and no misting from July through the following April (Manter et al., 2005). The positive effect of sum-

mer temperature on foliage retention in the current analysis appears contradictory, but the progression of pseudothecia counts

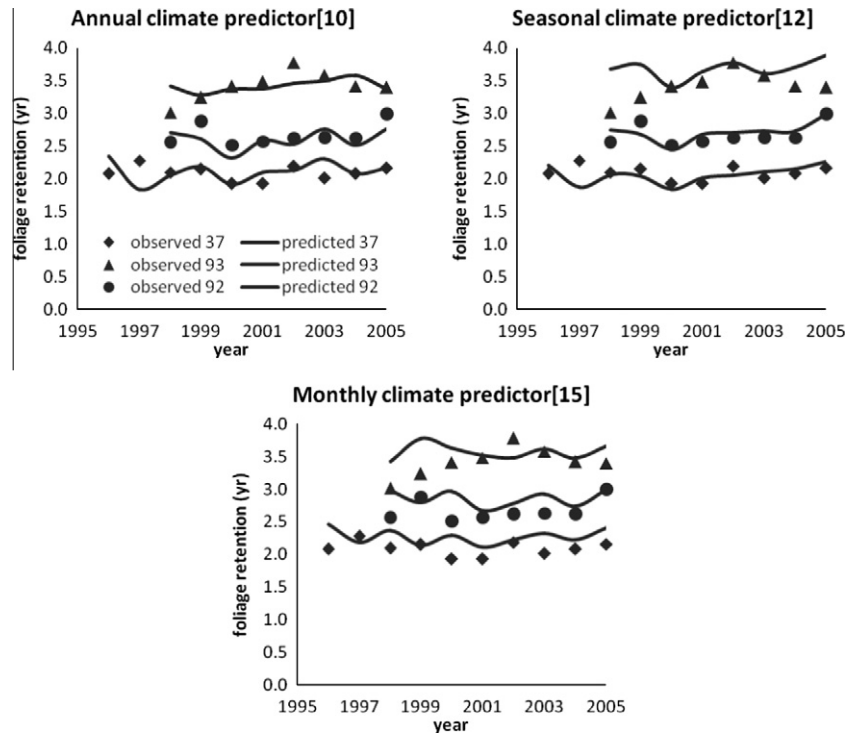


Fig. 8. Annual foliage retention predicted from the selected models using annual (model 10), seasonal (model 12), or monthly climatic variables (model 15) relative to observed retention in the validation dataset.

from July through April in Manter et al.'s (2005) study suggested that the promoting effect of more intense sun and presumably higher temperatures on pseudothecia development began only in November. It remains possible that higher temperatures during the summer may have stimulated fungal development within needles and contributed to the effect of higher winter temperatures on pseudothecia development. However, lacking any direct assessment of mycelia development during the summer, the consistently positive influence of summer temperature on needle retention in our analysis strongly suggested that other mechanisms must be operating during the summer. One alternative mechanism may be the negative effects of high vapor pressure deficits, low water potential within the foliage, and low water availability to fungal hyphae. Likewise, water stress on the tree itself may limit the amount or quality of feeding substrate available to the fungus. Littell et al. (2008) documented the influence of summer temperature on Douglas-fir growth, due to its influence on evapotranspirational demand and vapor pressure deficit. Also, the increase in foliage retention with lower productivity is well documented in the literature (Reich et al., 1995); therefore, climatic effects may have been influencing multiple drivers of needle retention in coastal Douglas-fir stands. It may also be important to note that summer temperature and continentality index were closely correlated with distance from the coast, a consistently strong predictor of Swiss needle cast intensity and foliage retention, even in the presence of the 85 climatic variables. Distance from coast represents a complex gradient of moisture, temperature, and fog. To start understanding the ultimate factors by which distance from coast influences foliage retention and SNC, our analysis intentionally focused on detailed climatic variables alone.

The continentality index was influenced by the lower or cold end of the temperature range as well as the high end of the range. Our results with respect to both continentality index and winter temperature alone (Tave_wt, Tmin_wt, or Tmin12) are therefore more consistent with both greenhouse and field studies (Manter et al., 2005); i.e., colder winters were inferred to impede hyphal

and/or pseudothecia development. Furthermore, the positive effect of DD0 (degree-days below 0 °C) on foliage retention in our selected model ([2]) was consistent with the effect of winter degree days in the model presented by Coop and Stone (2007).

Another important annual climatic predictor was mean annual precipitation (MAP) as a general measure of moisture availability. The negative effect of this variable suggested that wetter conditions promoted disease development, probably by facilitating colonization of new foliage in the late spring and early summer. The finer resolution of models based on seasonal and monthly variables offered a potentially stronger case for specific mechanisms driving foliage retention. At the seasonal level, the combined negative effects of spring precipitation (PPT_sp) and spring mean maximum temperature (Tmax_sp) suggested that warm, wet springs did in fact create conditions that maximized colonization of new needles by *Phaeocryptopus*. Likewise, at a monthly resolution, precipitation during any of the summer months (PPT07 or PPT08) probably indicated potential leaf wetness (cf. Manter et al., 2005), and combined with the effect of maximum mean temperature in June (Tmax06), again suggested that warm wet conditions in spring and early summer were probably very conducive to infection of new foliage.

Stone et al. (2007) found that variation in SNC severity in New Zealand was influenced by climatic factors similar to those identified in western Oregon. Unfortunately, direct comparisons are complicated by use of a colonization index as the measure of SNC severity in New Zealand (Stone et al., 2007). Colonization index was the product of percent of needles with visible pseudothecia and the average proportion of occluded stomates. Its correlation with foliage retention has not been well quantified.

4.3. Forecasts with the average foliage retention model

According to the best foliage retention models based on annual or monthly climate variables (model 2 or 7), foliage retention was predicted to increase gradually from 2020 to 2080. These predicted increases could be attributed primarily to increasing continentality

indices (TD) predicted by the GCMs at the annual resolution, and to increasing August average temperature (Tave08) and decreasing July precipitation (PPT07) predicted at the monthly resolution. Apparently the strong decline in chilling degree days (DD0) and relative stability in annual precipitation (MAP) predicted by the GCMs were not great enough relative to the increase in continentality to imply a net decrease in foliage retention in the annual model. Likewise, the increase in December minimum temperature (Tmin12) in the monthly model was not great enough relative to the increase in August average temperature and decrease in July precipitation to cause a net decrease in foliage retention in the monthly model. However, according to the best seasonal model (model 4), average foliage retention was predicted to decrease gradually from 2020 to 2080, primarily due to the marked increase in average winter temperature predicted by the GCMs.

Stone et al. (2008) suggested that the severity and distribution of Swiss needle cast is likely to increase in the coming decades as a result of climate change, with significant consequences for Pacific Northwest forests. It is significant to note that their model, like model 4 in the current analysis, was based on seasonal climatic variables, and that both models predicted a gradual decline in foliage retention under future climate scenarios. Uncertainty in future climate variables would probably be least at the annual resolution, moderate at the seasonal resolution, and relatively high at a monthly resolution. However, the fact that the monthly and annual models were consistent and different from the seasonal model suggested that differences could not be attributed to the relative uncertainty associated with climatic predictions at different temporal resolutions. Of possible relevance was the relatively small decline in spring precipitation compared to the more dramatic decline in July precipitation predicted by the GCMs (Fig. 6). If spring moisture becomes limiting to successful colonization by *P. gaumannii*, then winter temperatures may become irrelevant to

disease severity and foliage retention. Unfortunately, the uncertainty in GCM predictions of future precipitation is considered greater than that for temperature (Buytaert et al., 2009), underscoring the challenge of predicting the course of Swiss needle cast under future climate scenarios.

With respect to actual observations over the last 14 years in western Oregon, annual foliage retention has fluctuated too widely within specific sets of plots and geographic locations to claim a long-term increase or decrease over the period between 1996 and 2009 (Fig. 9). Annual aerial surveys for SNC suggested the total area with SNC symptoms detectable from the air increased about 3-fold from 1996 to 2010; however, annual variation in these symptoms similarly limits any conclusions about long-term trends (Kanaskie and Mc Williamms, 2010).

Across the age range, management intensity, and site conditions sampled in the Swiss needle cast growth impact study in north coastal Oregon, Douglas-fir retained foliage up to almost 4 years, but under severe Swiss needle cast as low as 1 year (Maguire et al., 2002). Fewer plots were predicted to retain foliage for less than 2 years under future climate scenarios, and the number of plots retaining foliage for longer than 5 years was also predicted to increase. Because averaging the 13 predictions for each plot potentially damped the effect of extreme values and narrowed the potential variability and frequency distributions, it was important to consider the range of plot-level maxima and minima as well. However, the same general conclusion was reached with regard to a slight increase in foliage retention under predicted future climates.

4.4. Annual foliage retention model

Previous analyses of needle retention focused on geographic variation; i.e., retention was averaged over a period of approximately

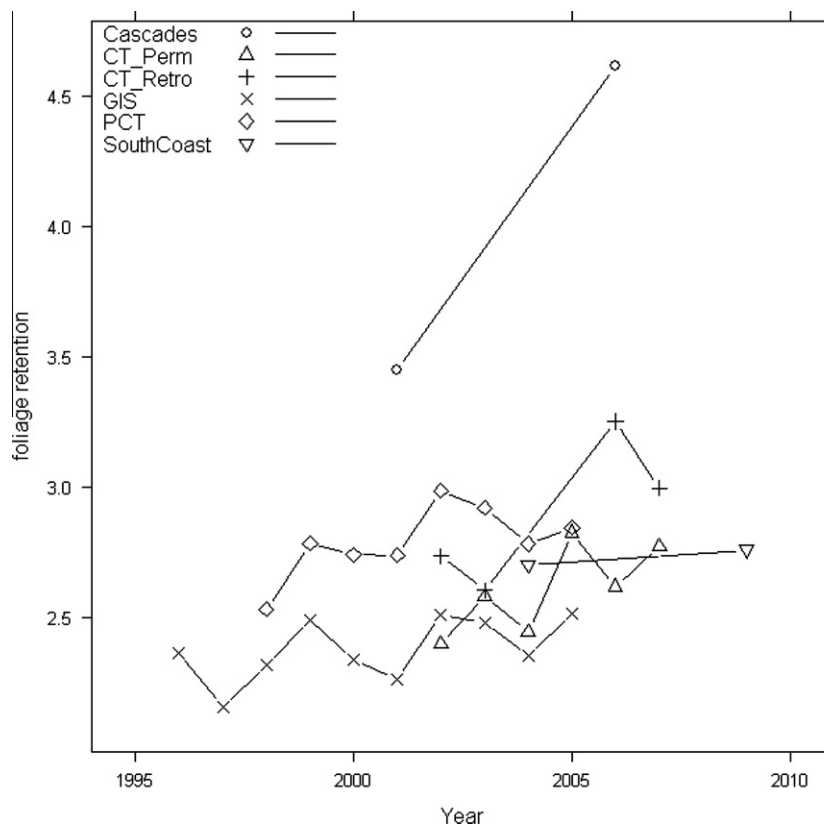


Fig. 9. Average foliage retention for each year of observation in the six Swiss needle cast studies used in development of foliage retention models.

10 years for a number of sites and then was correlated with long-term climatic variables specific to those sites. From this correlation between needle retention and climatic conditions, the link between weather, *P. gaumannii*, and foliage retention was inferred. Contemporaneous fluctuation in annual foliage retention and climatic variables lent further support to the hypothesis that weather controls foliage retention either directly through physiological effects or indirectly through mediating processes such as colonization by *P. gaumannii* and subsequent development of Swiss needle cast. Coop and Stone (2010) developed a model to predict normalized colonization index (CI) averaged over a five-year period (2001–2005). Because this colonization index requires pseudothecia counts, only 29 sites were available for model development, and climatic variables presumably represented 10-year averages from PRISM. In this and other studies using either CI or foliage retention as an index of SNC severity, monthly or bi-monthly climatic variables were considered rather than annual variables to ensure a closer match between known and hypothesized mechanisms driving SNC epidemiology. However, our mixed-effects model predicted annual foliage retention surprisingly well from annual climatic variables lagged by one to 4 years.

The best annual and seasonal predictors in the models for describing annual fluctuations in foliage retention were consistent with the best predictors in the geographic analysis of periodic average foliage retention. A lag time of 2 years generally was most effective for predicting annual retention. However, in the models fitted using monthly climatic variables, the predictors were often quite different from the monthly variables in the periodic average retention models, especially in those models with four predictors. Optimal lag times generally shifted to 3 years, which is consistent with the large majority of plots holding foliage for 2–3 years; i.e., climatic conditions during the year of formation of two- and three-year-old needles has a strong influence on their continued longevity. However, due to close correlations between monthly climate variables in adjacent months of the same year, and between monthly climate variables in different years, the specific predictors that perform best in alternative models depended on their relationship with other variables already in the model.

Alternative models were screened based on ordinary least squares in an all-subsets approach, with selected models required to have all parameter estimates significantly different from zero at $\alpha = 0.05$. A random plot effect appeared sufficient for addressing autocorrelation among repeated observations within a plot, with no additional gains from modeling the variance-covariance structure of the residual errors directly. Introducing the random plot effect led to adjustments in parameter estimate standard errors and accompanying shifts in significance of parameter estimates. Given the evidence in this large dataset, the annual foliage retention model with annual climate predictors (model 10) is probably most appropriate for regional risk rating assessments, but if large changes occur in the relationship between annual, seasonal, and monthly variables, or if extreme events become predominant drivers, models with climatic variables at finer temporal resolution may be required.

5. Conclusions

Geographic variation in long-term average foliage retention, as well as annual fluctuation in foliage retention, were predicted well by climate variables from ClimateWNA. Climatic variables at an annual resolution (versus seasonal or monthly) seemed adequate for explaining both the geographic and temporal variation in recent past foliage retention. However, monthly climatic variables may have a more dominating influence on foliage retention if future climates are characterized by greater monthly variation and relatively little change in annual averages. When predicting average

foliage retention under future climate scenarios, the periodic average foliage retention model with climatic variables at an annual resolution may be more reliable because this resolution more appropriately matched the precision of GCM predictions. The average foliage retention model developed from the six Swiss needle cast studies suggested that foliage retention would increase under current predictions from GCMs. The GCMs predicted greater continentality (difference between mean warmest month temperature and mean coldest month temperature) and only a very slight increase in mean annual precipitation. However, predictions of foliage retention were very sensitive to the monthly distribution of precipitation, underscoring the importance of finer resolution in climatic variables for predicting the consequences of climate change. Models for predicting annual fluctuations in foliage retention are probably more appropriate for understanding the mechanisms driving the effect of *P. gaumannii* or other factors on the survival of individual foliage cohorts. Ultimately, models describing geographical and temporal trends in foliage retention should be similar to those that describe the same trends in counts or indices of pseudothecia frequency (e.g., Manter et al., 2005; Stone et al., 2007).

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Ten-year growth and mortality in young Douglas-fir stands experiencing a range in Swiss needle cast severity

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Abstract: Swiss needle cast, a foliar disease caused by the Ascomycete *Phaeocryptopus gaeumannii* (T. Rohde) Petr., continues to afflict Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in north coastal Oregon. Permanent plots were installed in 1998 to assess growth impacts and monitor disease severity. Gross periodic annual increment was measured for three 2-year growth periods and one 4-year growth period and ranged from 0.37 to 31.74 m³·ha⁻¹·year⁻¹. Foliage retention, defined as the average number of annual needle age classes held by a tree, was also estimated as an index of disease severity. Assuming negligible losses in stands with maximum needle retention (approximately 3.9 years), growth losses in net periodic annual increment reached slightly over 50% in stands with the lowest needle retention (approximately 1 year). Mixed-effects regression models supported a consistent relationship between foliage retention and both gross and net periodic annual increment among the four growth periods. Periodic annual mortality ranged from 0 to 19.12 m³·ha⁻¹·year⁻¹ but was not significantly influenced by Swiss needle cast as measured by average foliage retention. Minimum and maximum foliage retention has fluctuated annually from 1998 to 2008 on the permanent plots, but growth losses at a given level of foliage retention appear to have remained stable. Estimated growth losses are similar to those reported for comparable levels of defoliation by other agents.

Résumé : La rouille suisse, une maladie des feuilles causée par l'Ascomycète *Phaeocryptopus gaeumannii* (T. Rohde) Petr., continue d'infecter le douglas vert (*Pseudotsuga menziesii* (Mirb.) Franco) dans la région côtière du nord de l'Oregon. Des placettes permanentes ont été installées en 1998 pour évaluer les impacts sur la croissance et suivre l'évolution de la sévérité de la maladie. L'accroissement annuel périodique brut a été mesuré pour trois périodes de deux ans et une période de quatre ans; il variait de 0,37 à 31,74 m³·ha⁻¹·an⁻¹. La conservation du feuillage, définie comme le nombre moyen de classes d'âge annuelles des aiguilles conservées par un arbre, a aussi été estimée en tant qu'indice de sévérité de la maladie. En assumant des pertes négligeables dans les peuplements où la conservation des aiguilles durait le plus longtemps (approximativement 3,9 ans), les pertes de croissance en accroissement annuel périodique net atteignaient un peu plus de 50 % dans les peuplements où la conservation des aiguilles durait le moins longtemps (approximativement 1 an). Selon les modèles de régression à effets mixtes, il y avait une relation constante entre la conservation du feuillage et les accroissements annuels périodiques net et brut pendant les quatre périodes de croissance. La mortalité annuelle périodique variait de 0 à 19,12 m³·ha⁻¹·an⁻¹ mais n'était pas significativement influencée par la rouille suisse telle que mesurée par la durée moyenne de conservation du feuillage. La durée minimale et maximale de conservation du feuillage a fluctué annuellement de 1998 à 2008 dans les placettes permanentes mais les pertes de croissance correspondant à un niveau donné de conservation du feuillage semblent être demeurées stables. Les pertes de croissance estimées sont semblables à celles qui ont été rapportées pour des niveaux comparables de défoliation causée par d'autres agents.

[Traduit par la Rédaction]

Introduction

Swiss needle cast (SNC) is a foliar disease of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) caused by the Ascomycete *Phaeocryptopus gaeumannii* (T. Rohde) Petr. (Hansen et al. 2000). This pathogen causes premature loss of older foliage, resulting in needle longevity of only 1 year in the most severe cases, relative to a maximum of approximately 4 years in unaffected plantations of similar age and geographic location (Hansen et al. 2000; Maguire et al.

2002). Annual growth losses under severe SNC have been shown to average approximately 23% of stem volume increment and reach 50% under the lowest levels of foliage retention (Maguire et al. 2002). Although the majority of growth loss under low needle retention is imposed by reduction in tree and stand foliage mass, some growth loss also accrues from inhibition of gas exchange on surviving foliage due to stomatal occlusion by fungal fruiting bodies, or pseudothecia (Manter et al. 2000).

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Numerous agents cause direct loss of foliage in coniferous trees, including various classes of herbivores (Pook et al. 1998) and foliar pathogens (Kurkela et al. 2009). Defoliating insects have been shown to cause growth reductions, with the amount of growth loss dependent on the degree and duration of defoliation (Williams 1967; Alfaro and Shepherd 1991). Some insects progressively consume foliage of the youngest age classes, e.g., *Choristoneura fumiferana* Clem. on balsam fir (*Abies balsamea* (L.) Mill.) (Piene et al. 2003), while others cause premature loss of older foliage, e.g., the aphid *Essigella californica* (Essig) on radiata pine (*Pinus radiata* D. Don) (Hopmans et al. 2008) and the aphid *Elatobium abietinum* (Walker) on Sitka spruce (*Picea sitchensis* (Bong.) Carrière) (Straw et al. 2005). Because photosynthetic efficiency declines with needle age (Ethier et al. 2006), insects like *Choristoneura fumiferana* should have a more deleterious effect on growth for a given amount of foliage loss than agents causing premature loss of older foliage. Artificial defoliation studies generally support this expectation, particularly for 1-year-old and (or) 2-year-old versus older needles (e.g., Linzon 1958; Kulman 1965). *Dothistroma* blight on radiata pine does not seem to impact tree growth until 20%–25% of the foliage is affected (Gibson et al. 1964), probably because the disease starts on the oldest and most shaded foliage, with subsequent spread to younger and more photosynthetically efficient foliage (Gibson 1972, 1974). Given its similar progression from older to younger foliage, SNC might also be expected to cause a relatively low growth impact at low levels of foliage loss followed by an exponentially increasing growth impact as foliage loss proceeds to younger foliage; however, superimposed on this pattern of foliage loss is an advance wave of physiological disruption as a precursor to premature abscission (Manter et al. 2000).

In an effort to gauge the degree of growth loss from recent intensification of SNC in north coastal Oregon, a retrospective study was implemented by the Swiss Needle Cast Cooperative (<http://sncc.forestry.oregonstate.edu/>) at Oregon State University in 1997 (Maguire et al. 2002). In this phase, trees were destructively sampled to demonstrate that growth losses over the previous several years were proportional to current foliage retention. In the following year, a network of permanent plots was established in the same young Douglas-fir plantations to monitor tree growth and disease symptoms concurrently. Because stands that have expressed severe SNC for multiple years have experienced substantial cumulative growth loss that could potentially impose a general decline in physiological condition, it is uncertain whether the quantitative relationship between foliage retention and either growth loss or mortality may have shifted over time. Therefore, 10 years of permanent plot data were analyzed to meet the following objectives: (i) to verify the relationship between foliage retention and Douglas-fir stem volume growth estimated from the retrospective study, (ii) to quantify current growth losses attributable to SNC by combining permanent plot data from all growth periods over the last 10 years, (iii) to test the null hypothesis that the relationship between foliage retention and stem volume growth loss has remained stable over successive growth periods, and (iv) to test the null hypothesis that Douglas-fir mortality rate is not affected by SNC severity.

Methods

The target population for the Swiss Needle Cast Cooperative Growth Impact Study was the collection of 10- to 30-year-old Douglas-fir plantations in north coastal Oregon. Symptoms of SNC had been intensifying throughout the early 1990s in this region and the disease was increasingly recognized as a potential impediment to growing Douglas-fir near the Pacific Coast. Concern was also growing that some of these plantations would not survive to commercial size or that they would grow so slowly as to be economically nonviable.

Field work

A list of 4504 10- to 30-year-old Douglas-fir stands was first compiled in 1996, with geographic bounds defined by Astoria to the north (46°11'N, 123°50'W), Newport to the south (44°38'N, 124°04'W), the Pacific Coast to the west (124°05'W), and the crest of the Oregon Coast Ranges to the east (123°30'W). A set of 76 stands was randomly selected from this list and permanent plots were established in the late winter – early spring of 1998. Plots were square, 0.08 ha in area (28.45 × 28.45 m), and centered on the fifth point of an 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) (nearest 0.1 cm) greater than 4 cm were tagged at a height of 1.37 m, and at least 40 Douglas-fir were measured for total height (nearest 0.01 m) and height to crown base (nearest 0.01 m) at time of plot establishment. Trees with DBH < 4 cm were measured for DBH but were not tagged. On several plots with dense natural regeneration of hardwoods or other conifers, these smaller trees were measured only on a 0.02 ha circular plot in the center of the 0.08 ha plot. After two, four, six, and 10 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. During the 10-year study period, some plots were inadvertently thinned or otherwise disturbed by management activities, so were excluded from further remeasurement. These losses resulted in 284 observations rather than the 304 that would be expected if all 76 plots had been observed for all four growth periods. Douglas-fir trees averaged 20.6 cm DBH at the start of any given growth period but ranged from 0.1 to 59.3 cm (Table 1). Some plots contained a significant amount of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) as well as various broadleaved species, most commonly cascara (*Rhamnus purshiana* DC.), red alder (*Alnus rubra* Bong.), and red elderberry (*Sambucus racemosa* L.) (Tables 1 and 2). Other conifers that occurred less frequently included Sitka spruce, western redcedar (*Thuja plicata* Donn ex D. Don), noble fir (*Abies procera* Rehder), and grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.). Other hardwood species included bitter cherry (*Prunus emarginata* (Dougl. ex Hook.) D. Dietr.) and bigleaf maple (*Acer macrophyllum* Pursh).

Ten dominant or codominant Douglas-fir on each plot were also scored for SNC at the time of plot establishment in 1998 and just prior to bud break in the years 1999–2004. A tree was scored for SNC by dividing the crown vertically

Table 1. Initial tree attributes for all growth periods from the Growth Impact Study established in early 1998 by the Swiss Needle Cast Cooperative.

Species	Attribute	<i>n</i>	Minimum	Mean (SD)	Maximum
Douglas-fir	DBH (cm)	17638	0.1	20.6 (8.9)	59.3
Douglas-fir	Height (m)	12844	1.63	16.0 (5.4)	38.6
Douglas-fir	Crown ratio	12807	0.01	0.69 (0.19)	1.00
Western hemlock	DBH (cm)	5993	0.1	11.8 (9.8)	105.4
Western hemlock	Height (m)	1585	1.48	14.41 (5.36)	32.5
Western hemlock	Crown ratio	1542	0.03	0.79 (0.15)	1.00
Sitka spruce	DBH (cm)	1304	0.1	7.8 (5.8)	46.1
Western redcedar	DBH (cm)	136	0.1	6.7 (6.0)	23.4
Noble fir	DBH (cm)	202	1.9	23.6 (13.6)	58.8
Grand fir	DBH (cm)	21	1.4	5.0 (4.4)	13.3
Cascara	DBH (cm)	2732	0.1	4.6 (3.1)	27.4
Red alder	DBH (cm)	2108	0.1	12.4 (7.5)	43.4
Red elderberry	DBH (cm)	1528	0.1	3.5 (3.0)	17.0
Bitter cherry	DBH (cm)	448	0.2	8.9 (5.4)	24.6
Bigleaf maple	DBH (cm)	103	1.4	14.5 (7.5)	37.6

Table 2. Initial plot attributes and growth rates for all growth periods from the Growth Impact Study established in early 1998 by the Swiss Needle Cast Cooperative (*n* = 284).

Variable	Minimum	Mean (SD)	Maximum
Douglas-fir tree density (trees·ha ⁻¹)	86	602 (274)	1692
Douglas-fir basal area (m ² ·ha ⁻¹)	0.62	21.91 (9.44)	48.35
Douglas-fir SDI (trees·ha ⁻¹)*	26	449 (171)	838
Douglas-fir stem volume (m ³ ·ha ⁻¹)	0.93	150.51 (87.71)	402.18
Douglas-fir breast height age (years)	5.9	17.5 (5.4)	34.9
Douglas-fir top height (m)	4.89	20.83 (5.98)	41.93
Douglas-fir site index (m at 50 years)	13.4	41.4 (6.6)	64.6
Basal area of other conifers (m ² ·ha ⁻¹)	0.00	4.28 (7.32)	46.98
Basal area of broadleaved species (m ² ·ha ⁻¹)	0.00	1.68 (2.67)	17.29
Total tree density (trees·ha ⁻¹)	247	1380 (933)	5705
Total plot basal area (m ² ·ha ⁻¹)	1.71	28.01 (10.85)	65.37
Total SDI (trees·ha ⁻¹)*	84	633 (221)	1447
Foliage retention (years)	1.01	2.38 (0.45)	3.85
Total basal area growth (m ² ·ha ⁻¹ ·year ⁻¹)	0.03	4.40 (2.05)	12.61
Douglas-fir basal area growth (m ² ·ha ⁻¹ ·year ⁻¹)	0.15	3.29 (1.80)	10.40
Douglas-fir top height growth (m·year ⁻¹)	0.19	0.90 (0.24)	1.58
Douglas-fir gross volume growth (m ³ ·ha ⁻¹ ·year ⁻¹)	0.37	15.98 (6.64)	31.74
Douglas-fir net volume growth (m ³ ·ha ⁻¹ ·year ⁻¹)	0.37	15.51 (6.70)	31.68
Douglas-fir volume mortality (m ³ ·ha ⁻¹ ·year ⁻¹)	0.00	1.34 (2.68)	19.12

*SDI is stand density index = (trees·ha⁻¹)(Dq/25.4)^{1.605}, where Dq is quadratic mean DBH.

into thirds and visually estimating the average number of years (nearest 0.1 year) that foliage was retained in each crown third. Plot ratings were computed as the average of all crown thirds from all 10 trees.

Statistical analysis

Missing total heights and heights to crown base for Douglas-fir trees were estimated as a function of DBH by fitting regression models specific to each plot and growth period. Cubic stem volume of each Douglas-fir was estimated with equations previously developed for second-growth Douglas-fir (Bruce and DeMars 1974). Plot-level periodic annual increment (PAI) of Douglas-fir trees was first computed as gross increment, i.e., net change in standing live stem volume plus mortality. Douglas-fir ingrowth was zero for the vast majority of plots and trivial for the rest. The basic statistical

model described gross PAI at the plot level as a function of initial Douglas-fir basal area, initial breast height age, site quality, foliage retention, and basal area of competing conifer and hardwood species:

$$[1] \quad \ln[\text{gPAI}] = \beta_{10} + \beta_{11} \ln(\text{BA}_{\text{DF}}) + \beta_{12} \ln(\text{AGE}_{\text{BH}}) + \beta_{13} \ln(\text{SI}) + \beta_{14} \text{BA}_{\text{OC}} + \beta_{15} \text{BA}_{\text{HARD}} + \beta_{16} \ln(\text{FR} - 0.5) + \varepsilon_1$$

where gPAI is gross periodic annual stem volume increment of Douglas-fir trees (m³·ha⁻¹·year⁻¹), BA_{DF} is initial Douglas-fir basal area (m²·ha⁻¹), AGE_{BH} is initial age at breast height (years), SI is Bruce's (1981) site index (m at 50 years), BA_{OC} is initial basal area in other conifers (m²·ha⁻¹), BA_{HARD} is initial basal area in broadleaved species (m²·ha⁻¹), FR is foliage retention (years), ε_1 is a random error term with

$\varepsilon_1 \sim N(0, \sigma_1^2)$, and β_{1k} are parameters estimated from the data. This basic model form resulted from considering the response and predictor variables as both untransformed and log-transformed variables to address expected and demonstrated nonlinear effects. A range of constants (0.1, 0.2, ..., 0.9) was also considered for translating the response along the foliage retention axis to represent better the observed growth as foliage retention approached its minimum value. Plot PAIs were measured repeatedly over time, and tree growth fluctuated with annual climatic conditions; therefore, the error structure of the model was potentially more complex than indicated by the distribution of ε_1 in model 1. Mixed-effects models were fitted to the data under several different assumptions using PROC MIXED in SAS version 9.2 (Littell et al. 2006). These assumptions included a random plot effect, a random growth period effect, both random plot and random growth period effects, and alternative error covariance structures that recognized repeated observations within a plot. Model comparisons were based on Akaike's information criterion (AIC), which is a function of the maximum likelihood and number of parameters from the fitted model (Burnham and Anderson 2002). Normality and homoscedasticity of residuals were verified for the final models by standard graphical analysis. This same model was fitted to data representing net PAI and similar comparisons were made among alternative random effects and error structures. Variables were considered significant at $\alpha = 0.05$, but those with p values between 0.05 and 0.10 were identified as marginally significant. Final models were required to have only significant variables.

To meet the first objective of verifying growth losses estimated from the retrospective phase of the growth impact study, plot-level data from 1997 and an indicator variable were added to model 1 for both gross and net increment. Interactions between the retrospective indicator and predictors were included, and the model was reduced by backward elimination of nonsignificant variables ($\alpha = 0.05$).

SNC generally does not seem to cause direct mortality of Douglas-fir trees, but this general observation had not been rigorously tested in the subject population. To perform this test with the permanent plot data, mortality was assessed in two phases. In the first phase, occurrence of Douglas-fir mortality on a given plot during any given growth period was regarded as a binary response, with the "event" defined as mortality in at least one year within the period. This analysis of mortality differed from more conventional analysis of individual-tree mortality because plot-level mortality could have occurred repeatedly in all years of a given growth period or in only one of the years. The following binomial regression model (McCullagh and Nelder 1989) was fitted to the data from the SNCC Growth Impact Study to test whether the occurrence of Douglas-fir mortality was influenced by intensity of SNC:

$$[2] \quad \eta = \ln[\mu/(1 - \mu)] = \beta_{20} + \beta_{21}f(\text{BA}_{\text{DF}}) + \beta_{22}f(\text{BA}_{\text{OC}}) + \beta_{23}f(\text{BA}_{\text{HARD}}) + \beta_{24}f(\text{AGE}_{\text{BH}}) + \beta_{25}f(\text{SI}) + \beta_{26}f(\text{FR}) + \beta_{27}f(\text{GP})$$

where μ is the probability of observing Douglas-fir mortality on the plot during the growth period, f is the identity function (untransformed variable) or natural logarithm, β_{2k} are

parameters estimated from the data, GP is growth period length (2 or 4 years), and BA_{DF} , BA_{OC} , BA_{HARD} , AGE_{BH} , SI, and FR are defined above. GP was included to accommodate the 2- and 4-year growth periods and to address the lack of further information about the number of years that the plot experienced mortality within the growth period. To address covariance among repeated observations within a plot, random plot and growth period effects and alternative error structures were explored using PROC GLIMMIX in SAS version 9.2. All forms of predictor variables (untransformed and log-transformed) were initially included in a full model that was reduced by backward elimination of nonsignificant variables ($\alpha = 0.05$). Alternative model formulations were compared using AIC.

In the second phase of assessing SNC effects on mortality, cubic volume of Douglas-fir mortality was regarded as conditional on occurrence of mortality in a given plot (i.e., only those plots experiencing mortality were included). The statistical model took the following form:

$$[3] \quad \ln[\text{PAM}] = \beta_{30} + \beta_{31} \ln(\text{BA}_{\text{DF}}) + \beta_{32} \ln(\text{AGE}_{\text{BH}}) + \beta_{33} \ln(\text{SI}) + \beta_{34} \text{BA}_{\text{OC}} + \beta_{35} \text{BA}_{\text{HARD}} + \beta_{36} \ln(\text{FR} - 0.5) + \varepsilon_3$$

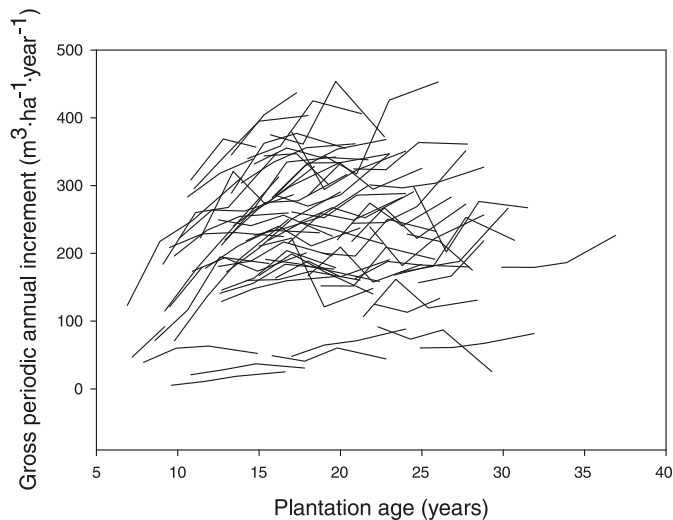
where PAM is the conditional periodic annual mortality of Douglas-fir trees ($\text{m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$), β_{3i} are parameters estimated from the data, ε_3 is a random error term with $\varepsilon_3 \sim N(0, \sigma_3^2)$, and BA_{DF} , AGE_{BH} , SI, BA_{OC} , BA_{HARD} , and FR are defined above. As with gross and net PAI, the model was fitted with various combinations of random plot and growth period effects and specific covariance structures to account for repeated observations within a plot. All models were fitted with PROC MIXED in SAS version 9.2 (Littell et al. 2006), alternative models were compared using AIC, and normality and homoscedasticity of residuals were verified by standard graphical analysis.

Results

Trends in gross PAI and periodic annual mortality over four growth periods showed strong plot effects attributable primarily to differences in inherent site quality and secondarily to differences in growing stock (Figs. 1 and 2). Periodic variation in gross PAI for a given plot reflects a combination of age effects, annual weather fluctuations, episodic mortality, and some residual measurement error. Over the range of plantation ages sampled in 1998 (10 to 30 years old), PAI generally depicted the expected trend of increasing growth potential with increasing age and the accompanying increase in site occupancy (combination of leaf area index and cambial surface area). Gross PAI ranged from 0.37 to 31.74 $\text{m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ (Table 2).

The importance of accounting for covariance among repeated observations of individual plots was underscored by the significant improvement (reduction) in AIC achieved by all models that assumed any error structure beyond independence of observations (Table 3). Likewise, the correctly specified error structures demonstrated how some variables that were incorrectly identified as significant under the assumption of independence were in fact not significant when autocorrelation was accounted for. Random plot effects did

Fig. 1. Observed plot-level trends in gross periodic annual increment of Douglas-fir (*Pseudotsuga menziesii*) over plantation age at the start of each growth period.

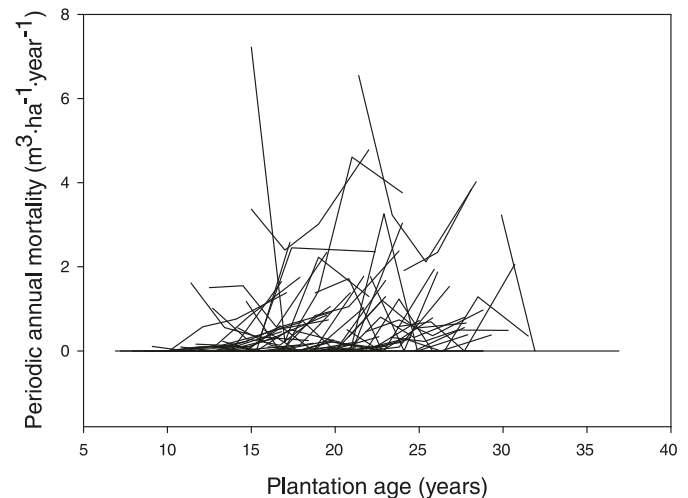


improve the fit of the models, presumably by addressing, at least in part, covariance among repeated observations within a plot; however, direct estimation of the variance–covariance matrix was more effective. In the selected model, the variance–covariance matrix was block diagonal, consistent with independence of individual plots and nonzero covariance of repeated observations within plots. In one simple form, the nonzero diagonal blocks are a Toeplitz or diagonal-constant matrix that assumes equal variance among plots and years and equal covariance among observations separated by the same time interval. However, the variation applied in the final PAI model was a heterogeneous Toeplitz covariance structure (Littell et al. 2006), which assumed constant variance among plots for a given growth period but unequal variance among growth periods (diagonals $\sigma_1^2, \dots, \sigma_4^2$). Covariances among repeated observations within a plot were constrained to be the product of the two growth period standard deviations and a constant ρ (off-diagonals $\rho\sigma_1\sigma_2, \dots, \rho\sigma_3\sigma_4$). The effect of site index was nonsignificant under this error structure ($p = 0.49$) but would have been incorrectly inferred as very significant under the assumption of independent observations ($p < 0.0001$). All other variables were strongly significant after dropping site index (all $p < 0.007$), resulting in the following final model for gross PAI of Douglas-fir (standard errors for parameter estimates shown in parentheses):

$$\begin{aligned}
 [4] \quad \ln[\text{gPAI}] = & 1.6597 + 0.9245 \times \ln(\text{BA}_{\text{DF}}) \\
 & (0.1360) \quad (0.03672) \\
 & -0.6727 \times \ln(\text{AGE}_{\text{BH}}) - 0.00600 \times \text{BA}_{\text{OC}} \\
 & (0.06985) \quad (0.002202) \\
 & -0.01928 \times \text{BA}_{\text{HARD}} + 0.3589 \times \ln(\text{FR} - 0.5) \\
 & (0.007093) \quad (0.05052)
 \end{aligned}$$

Random growth period effects added very little to any of the alternative models. The average loss in gross PAI implied by the final model was 18.7%, with a maximum loss of 49.1%. The average losses in gross PAI implied by the same model fitted separately to each growth period ranged from 17.4% to

Fig. 2. Observed plot-level trends in periodic annual mortality of Douglas-fir (*Pseudotsuga menziesii*) over plantation age at the start of each growth period.



25.6%, with maxima ranging from 36.6% to 58.2% (Table 4). Pairwise tests among foliage retention parameter estimates for specific growth periods failed to reject the null hypothesis that the relationship between foliage retention and gross increment remained consistent over the 10-year study period.

Similar results were obtained for the model describing net PAI (Table 4). The lowest AIC was associated with the model assuming a heterogeneous Toeplitz covariance structure. As was the case for gross PAI, site index was not significant under this error structure ($p = 0.76$) but would have been incorrectly identified as very significant under the assumption of independent observations ($p = 0.0002$). All other variables were significant after dropping site index (all $p \leq 0.021$), resulting in the following final model for net PAI (nPAI) of Douglas-fir (standard errors for parameter estimates shown in parentheses):

$$\begin{aligned}
 [5] \quad \ln[\text{nPAI}] = & 1.7551 + 0.9420 \times \ln(\text{BA}_{\text{DF}}) \\
 & (0.1545) \quad (0.04257) \\
 & -0.7403 \times \ln(\text{AGE}_{\text{BH}}) - 0.00621 \times \text{BA}_{\text{OC}} \\
 & (0.08125) \quad (0.002673) \\
 & -0.02633 \times \text{BA}_{\text{HARD}} + 0.3859 \times \ln(\text{FR} - 0.5) \\
 & (0.008611) \quad (0.06153)
 \end{aligned}$$

Random growth period effects again provided no significant improvement in any of the alternative models. The average loss in net PAI implied by this model was 20.0%, with a maximum loss of 51.6%. The average losses in net PAI implied by the same model fitted separately to each growth period ranged from 18.3% to 20.3%, with maxima ranging from 36.2% to 58.6% (Table 4). As with gross increment, pairwise tests among foliage retention parameter estimates for specific growth periods failed to reject the null hypothesis that the relationship between foliage retention and net increment remained consistent over the 10-year study period. Curves depicting loss in net PAI for individual growth periods yielded a set of very similar curves that fell within the confidence envelope for model 5, assuming average levels of Douglas-fir ba-

Table 3. Models tested for predicting gross periodic annual increment (gPAI) (m³·ha⁻¹·year⁻¹) and net periodic annual increment (nPAI) (m³·ha⁻¹·year⁻¹) of 76 permanent plots installed as part of the Swiss Needle Cast Cooperative Growth Impact Study.

Response	Symbols of included variables	Error structure	AIC
ln(gPAI)	lbadf, baoc, bahard, lage, lsib, lretm	Independent	-85.8
	lbadf, baoc, bahard, lage, lsib , lretm	Random plot (compound symm)	-164.3
	lbadf, baoc, bahard, lage, lretm	Random plot (compound symm)	-164.0
	lbadf, baoc, bahard, lage, lretm	Unstructured	-173.6
	lbadf, baoc, bahard, lage, lretm	Compound symm hetero	-173.1
	lbadf, baoc, bahard, lage, lretm	Toeplitz	-167.1
	lbadf, baoc, bahard, lage, lretm	Toeplitz hetero	-175.9
	lbadf, baoc, bahard, lage, lretm	AR(1)	-146.4
	lbadf, baoc, bahard, lage, lretm	SP(POW)	-145.0
	lbadf, baoc, bahard, lage, lsib, lretm	Independent	2.1
ln(nPAI)	lbadf, baoc, bahard, lage, lsib , lretm	Random plot	-77.7
	lbadf, baoc, bahard, lage, lretm	Random plot	-78.7
	lbadf, baoc, bahard, lage, lretm	Unstructured	-85.6
	lbadf, baoc, bahard, lage, lretm	Compound symm hetero	-88.8
	lbadf, baoc, bahard, lage, lretm	Toeplitz	-79.9
	lbadf, baoc, bahard, lage, lretm	Toeplitz hetero	-88.0
	lbadf, baoc, bahard, lage, lretm	AR(1)	-67.0
	lbadf, baoc, bahard, lage, lretm	SP(POW)	-65.2

Note: All variables are significant ($p \leq 0.05$) except for variables in bold ($p > 0.10$). lbadf = ln(BA_{DF}), lsib = ln(SI), lage = ln(AGE_{BH}), baoc = BA_{OC}, bahard = BA_{HARD}, lret = ln(FR).

Table 4. Average and minimum foliage retention and average and maximum loss in gross and net periodic annual increment of Douglas-fir (*Pseudotsuga menziesii*) (estimated from models 4 and 5 fitted separately to each growth period).

Attribute	Growth period			
	1998–1999	2000–2001	2002–2003	2004–2007
Foliage retention				
Average	2.32	2.34	2.51	2.41
Minimum	1.07	1.01	1.62	1.47
Gross increment				
Average growth loss (%)	18.1	17.8	25.6	17.4
Maximum growth loss (%)	58.2	53.9	46.8	36.6
Net increment				
Average growth loss (%)	18.3	18.4	19.0	20.3
Maximum growth loss (%)	58.6	55.2	36.2	41.9

sal area, broadleaved basal area, other conifer basal area, and breast height age (Fig. 3). The 95% confidence intervals for the parameter estimates associated with FR in eqs. 4 and 5 (0.36 ± 0.11 and 0.30 ± 0.12 , respectively) did not include 1.0, indicating that the relationship between periodic annual increment and foliage retention was significantly nonlinear.

Reanalysis of models 4 and 5 with the retrospective indicator variable and its interaction with other covariates failed to detect any differences in the relationship between plot-level increment and foliage retention in the retrospective and permanent plot phases of the growth impact study.

The selected binomial model for predicting probability of Douglas-fir mortality incorporated a simple Toeplitz covariance structure (Table 5). As described above, this structure assumed equal variance among plots and growth periods; however, covariances among repeated observations within plots were assumed to be nonzero and equal for any set of growth periods separated by the same time interval (diagonal-constant). The greater flexibility provided by the heterogeneous Toeplitz structure offered little gain in the binomial

mortality model (Table 5). Foliage retention had no significant effect on the probability that a plot would experience Douglas-fir mortality during any given growth period ($p = 0.94$), leading to the following final model (standard errors of parameter estimates shown in parentheses):

[6]

$$\ln[p/(1 - p)] = -3.0091 + 0.5882 \times \ln(\text{BA}_{\text{DF}}) + 0.2069 \times \ln(\text{BA}_{\text{OC}}) + 0.6168 \times \ln(\text{BA}_{\text{HARD}}) + 0.6231 \times \text{GP}$$

(0.8776)

(0.2896)

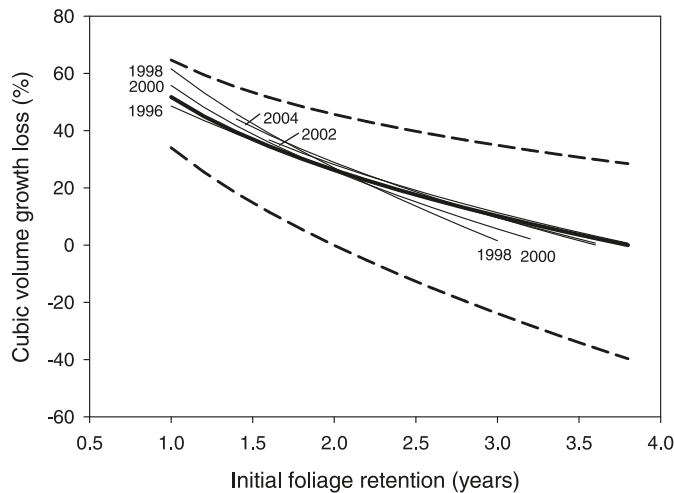
(0.08831)

(0.1305)

(0.1588)

where p is the predicted probability of observing Douglas-fir mortality within the growth period and all other variables are defined above. As would be expected, the probability of Douglas-fir mortality increased with increasing basal area in all three stand components, i.e., Douglas-fir, other conifers,

Fig. 3. Estimated net growth loss (model 5) for Douglas-fir (*Pseudotsuga menziesii*) cubic stem volume by initial foliage retention (index of Swiss needle cast severity). The heavy solid line represents the comprehensive model fitted to pooled data from three 2-year periods and one 4-year growth period on permanent plots in the Swiss Needle Cast Cooperative Growth Impact Study. The broken lines represent the 95% confidence envelope for the prediction model and the light solid lines represent model 5 fitted separately to each of the four growth periods in this study and to the retrospective study.



and broadleaved species. The influence of broadleaved basal area was particularly strong, with a very rapid increase in the probability of mortality with even low amounts of hardwood basal area (Fig. 4). Not surprisingly, the probability of mortality was higher for the 4-year growth period.

As was the case for the binomial mortality model, the simple Toeplitz covariance structure was sufficient for accounting for repeated observations in the conditional model for volume of Douglas-fir mortality. Mortality volume was not influenced by foliage retention under this structure ($p = 0.49$). The following final model for Douglas-fir mortality retained only initial Douglas-fir basal area and the competitive effects depicted by basal area of broadleaved species and western hemlock (standard errors of parameter estimates shown in parentheses):

$$[7] \quad \ln[\text{PAM}] = -5.2712 + 1.3323 \times \ln(\text{BA}_{\text{DF}}) + 0.1332 \times \text{BA}_{\text{HARD}} + 0.04507 \times \text{BA}_{\text{WH}}$$

(0.6252) (0.1928) (0.03208) (0.01649)

Periodic annual Douglas-fir mortality increased as initial basal area of Douglas-fir, broadleaved species, and western hemlock increased. As with probability of mortality, foliage retention was not a significant predictor of conditional Douglas-fir mortality. For a given amount of initial basal area, broadleaved species had a relatively strong effect on mortality (Fig. 5), probably because bitter cherry, bigleaf maple, and red alder are all capable of overtopping Douglas-fir due to more rapid juvenile height growth.

Discussion

Periodic annual stem volume increment

In the retrospective phase of the growth impact study, stem volume increment of Douglas-fir during the 1996 growing season was estimated by destructively sampling 0.02 ha fixed area plots in the spring of 1997 (Maguire et al. 2002). The 1996 annual increment was regressed on standard plot-level covariates backdated to their initial conditions, with the exception that foliage retention was available only for the spring of 1997 (time of destructive sampling). In contrast, volume increment was regressed on initial foliage retention for the growth periods in the permanent plot analysis. Likewise, mortality was unknown for the 1-year retrospective growth period, so the 1996 annual increment was limited to survivor growth. Despite these unavoidable inconsistencies between the retrospective and permanent plot phases of the growth impact study and, hence, the possibility of differences in the estimated relationship between foliage retention and volume increment, the retrospective estimates of growth losses for a given level of foliage retention did not differ significantly from those of the permanent plot phase. Likewise, the fundamental relationship between foliage retention and growth loss remained consistent over successive growth periods comprising the 10-year permanent plot phase of the growth impact study. In short, all evidence failed to reject the null hypothesis of stability in the relationship between foliage retention and growth loss. Although by convention, this result does not prove the null hypothesis, no gradual decline in growth vigor at a given level of foliage retention could be detected in these permanent plot data.

The increase in growth loss with declining foliage retention exhibited some curvature but lacked evidence of any obvious threshold of foliage retention at which growth loss suddenly appeared or worsened. Instead, the model described a relatively steady decline in growth with decreasing foliage retention, a trend that would be expected with significant physiological disruption of gas exchange in younger foliage, in advance of premature abscission (Manter et al. 2000).

To our knowledge, no other links between foliage retention and growth loss have been quantified in other regions of the world where Douglas-fir is grown. Douglas-fir in New Zealand experienced a growth decline attributed to *Phaeocryptopus gaeumannii* starting in 1963, and comparison of pre-1963 with post-1963 growth suggested a growth loss of 26%–40%; however, foliage retention was not reported (Manley 1985). Cameron et al. (1978) observed that infected trees in Hanmer Forest in New Zealand generally retained 20%–30% less foliage than uninfected trees, with 7-year-old infected trees at Rotorua holding 95%, 43%, 8%, and 0% of 1-, 2-, 3-, and 4-year-old needles, respectively. In a more comprehensive analysis using 312 permanent sample plots on both North and South Islands, Kimberley et al. (2011) compared growth rates for the years before SNC detection (prior to 1959) with growth for the years following detection. Average volume growth loss was estimated to be 32% but was greater on the North Island (35%) than on the South Island (23%). These estimates were similar to the average loss of 27% derived from the relationship between foliage retention and growth loss in the retrospective phase of the north coastal Oregon study (Maguire et al. 2002) but were higher

Table 5. Models tested for predicting probability of Douglas-fir (*Pseudotsuga menziesii*) mortality and conditional periodic annual mortality (PAM) ($\text{m}^3\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) of 76 permanent plots installed as part of the Swiss Needle Cast Cooperative Growth Impact Study.

Response	Symbols of included variables	Error structure	AIC
$\ln[p/(1 - p)]$	lbadf, lbaoc, lbahard, lsib, per, lretm	Random plot	1343
	lbadf, lbaoc, lbahard, lsib , per	Random plot	1339
	lbadf, lbaoc, lbahard, per	Random plot	1328
	lbadf , lbaoc, lbahard, per	Unstructured	1313
	lbadf, lbaoc, lbahard, per	Compound symm	1295
	lbadf, lbaoc, lbahard, per	Compound symm hetero	1289
	lbadf, lbaoc, lbahard, per	Toeplitz	1288
	lbadf, lbaoc, lbahard, per	Toeplitz hetero	1306
	lbadf, lbaoc, lbahard, per	AR(1)	1309
	lbadf, lbaoc, lbahard, per	SP(POW)	1310
	ln(PAM)	Independent	434.9
		Random plot	432.5
		Random plot	433.7
		Random plot	435.1
		Unstructured	424.8
		Compound symm hetero	434.3
		Toeplitz	422.3
		Toeplitz hetero	422.7
		AR(1)	427.1
		SP(POW)	427.7

Note: Bold italicized variables are marginally significant ($0.05 < p \leq 0.10$), bold variables are not significant ($p > 0.10$), and all other variables are significant ($p \leq 0.05$). lbadf = $\ln(\text{BA}_{\text{DF}})$, lsib = $\ln(\text{SI})$, lage = $\ln(\text{AGE}_{\text{BH}})$, baoc = BA_{OC} , bahard = BA_{HARD} , lret = $\ln(\text{FR})$.

Fig. 4. Estimated effects (model 6) of initial hardwood basal area and initial basal area in other conifers on probability of Douglas-fir (*Pseudotsuga menziesii*) mortality during the growth period (a 2-year growth period is assumed with initial Douglas-fir basal area set at an average level of $21.9 \text{ m}^2\cdot\text{ha}^{-1}$).

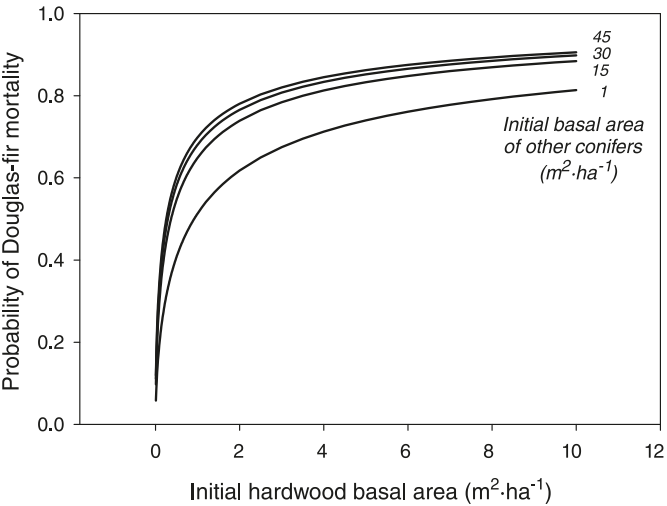
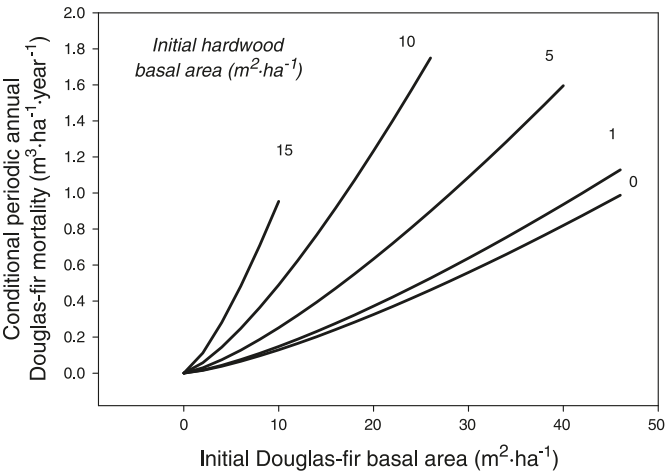


Fig. 5. Estimated effects (model [7]) of initial Douglas-fir (*Pseudotsuga menziesii*) basal area and initial hardwood basal area on conditional periodic annual Douglas-fir mortality (initial western hemlock (*Tsuga heterophylla*) basal area set at an average level of $3.5 \text{ m}^2\cdot\text{ha}^{-1}$).



than the average loss of 20% in net increment reported above for the permanent plot phase.

Douglas-fir mortality

Data from the permanent plots supported the hypothesized lack of any SNC effect on Douglas-fir mortality. Formal analysis of permanent plots in New Zealand similarly failed to detect any acceleration of mortality after the appearance of *Phaeocryptopus gaemmannii* in 1959 (Kimberley et al. 2011).

As is consistent with many previous analyses and models of mortality at both the individual-tree level (e.g., Hamilton 1986) and stand level (e.g., Zhao et al. 2007), the probability of Douglas-fir mortality on the SNC permanent plots increased with stand density. In the case of Douglas-fir plantations in north coastal Oregon, increasing basal area of hardwood and other conifer species that regenerated naturally in these stands further contributed to increasing probability of mortality.

As with probability of mortality, the conditional amount of Douglas-fir mortality was driven by density of the major stand components, with the exception that other coniferous species contributed little beyond the effects of western hemlock alone. This particular aspect of stand dynamics can be best understood by considering the vertical structure of Douglas-fir plantations. Western hemlock comprised the bulk of basal area in other conifers, and the average height of this species (Table 1) supported field observations that it typically maintained a position in the main canopy. With the exception of noble fir on only very few plots, the additional basal area in other conifers was contributed by western redcedar and Sitka spruce, both of which were much shorter on average than Douglas-fir and therefore occupied the suppressed crown class (Table 1). While these latter two species influenced the probability of Douglas-fir mortality, they did not provide sufficient competition to larger Douglas-fir to influence significantly the volume of mortality experienced by plots.

Other assessments of conditional mortality have targeted number of trees as the response variable rather than stem volume (Affleck 2006; Zhao et al. 2007); however, in all cases, initial stand density was the primary driver of conditional mortality. A two-stage approach has been previously applied to stand-level mortality in loblolly pine (*Pinus taeda* L.) plantations (Affleck 2006; Zhao et al. 2007). Likewise, zero-inflated Poisson, zero-inflated negative binomial, and especially hurdle models have been shown to offer a single-stage alternative for accommodating the common mixture of many plots without mortality and relatively few plots with mortality (Affleck 2006). Regardless, all approaches lead to similar inferences about the predominant effect of stand density on mortality.

Assumptions required for estimating SNC growth impact

Estimating the growth impact from SNC requires a reference point that can be considered the potential or expected growth in absence of the disease. Four general approaches can be taken to quantify expected growth rate. The first assumes that foliage retention is controlled exclusively by *Phaeocryptopus gaeumannii* (this assumption is addressed in next section), that sampling has spanned the full range of SNC severity, and that disease severity acts independently of other factors that may influence growth (e.g., annual and seasonal weather). Under these conditions, plots exhibiting the highest foliage retention are interpreted as disease-free. After accounting for the effects of other covariates influencing growth, the marginal effect of foliage retention in the regression models allows estimation of growth loss relative to maximum possible foliage retention. As described above, SNC growth impacts on gross and net periodic stem volume increment of Douglas-fir were estimated in this way on the Swiss Needle Cast Cooperative growth impact plots.

A second approach is possible if the exact date of an introduction or start of an epidemic is known. In this case, the growth of permanent plots prior to the known date can be compared with subsequent growth, assuming correction for other covariates influencing growth. This approach was possible in New Zealand due to the extensive network of Douglas-fir plots that was established well before the introduction of SNC in 1959 (Manley 1985; Kimberley et al. 2011). A

similar approach involved application of dendrochronological techniques to Douglas-fir and adjacent western hemlock in north coastal Oregon; in this case, the start of the SNC epidemic was identified as the date when the radial increment of Douglas-fir diverged from the increment of adjacent western hemlock (Black et al. 2010).

A third approach relies on predictions from established models to provide the expected growth rate. Departures from expectation can then be related formally or informally to foliage retention. SNC growth impacts at the stand level have been compared with predictions from the ORGANON growth model (Weiskittel and Maguire 2004), and impacts on individual-tree diameter and height growth have been quantified relative to the regional trends represented in ORGANON (Weiskittel and Maguire 2004; Garber et al. 2007). Similar approaches have been applied to estimate other growth losses, for example, from the western spruce budworm (Crookston 1985).

The fourth approach to estimating growth impacts requires elimination of the pathogen by fungicide in a controlled experiment (e.g., Hocking 1967; Stone et al. 2007). Growth of newly planted radiata pine in Chile protected from *Dothistroma septospora* (Dorog.) Morelet for 2 years exceeded that of unprotected trees by 20%, implying a 17% growth loss in the first 2 years after planting. Relative to the most effective fungicide treatments, height growth of unprotected radiata pine seedlings was reduced 31% by *Dothistroma* blight (Hocking 1967). Aerial application of chlorothalonil to Douglas-fir stands with severe SNC increased stem volume growth 35% over unsprayed controls during the full 5-year period of application, but the increase was 60% over the final 3 years alone (Mainwaring et al. 2002).

Factors influencing foliage retention

A fundamental assumption behind assessment of SNC growth impact is that foliage retention or needle longevity is controlled exclusively by the presence, abundance, and (or) activity of *Phaeocryptopus gaeumannii*. However, many other factors are well known to influence needle life span between and within species (Reich et al. 1995). Patterns observed between species can be quite complex and relate to many factors like crown and needle morphology, shade tolerance, and temperature regime and other aspects of the physical environment to which they are adapted. These interspecific patterns in leaf life span represent genetic adaptations that ensure survival and reproductive success, so are of limited interest from the perspective of intensive silviculture, except perhaps for implications in managing forests under various climate change scenarios. Of greater interest in the present context are plastic or phenotypic responses to aspects of the growing environment that are under some degree of silvicultural control.

In general, foliage retention declines along a gradient from lower to higher net primary production, whether imposed by inherent site quality (Weidman 1939; Oleksyn et al. 2003) or fertilization and irrigation (Gower et al. 1992). Although this trend may seem counterintuitive, it is important to recognize that lower foliage retention and shorter life span do not necessarily imply less foliage biomass. In fact, the trend imposed by greater productivity can largely be attributed to greater foliage production, more rapid turnover, and either stable or in-

creasing total amounts of foliage biomass. Foliated shoot length among different provenances of ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) was stable despite variation in needle retention from 3 years in some provenances to 8 years in others (Weidman 1939). This difference was attributed to phenotypic plasticity, given that needle retention was consistently 3–4 years for all provenances when grown in a common garden. A similar study confirmed that the amount of foliage per shoot remained constant in lodgepole pine (*Pinus contorta* Douglas ex Loudon) growing at different elevations, despite variation in needle retention from 5 to 18 years (Schoettle 1990). Results from fertilization studies are consistent with observations along productivity gradients. Based on needle litterfall rates, foliage retention was inferred to increase immediately after fertilizing Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) in the southern Rocky Mountains (Gower et al. 1992) but to decrease in the long term (Gower et al. 1992). In a more detailed study of crown architecture, foliated branch length remained constant among fertilized and unfertilized grand fir and Rocky Mountain Douglas-fir in the northern Rocky Mountains, even though foliage longevity declined (Balster and Marshall 2000).

If foliated branch length for a given level of light availability is constant, then the pattern observed among trees with differing growth rates described above should extend to within-tree differences in branch growth. Light measurements and detailed analysis of crown architecture indicate that needle longevity is controlled by the number of annual shoots required to accumulate sufficient foliage to reduce light below the compensation point (Schoettle and Smith 1991). An increase in foliage longevity with increasing depth into the crown has in fact been broadly observed and can be attributed to improved light conditions and greater shoot growth with increasing height in the crown (Schoettle and Smith 1991).

Biological interpretation of foliage retention

In light of the generally observed inverse relationship between foliage retention and forest productivity, the positive correlation between stem volume increment of Douglas-fir and foliage retention in north-central Oregon suggested that SNC was the predominant factor controlling needle retention in this region. This conclusion is further supported by the increase in foliage retention from 1.9 to 2.8 years after fungicidal elimination of *Phaeocryptopus gaeumannii* (Mainwaring et al. 2002), suggesting that the limiting factor on foliage retention was not maximum foliated length.

Although the mechanisms controlling foliage retention are complex, the fact that foliage retention is correlated with total foliage amount (at least in the presence of other covariates) was indicated by the significant effect of foliage retention in statistical models of periodic annual increment. Douglas-fir trees displaying maximum needle longevity in our target population received foliage retention ratings of slightly over 3.5 years. On a tree with this foliage retention, 31%, 28%, 19%, 11%, and 11% of the total foliage mass was contributed by 1-, 2-, 3-, 4-, and ≥ 5 -year-old needles, respectively (Weiskittel and Maguire 2006). For a tree of equal diameter, height, and crown length, a foliage retention of 1.5 years implied a shift in the distribution to 40%, 34%, 18%, 7%, and

1% across the same age classes; however, total foliage mass was approximately 27% less (Weiskittel and Maguire 2006). Although foliage retention must be used with caution as a predictor of tree- or stand-level foliage mass for the reasons outlined in the previous section, foliage retention does provide a rating that can be operationally implemented in stands ≤ 40 –50 years of age, and it has consistently served as a reliable index of growth loss in Douglas-fir plantations when accompanied by appropriate covariates (Maguire et al. 2002).

Growth losses from foliar fungi

Growth impacts of defoliation by SNC were comparable with growth impacts estimated at similar levels of defoliation by agents such as other foliar fungi and canopy insects as well as under simulated defoliation in designed experiments. However, major differences between effects of SNC and other agents include severity of defoliation, relative losses among age classes, duration or periodicity of defoliation, thresholds for mortality, and concomitant effects on other tree, stand, and ecosystem components. Assessing growth impacts of SNC was relatively simple compared with other defoliators in that defoliation was never complete or episodic; rather, it fluctuated annually but was relatively constant over the decade of observation. Likewise, SNC has not yet caused significant mortality in the sampled plantations of young Douglas-fir.

Dothistroma blight is a foliar disease that has caused significant defoliation in several coniferous species and can be sufficiently severe to cause mortality (Gibson 1972). The first signs of *Dothistroma* appear in the oldest and most shaded foliage, with subsequent spread to younger foliage in more exposed parts of the crown (Gibson 1972). *Dothistroma* was first recognized as a serious disease of commercial conifers after radiata pine was introduced into eastern and central Africa. Much of the early work on *Dothistroma* growth impact was based on comparison of height and diameter growth among trees with differing levels of defoliation (Gibson 1974). Because the older and shaded foliage was attacked first, 20%–30% of the foliage on radiata pine could be affected before impacts on diameter and height growth were detected (Gibson et al. 1964; Gibson 1972, 1974). Due to this pattern of disease progression, growth in older radiata pine was observed to follow a reverse sigmoid pattern as *Dothistroma* severity increased (Christensen and Gibson 1964), i.e., little detectable influence on diameter growth until 25% defoliation, 50% growth reduction at 50% defoliation, and 90% reduction at 75% defoliation. The onset of height growth loss was much later, reaching 50% reduction at 80% defoliation. Earlier observations in Kenyan radiata pine plantations had suggested that height growth losses from *Dothistroma* reached only 20% when 75% of the tree's foliage became affected (Gibson et al. 1964). In younger trees with relatively little older foliage, the relationship between defoliation and height growth was more linear (Gibson et al. 1964). Severe levels of infection have led to tree mortality in the past, but mortality did not appear to be as dominant a factor in stand-level growth loss relative to the more widespread effects of partial defoliation (Gibson 1974).

Lophodermium needle cast has been observed to start at the base of Scots pine (*Pinus sylvestris* L.) crowns and move upward (Martinsson 1979). This progression was attributed to

dispersal of spores from fruiting bodies that develop during a saprophytic phase on needles that have been cast during a parasitic phase on live needles combined with the influence of a more humid microclimate lower in the crown. After the trees reach a minimum height, perhaps as low as 2 m, the tree is less susceptible, particularly at the top. In a study of genetic resistance, trees were subjected to as many as three attacks by the fungus, but height growth losses were not detected until defoliation reached 65% (Martinsson 1979). Growth losses then increased to 24% at 80% defoliation and 50% at 96% defoliation.

Growth impacts from insect defoliation

Insects have perhaps received the greatest amount of attention as defoliators from a research perspective (e.g., Kulman 1971). MacLean (1985) provided a very comprehensive review of growth impact from the spruce budworm, including both eastern and western species. Budworm development is synchronous with bud flush, resulting in early larval instars feeding on new foliage emerging from the bud. Magnitudes of growth loss are a function of both the severity of budworm feeding in specific years and the temporal sequence of defoliation. Growth losses accrue from reduction in diameter and height growth, top kill, stem deformities in severely defoliated trees resulting from top kill, and mortality of entire trees (MacLean 1985). The net effect of these impacts were yield losses ranging from 10% to 81% and growth losses ranging from 19% to 54%, with much of the growth loss occurring after defoliation had ended (Batzer 1973). Mortality rate depends on severity and duration of defoliation, species and age range of trees, age class distribution, species composition, spacing, site, and others (MacLean 1985). Mortality starts usually after 4 or 5 years of severe defoliation (MacLean 1980).

Douglas-fir tussock moth (*Orgyia pseudotsugata* (McDunnough)) defoliates several conifer species, particularly Douglas-fir and grand fir, by partial consumption and induced shedding of individual needles (Brookes et al. 1978). The ratio of damaged foliage to consumed foliage averages 3.2 but can run as high as 8. Outbreaks generally last for 4 years and damage progresses from the top of the tree downward due to larval behavior and the preference for newer foliage. Severe defoliation is typically characterized by complete loss of foliage in the upper quarter to half of the crown and damage of most current foliage in the rest of the crown. Stand-level defoliation has typically been rated as very light, light, moderate, or heavy, corresponding approximately to 10%, 25%, 50%, and 90% average defoliation. Radial growth reductions of Douglas-fir suffering 50% defoliation or greater were estimated to average 58% in the Blue Mountains of Oregon.

Growth impacts from a variety of other insect defoliators have also been estimated. Pine sawfly defoliation of loblolly pine evoked a compensatory response in growth with defoliation rates up to 30%, but 50% defoliation over a 3-year period resulted in a cumulative loss of diameter increment of approximately 28% (Zeide and Thompson 2005). The pine butterfly *Neophasia menapia* (C. Felder and R. Felder) feeds preferentially on older foliage of ponderosa pine but moves to newer foliage during epidemics. During a 3-year epidemic, radial growth losses averaged about 60% on surviving trees that experienced defoliation levels averaging about 75%

(Cole 1966). A pandora moth (*Coloradia pandora* Blake) outbreak in central Oregon ponderosa pine resulted in average defoliation of 45% in 1992 and a second wave in 1994 resulted in average defoliation of 67% (Cochran 1998). These defoliation events caused a basal area growth loss of 25% in the first season after defoliation, 30% in the second season after defoliation, and 63% after the second wave of defoliation in 1994. Defoliation by the larch casebearer (*Coleophora laricella* (Hubner)) on two sites over a 10-year period started at light (1%–25%) to moderate (26%–50%) defoliation, reached severe (76%–100%) defoliation, and tapered off to moderate and light defoliation before ending (Alfaro et al. 1991). Diameter growth losses averaged approximately 29%.

Growth impacts from artificial defoliation

Most artificial defoliation experiments were designed to remove differing amounts of total foliage or specific age classes of needles. The latter experiments are more relevant to SNC growth impact, but their interpretation is complicated by differences in season of foliage removal and unknown contributions of each age class to total foliage biomass. Linzon (1958) concluded that 1-year-old foliage was more important to eastern white pine (*Pinus strobus* L.) growth than either current or 2-year-old foliage, but defoliation was implemented in May, well before formation of significant amounts of current foliage (Linzon 1958). In contrast, Kulman (1965) removed foliage from red pine (*Pinus resinosa* Aiton) trees in mid-July and found that removal of current needles had the largest effect on shoot growth and removal of 2-year-old needles the least effect; however, 61.7%, 18.9%, 15.6%, and 3.8% of the foliage on subject trees was current, 1-year-old, 2-year-old, and 3-year-old foliage, respectively. In another experiment on red pine, 0%, 33%, 66%, and 99% of the foliage was removed from each age class by clipping corresponding distal portions of needles (Krause and Raffa 1996). Growth reductions from 33% removal were proportionally lower than from 66% foliage removal, a response attributed to lower nutrient concentrations in the tips of needles. Results from these and other artificial defoliation experiments suggest that relative contribution to diameter and shoot growth depends on at least three key features of the specific needle age classes: (i) its relative contribution to total foliage amount, (ii) its nutrient relative concentration, and (iii) its photosynthetic efficiency.

Conclusions

Growth loss from SNC averaged approximately 50% after 75% reduction in foliage retention and approximately 25% after 50% reduction in foliage retention. Declines in foliage retention were not necessarily proportional to loss of foliage mass because foliage retention represented a complex succession of mechanisms influencing photosynthetic capacity through corresponding effects on stomatal blockage by pseudothecia, changes in light penetration and capture, translocation of foliar nutrients, and shifts in foliage distribution among age classes of differing inherent photosynthetic efficiency. Estimated growth losses from SNC were comparable with losses from other fungal and insect defoliators that caused similar magnitudes of foliage loss as well as growth losses documented in various artificial defoliation experiments.

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