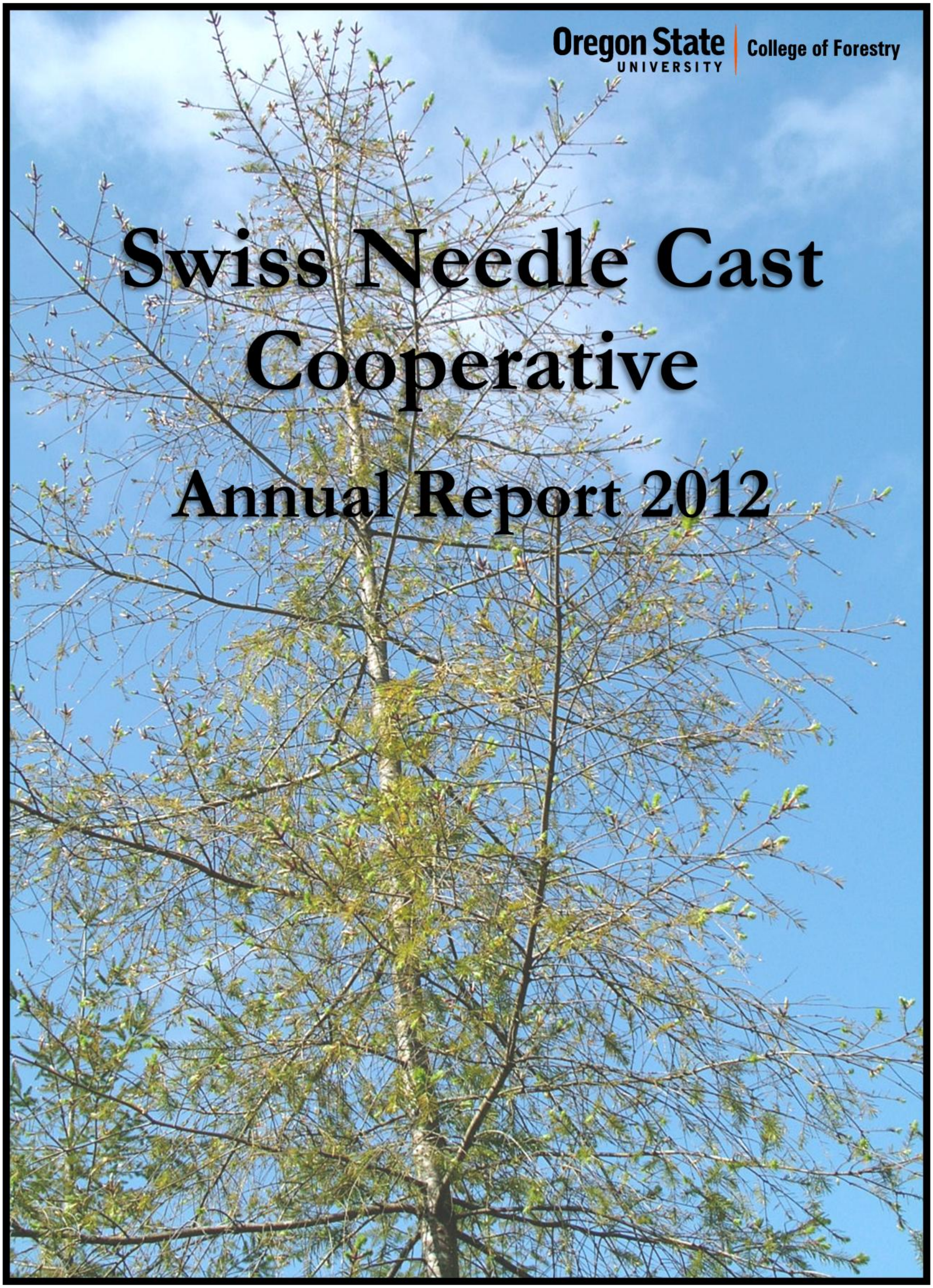
Oregon State University | College of Forestry

Swiss Needle Cast Cooperative

Annual Report 2012



SNCC Income Sources and Expenditures: 2012

Income

Membership dues	70,000
Oregon State Legislature	76,712
Carry-over	146,922
Total 2009 Budget	**$293,634**

Expenditures

Salaries and wages	80,077
Travel	3,667
Operating expenses	1,161
Contract Work	13,412
Materials and Supplies	14,061
Indirect Costs	4,350
Total 2010 Expenditures	**$116,728**

November 29, 2012.

To: Swiss Needle Cast Cooperative Members

From: David Shaw, Director, SNCC

Swiss needle cast has continued to intensify in the Oregon Coast Range this year, with the 2012 Aerial Detection Survey noting an all-time-high 519,502 acres with SNC symptoms.   This is a major increase from 2011 when we detected 444,287 acres, and 2010 when we noted 393, 923 acres. Each of these past three years has set a record. In short, although managers continue to adjust to the disease, we are seeing the disease intensify and move marginally west. This year, the Washington State Department of Natural Resources and the USFS Forest Health Protection group has surveyed coastal Washington from the air and with follow-up ground plots. We'll have a report from WA DNR at our Annual Meeting.

The focus of the Swiss Needle Cast Cooperative continues to be a blend of research, monitoring, and disease impact assessment to provide the framework for integrated pest management across the landscape of coastal Oregon and Washington. We also serve a function as an information source.

We have accumulated significant savings in our budget over the past several years in preparation for the 2013 field season and re-establishment of our Growth Impact Plot System, managed by Doug Maguire and SNCC. Our tentative plan, subject to approval by the members, is to spread the plot system out over the entire coast range, capturing the range of variation in needle retention, distance from coast and major soil bedrocks. This will allow for a better understanding of mensuration-based growth impacts, monitoring of SNC changes over time, and epidemiology research. Currently, our growth impact plots are nested into the NW Coast Range only, representing only a portion of the environment.

The 2012 Annual Report reflects the strong focus of SNCC on management implications of the disease and methods for managing the disease, while continuing to study details of biology and epidemiology. We hope the members find this useful, while our website contains the PDF's of published papers listed at the end of the Annual Report.

The SNCC continues to serve the forestry community in the PNW.

Sincerely,

David Shaw

SNCC Background

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. The SNCC is located in the Department of Forest Engineering, Resources and Management within the College of Forestry at Oregon State University. The Membership is comprised of private, state, and federal organizations. Private membership dues are set at a fixed rate. An 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

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.

Contents

Appendix

Swiss Needle Cast Aerial Survey, 2012

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 slope of the Coast range. The 2012 survey mapped 519,375 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 slope of the Coast range. 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 from late April to early June.

Methods

The 2012 Oregon Coast Range survey was flown on May 8, 9, 10, 11, and 14 and covered approximately 2.81 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 the northern border of Curry County, and from the coastline eastward until obvious symptoms were no longer visible. We did not survey the Cascade Range in 2012, but Swiss needle cast does occur at damaging levels in a few areas.

Results and Discussion

Weather conditions were excellent for symptom development and aerial observation. The survey mapped 519,375 acres of Douglas-fir forest with obvious symptoms of Swiss needle cast (Figure 1), reaching an all-time high for the third year in a row. 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 2012. 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 and increasing the amount of non-host tree species such as hemlock, cedar and red alder.

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 Michael 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://www.oregon.gov/ODF/privateforests/fhMaps.shtml

Acknowledgements

The 2012 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 and the Oregon Department of Forestry. Martin Kimbrel (ODFW) and Wayne Cartwright (ODF) piloted the plane. Mike McWilliams (ODF) is the survey coordinator and primary aerial observer; Ben Smith (USFS), Bob Schroeter (USFS), Keith Sprengel (USFS) and Rob Flowers (ODF) were the other aerial observers.

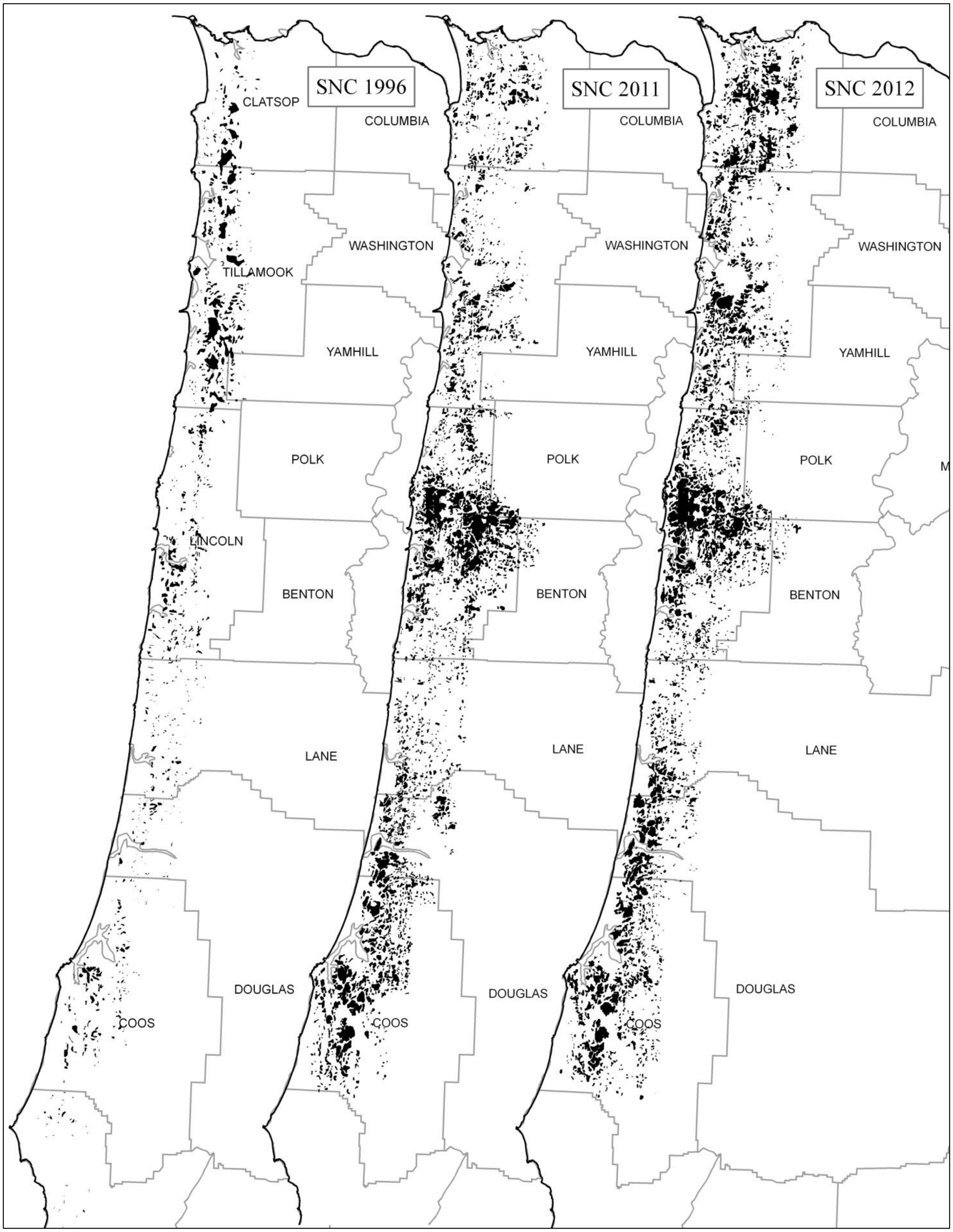


__Figure 1__. Swiss Needle Cast (SNC) aerial survey: areas of Douglas-fir forest with symptoms of Swiss Needle Cast detected in the 1996, 2011 and 2012 surveys. Solid black polygons (blotches) depict areas with severe or moderate damage from SNC.

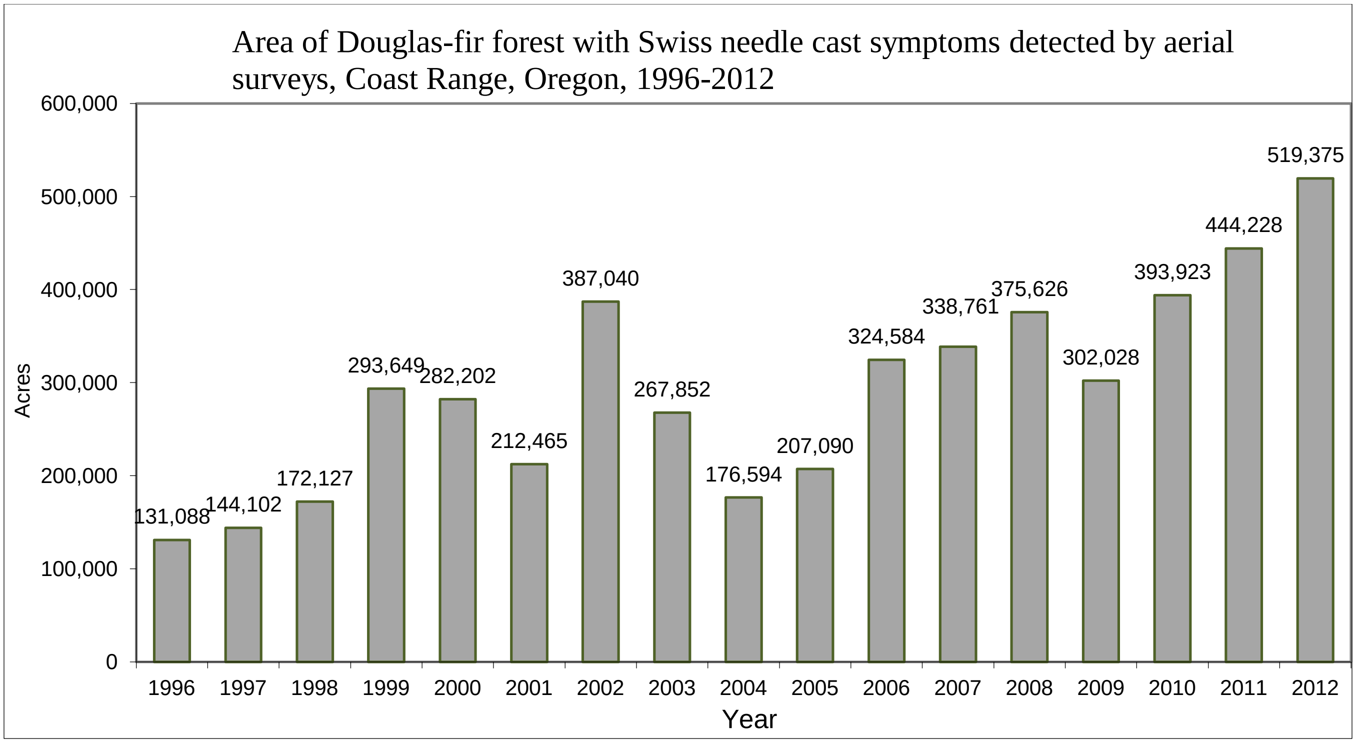


***Figure 2**. Trend in area of Douglas-fir forest in western Oregon with symptoms of Swiss needle cast detected during aerial surveys in April and May, 1996-2012. Results for 2008 were estimated by extrapolating from 3 sample survey blocks.*

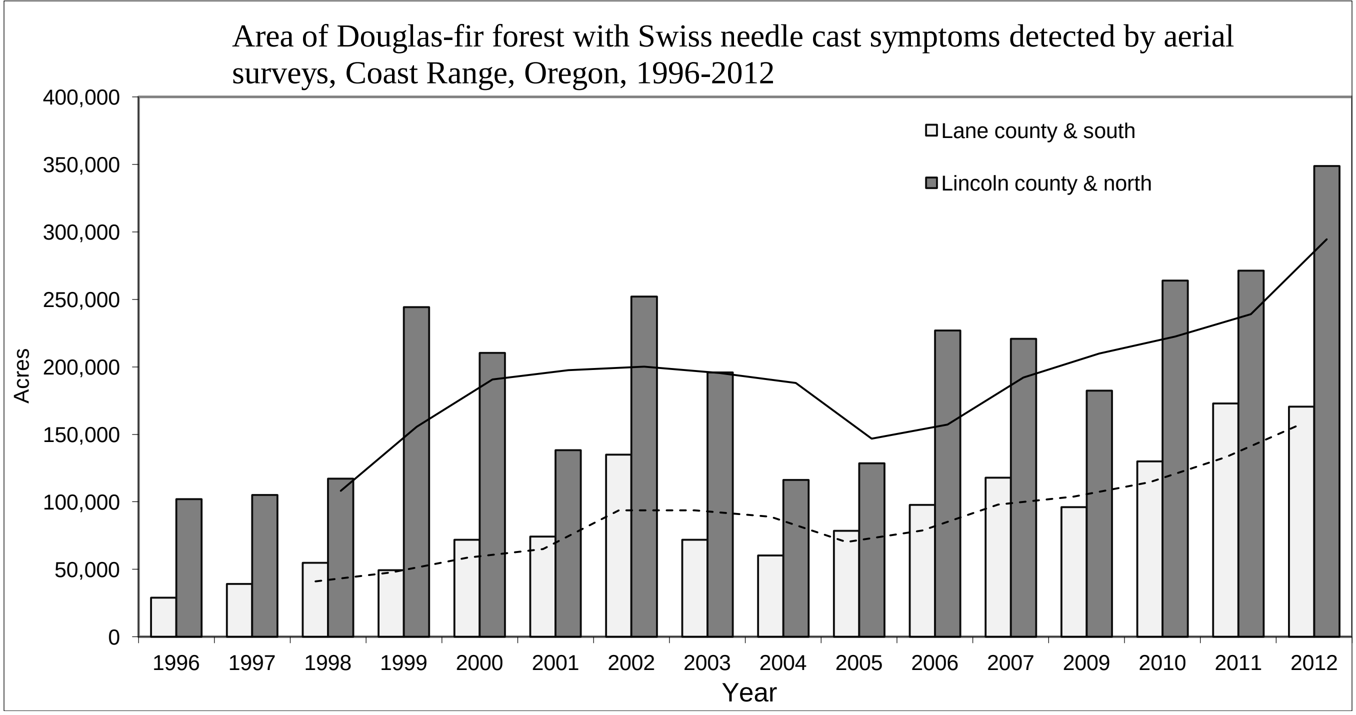


***Figure 3**. Trend in area of Douglas-fir forest in western Oregon with symptoms of Swiss needle cast detected during aerial surveys in April and May, 1996-2012. North region = Lincoln county & north; South region = Lane county & south. Trend lines are 3-year rolling averages.*

Incidence and Severity of Swiss Needle Cast in Coastal Washington, 2012

Daniel Omdal[1], Amy Ramsey-Kroll[1], Aleksandar Dozic[1], Ben Smith[2], and Hannah Peterson[1]
[1]Washington Department of Natural Resources, Olympia, WA
[2]USDA Forest Service Forest Health Protection, Sandy, OR

Report prepared for Swiss Needle Cast Cooperative Annual Meeting, November, 29, 2012.

Abstract

In May, an aerial survey, covering 2.7 million acres, was flown to detect and map the distribution of Swiss Needle Cast (SNC) symptoms in coastal Washington. Nearly 230,000 acres of symptomatic Douglas-fir were mapped. Seventy-five ground sites were also surveyed for Douglas-fir needle retention, the percentage of Douglas-fir in the stand and SNC incidence and severity, determined by pseudothecia counts. The greatest percentage of pseudothecia occluded stomata was found in ground sites that were not associated with any of the mapped aerial survey polygons. The average percentage of pseudothecia occluded stomata on all sites was nearly 3.5% for 2011 foliage (1-year-old) and nearly 18% for 2010 foliage (2-years-old).

Introduction

The fungus that causes SNC , *Phaeocryptopus gaeumannii*, is found throughout the range of its host, Douglas-fir (Shaw et al. 2011). The disease is most damaging near the coast due to the fungi-favorable climatic and topographic conditions. Swiss Needle Cast can reduce growth of host trees, as well as alter wood properties and affect stand structure and development (Kanaskie and McWilliams 2011). Over 300,000 acres of SNC symptomatic Douglas-fir have been mapped aerially since 2006 in Oregon (Kanaskie and McWilliams 2011), but there has not been a SNC aerial survey in Washington since 2000.

The 2012 SNC aerial survey in Washington was coupled with a ground survey. Swiss needle cast ground surveys have been conducted annually in Washington since 1997. The objective of the ground survey was to validate the aerial survey and determine how accurately the data collected from the air reflected what was happening on the ground.

Methods

The 2012 Washington SNC survey was flown on May 7, 10, 11, and 14 and covered approximately 2.7 million acres of forest. The aerial survey methods were similar to those described in Kanaskie and McWilliams (2011), except trees younger than approximately ten years were not mapped. The survey area extended from the Columbia River to the northern coast of the Washington peninsula, and from the western coastline east until obvious SNC symptoms were no longer visible.

Seventy five ground sites were included in the SNC ground survey. Fourteen sites were associated with “severe” SNC aerial survey polygons, 26 with “moderate” polygons and 35 were not associated with any aerial survey polygons (referred to as, "other" in the results). Stand color, landscape position, elevation, aspect and average tree age were recorded for each site. Needle retention, diameter at breast height and crown color were recorded for ten trees along a transect at each site. Foliage from 2011 and 2010 were collected from the upper third of each of the ten trees at each site and taken back to the lab for microscopic examination of pseudothecia density. Three hundred stomata on each of ten needles from each foliage cohort were microscopically examined for pseudothecia occurrence. ANOVA were used to compare variables across the three site categories and linear regression was used to analyze relationships between needle retention and percent occluded stomata.

Results and Discussion

The aerial survey mapped 228,500 acres of Douglas-fir with obvious symptoms of SNC (Figure 1). The easternmost area with obvious SNC symptoms was approximately 30 miles inland in southwest Washington and approximately 15 miles inland further north on the Olympic Peninsula. Table 1 shows how the 2012 SNC aerial survey compares to the 1998, 1999 and 2000 SNC aerial survey in Washington. Approximately 8.5% of the total acres surveyed in 2012 were symptomatic, which is a lower percentage than those acres mapped in 1999 and 2000. The severe polygons were on average about 9.5 miles from the western coast and the moderate polygons were on average about 13.9 miles from the coast. These distances were statistically different ($\alpha = 0.05$, $p = 0.000$).

Differences among site characteristics from the ground survey varied across site type. The percentage of Douglas-fir in the stands was greatest in the "other" and "moderate" sites, with significantly less in the "severe" sites (Figure 2). The average needle retention, in years, was significantly less in the "severe" and "moderate" sites when compared to the "other" sites (Figure 3). Crown color, however, was significantly more yellow in the "severe" sites when compared to the "other" and "moderate" sites (Figure 4). Since crown color is the characteristic used to aerially map SNC symptoms, significantly more yellowing in the "severe" sites was expected, but a significantly less Douglas-fir component in the "severe" sites was not expected.

Phaeocryptopus gaeumannii incidence was greater than 90% in both the 2011 and 2010 foliage across all sites, except for the "severe" sites. The incidence in the 2010 foliage in the "severe" sites was greater than 90%, but incidence in the 2011 foliage was 86%. The "other" sites had significantly greater pseudothecia incidence than the "moderate" and "severe" sites (Figure 5). The percent pseudothecia occluded stomata in 2011 foliage were statistically the same across sites, but significantly decreased from "other" to "severe" in the 2010 foliage, with the "severe" sites having the lowest percent of pseudothecia occluded stomata (Figure 6). The percent pseudothecia occluded stomata data does not reflect the results from the aerial survey.

Similar to the Oregon Department of Forestry SNC aerial survey, caution should be advised when interpreting aerial survey data. The SNC survey should be considered a conservative estimate of the acreage affected by SNC because aerial observers can only map areas where disease symptoms have developed enough to be visible from the air. SNC aerial survey can be used to coarsely document trends in damage over time. The ground data shows that SNC is present in areas that were not mapped during the aerial survey. While the aerial survey can be used as a guide for identifying areas impacted by SNC, on the ground surveys should be conducted in stands of interest before SNC mitigating management decisions are made.

Additional Notes

We appreciate any information regarding the accuracy or usefulness of the maps. Please contact Daniel Omdal (daniel.omdal@dnr.wa.gov or 360-902-1692) or Amy Ramsey-Kroll (amy.kroll@dnr.wa.gov or 360-902-1309) if you have questions, comments or suggestions.

References

Kanaskie, A. and M. McWilliams. 2011. 2011 Swiss Needle Cast Aerial Survey. Oregon Dept. of Forestry, Office report, Salem, OR. Aerial survey data available online at www.oregon.gov/ODF/privateforests/fhMaps.shtml; last accessed Sept 20, 2011.

Shaw, D.C., G.M. Filip, A. Kanaskie, D.A. Maguire, and W.A. Littke. 2011. Managing an epidemic of Swiss needle cast in the Douglas-fir region of Oregon; the role of the Swiss Needle Cast Cooperative. *J. of For.* 109(2): 109-119.

Figure 1. Swiss Needle Cast aerial survey in Washington in 2012.

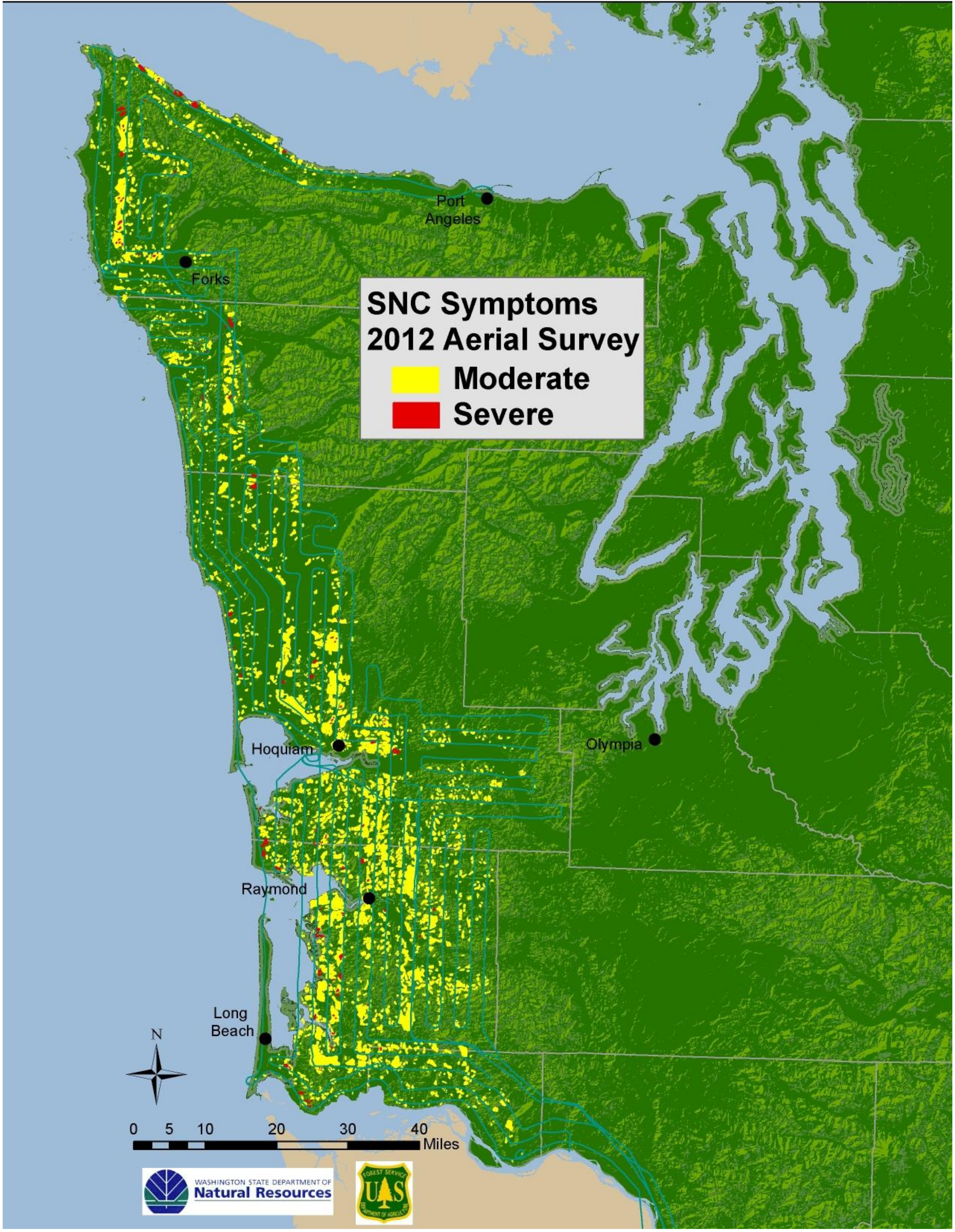


Table 1. Swiss Needle Cast aerial survey results for 1998, 1999, 2000 and 2012 survey.

Year	Total Acres Flown	Total Acres Mapped	Symptomatic Ac. (Moderate and Severe)		Severe Ac.	
1998	1,720,000	44,500	44,500	(2.6%)	3,100	(0.2%)
1999	1,100,000	200,000	200,000	(18.2%)	20,000	(1.8%)
2000	1,950,000	410,000	410,000	(21.0%)	278,500	14.3%)
2012	2,700,000	228,500	228,500	(8.5%)	6,500	(0.2%)

Figure 2. Percentage of Douglas-fir in Swiss needle cast (SNC) ground survey plots. Other plots were not associated with the SNC aerial survey polygons. Moderate and severe ground plots were associated with either the respective moderate or severe SNC aerial survey polygons. Standard error bars are shown for each bar. Different letters above each bar indicant statistically significant differences at the α ≤ 0.05 level.

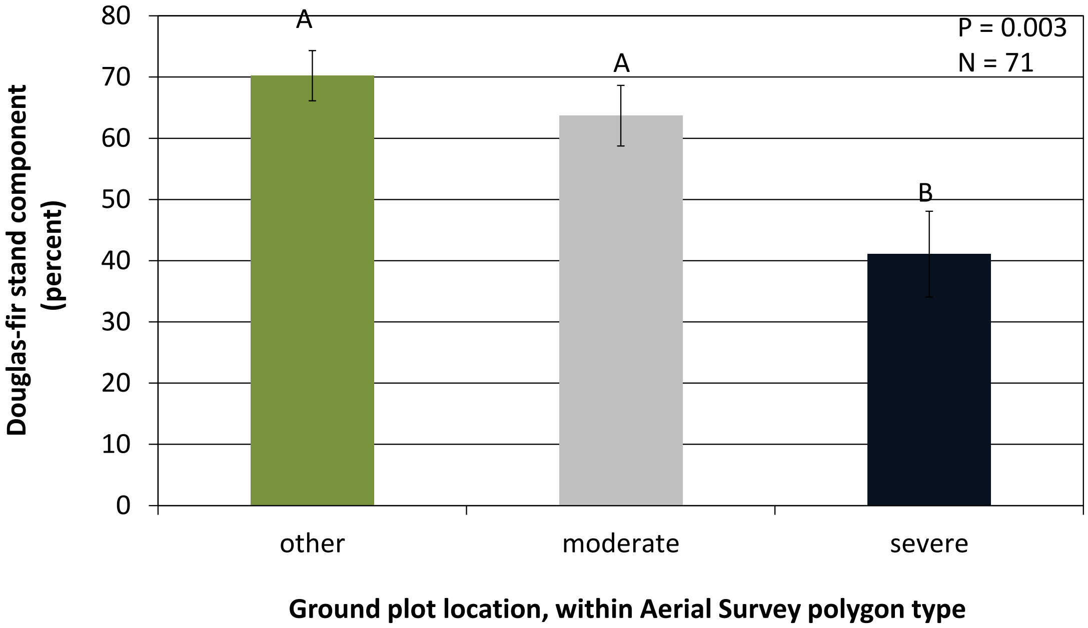


Figure 3. Average foliage needle retention, in years, for Douglas-fir in Swiss needle cast ground survey plots. Other plots were not associated with the SNC aerial survey polygons. Moderate and severe ground plots were associated with either the respective moderate or severe SNC aerial survey polygons. Standard error bars are shown for each bar. Different letters above each bar indicant statistically significant differences at the α ≤ 0.05 level.

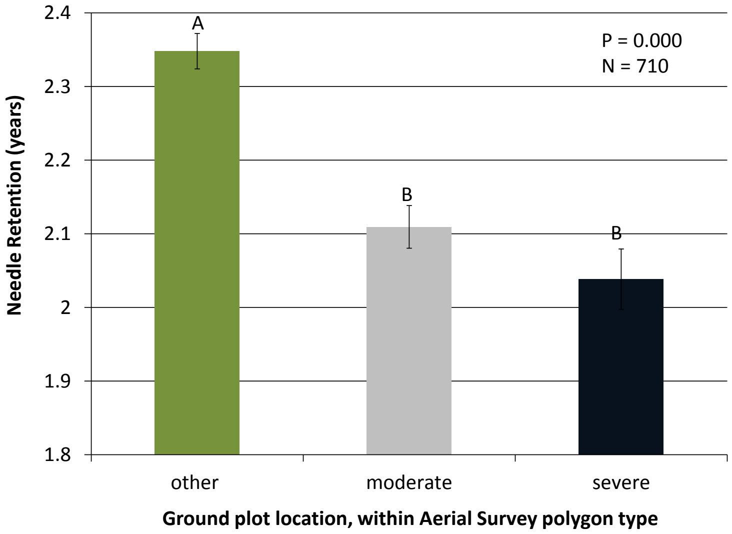


Figure 4. Crown color of Douglas-fir in Swiss needle cast ground survey plots. Other plots were not associated with the SNC aerial survey polygons. Moderate and severe ground plots were associated with either the respective moderate or severe SNC aerial survey polygons. Standard error bars are shown for each bar. Different letters above each bar indicant statistically significant differences at the α ≤ 0.05 level.

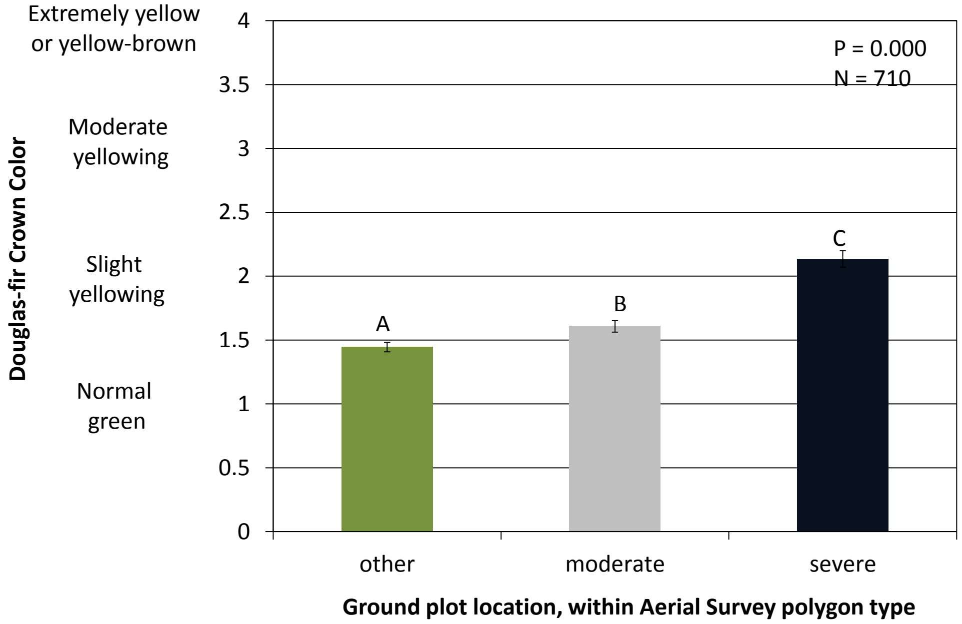


Figure 5. *Phaeocryptopus* incidence (percent pseudothecia occluded stomata) in ground surveyed Douglas-fir stands, by foliage year. Other plots were not associated with the SNC aerial survey polygons. Moderate and severe ground plots were associated with either the respective moderate or severe SNC aerial survey polygons. Standard error bars are shown for each bar. Different letters above each bar indicant statistically significant differences at the α ≤ 0.05 level.

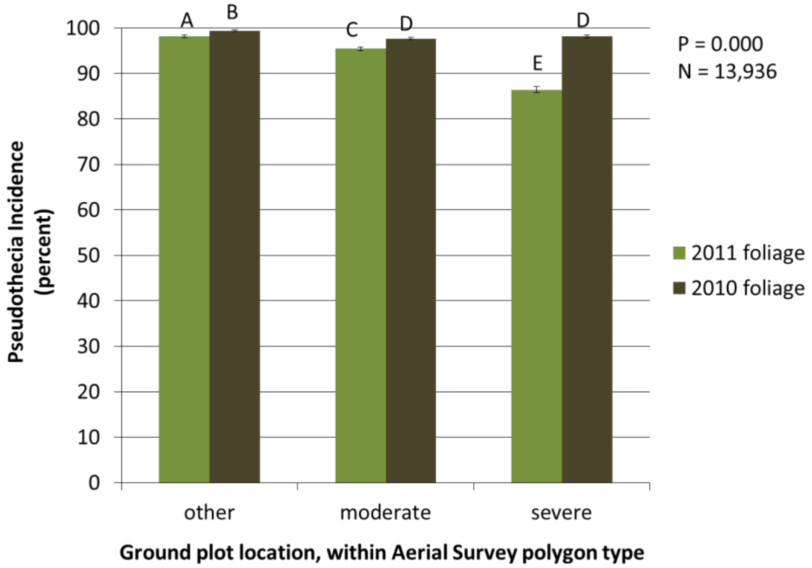
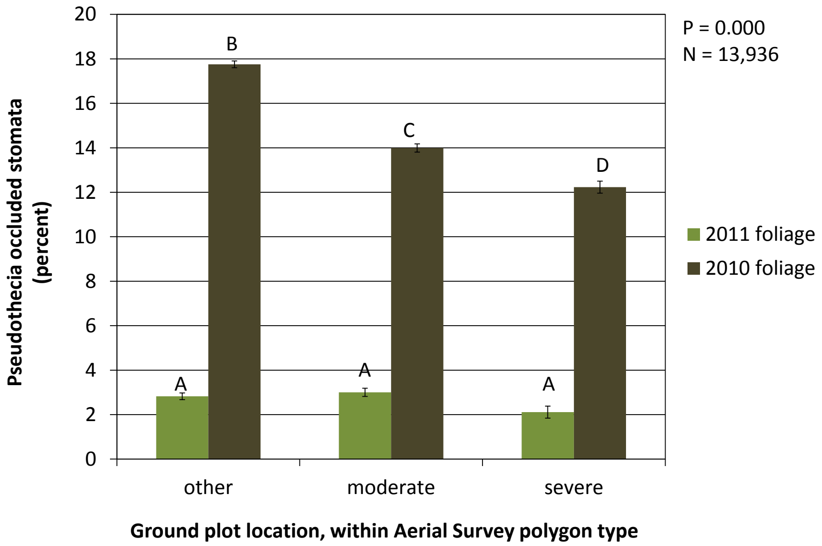


Figure 6. Severity of Swiss needle cast (percent pseudothecia occluded stomata) in ground surveyed Douglas-fir stands, by foliage year. Other plots were not associated with the SNC aerial survey polygons. Moderate and severe ground plots were associated with either the respective moderate or severe SNC aerial survey polygons. Standard error bars are shown for each bar. Different letters above each bar indicant statistically significant differences at the α ≤ 0.05 level.



Impact of Swiss Needle Cast Infection on Tree Carbohydrate Reserves

Brandy Saffell, Oregon State University, Forest Ecosystems and Society
Rick Meinzer, USDA Forest Service, PNW Research Station
David C. Woodruff, USDA Forest Service, PNW Research Station
David C. Shaw, Oregon State University, Forest Engineering, Resources, and Management
Steven L. Voelker, Southern Oregon University, Biology Department
Barbara Lachenbruch, Oregon State University, Forest Ecosystems and Society

Introduction

Trees can accumulate substantial nonstructural carbohydrate (NSC) pools, typically in the form of starch and free sugars. The physiological roles of NSC pools in organs such as leaves, stems and roots remain unclear and are a topic of vigorous debate (Sala et al. 2010, 2012; McDowell 2011; Ryan 2011; Johnson et al. 2012; Wiley and Helliker 2012). In some cases, NSC accumulation may be a purely passive process signifying that the supply of photosynthate exceeds demand from carbon sinks such as growth and respiratory metabolism. In other cases, trees may actively accumulate NSCs to a level that would enhance their chances of survival during prolonged periods of stress.

Because growth is more sensitive to certain environmental stresses than photosynthesis, NSCs often accumulate under moderate to severe stresses such as water deficits (Galvez et al. 2011; Woodruff and Meinzer 2011) and low temperatures (Hoch and Körner 2009). Nevertheless, the concentration of NSC in a plant part may not be indicative of its ability to be mobilized (hydrolysis of starch to sugars) and transported to support growth and respiration.

Recent trends in climate change and concurrent increases in drought-related tree mortality on a global scale have led to many questions and some dispute over the role of carbohydrates as an indicator of overall tree vigor; and more specifically, over their suitability as a reliable indicator of a tree's current demands for photosynthate (Sala et al. 2010, 2012; McDowell 2011, Ryan 2011). A first step towards resolving much of the uncertainty surrounding these issues could be achieved by developing a greater understanding of the different functions that may be performed by NSC that is stored within trees. Much of the uncertainty surrounding the role of stored NSC in maintaining tree survival pertains to the degree to which stored pools of NSC are sequestered (permanently stored and unusable) or whether they are capable of being mobilized when needed by the tree. Sequestration could occur, for example, if enzymes could no longer access NSCs within the xylem (Srichuwong and Jane 2007) or xylem conduits adjacent to parenchyma containing NSCs were embolized, restricting movement of NSCs into the phloem (Quick et al. 1992).

The impact of Swiss needle cast infection on tree NSC pools is unknown, but if NSC accumulation in Douglas-fir has an active component, then this competing sink for photosynthate would exacerbate the impact of SNC infection on growth and other carbon-dependent processes (see above). SNC provides a unique natural experiment to test for the relationship between carbon storage and infection symptoms because infection involves a substantial reduction in carbon assimilation under conditions of low environmental stress. Low water availability or low temperatures can often function as a confounding factor in evaluating the ability of trees to mobilize stored NSC because water stress can strongly impact the supply, demand and transport of carbon within a tree. If NSC pools remain largely undepleted under severe cases of SNC infection, this would provide evidence for prioritization of storage over sustaining growth, or the sequestration of stored NSC. If NSC pools become substantially depleted, this provides evidence for the ability of stored NSC to be mobilized when needed to maintain tree survival.

The goals of this research are: (1) to determine how SNC influences partitioning of assimilated carbon between growth and nonstructural carbohydrate reserves and if differences in infection severity influence relative partitioning of carbon between these two sinks, (2) to identify any seasonal differences in the impact of SNC on partitioning of carbon between growth and reserves, and (3) to establish the extent to which nonstructural carbon can be mobilized under natural conditions of high demand for carbon and low environmental stresses. Based on the previous research, we hypothesize that relative reductions in growth of trees with SNC will be greater than relative reductions in nonstructural carbon reserves and that seasonal fluctuations in nonstructural carbon will be smallest in the most heavily infected trees. We also expect that branches with different levels of infection severity on the same tree will show considerable autonomy with respect to patterns of NSC content, and radial and extension growth.

Methods

We selected a Douglas-fir stand with a range of SNC symptom expression located near Tillamook, Oregon, from an Oregon Department of Forestry unit named Prairie Hill. The stand was initially planted in 1990, with trees successively inter-planted through 1997. We selected trees that ranged in establishment from 1990 to 1995, so the largest age difference between trees would be five years. We sampled 15 trees, with five trees fitting into each of three categories of overall needle retention (0-1.0 years, >1.0-2.0 years, >2.0+ years). Needle retention was estimated in the field by dividing the crown into thirds and averaging the predominant needle retention from each third (Dave Shaw, personal communication). In view of our previous observations showing substantial seasonal variation in NSC content in Douglas-fir trees (Woodruff and Meinzer 2011) we sampled three times over a seasonal cycle: at bud break (late May/early June), mid-summer (mid-July), and late summer (late August/early September). We sampled trunk sapwood tissue with an increment borer to a depth of 2 cm, and leaves and twig sapwood from two branches of each tree, dividing the branches into 2011, 2010, and 2009 growth (2012 growth was sampled in September). We noted needle mass and twig length and width for each growth node from all branches sampled for leaves and twigs. NSC concentrations were assayed in leaves and twig and trunk sapwood tissue using a protocol refined in our laboratory that allows NSC to be expressed in terms of starch, free sugars (sucrose, glucose, fructose) and total NSC in mg g^{-1} dry weight tissue (Woodruff and Meinzer 2011).

To assess tree growth, we took two cores to pith from each tree and measured ring-widths with the program Measure J2X and cross-dated them with COFECHA (Holmes 1983; Grissino-Mayer 2001).

Results

There was an appreciable range in disease symptom expression throughout the Tillamook site (see Table 1).

Tab. 1 Tree characteristics at study site near Tillamook, Oregon. Data include diameter at breast height (DBH, cm), height (m), average basal area increment from 2000-2011 (BAI, cm^2), and average one-year-old needle mass per twig as of June 2012 (g, n=3 per tree). Trees are ordered by ascending average BAI.

Tree ID	Average BAI (cm^2)	DBH (cm)	Height (m)	One-year-old Foliage Mass (g)
7	2.75	9.1	14.0	0.05
3	3.23	9.9	20.1	0.25
1	4.11	10.2	17.9	0.23
13	5.11	12.1	15.9	0.36
5	7.27	11.5	14.5	0.24
10	8.18	14.0	15.4	0.06
8	9.34	10.5	8.7	0.19
14	9.95	12.7	14.7	0.18
2	11.67	18.5	23.1	0.36
9	13.43	13.5	11.0	0.36
15	15.52	21.5	20.6	0.66
4	15.82	18.3	23.0	0.34
12	18.75	19.1	24.1	0.50
6	33.56	25.8	17.9	0.36
11	35.27	21.2	18.4	0.62

There was a highly significant ($r^2=0.80$, $p<0.0001$) positive relationship between trunk NSC concentration and basal area increment (BAI) (see Figures 1 and 2). The slope of the relationship (0.67) suggested that the relative decline in growth was greater than that of NSC with increasing severity of SNC symptoms.

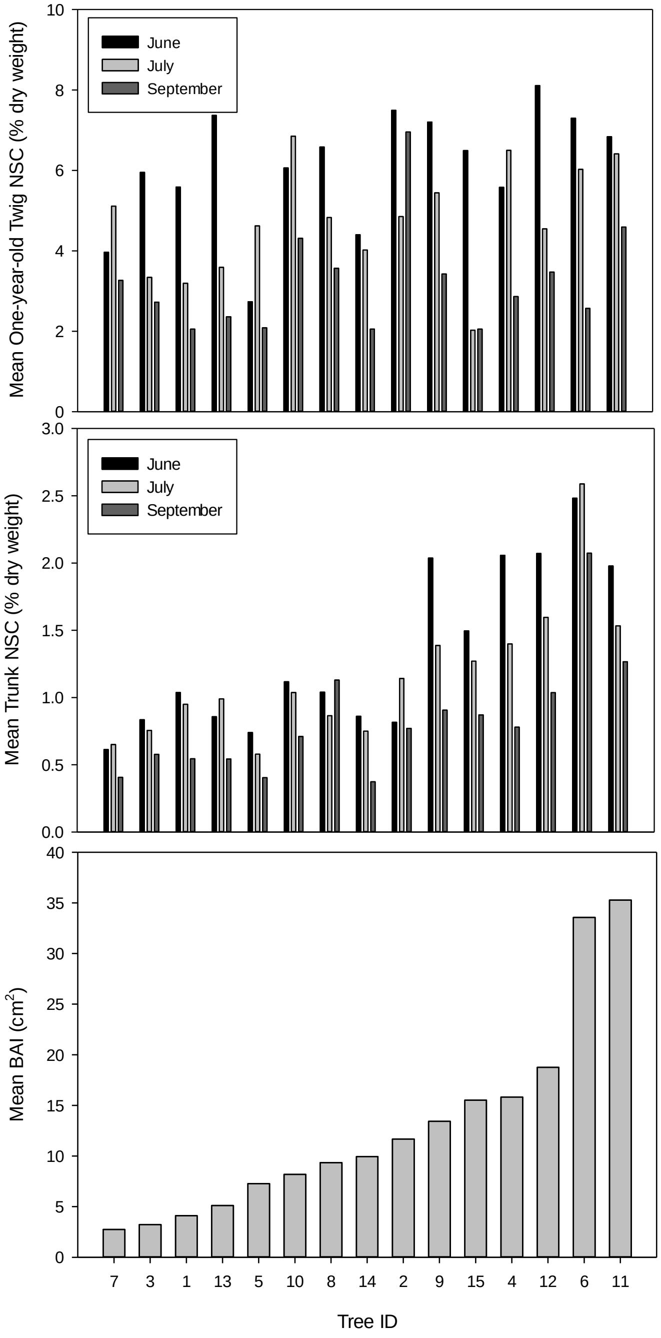


Fig 1. Histogram of mean one-year-old twig and trunk NSC concentration (% dry weight) and mean basal area increment (BAI, cm^2) from 2000-2011 for trees at study site near Tillamook, Oregon. NSC data are from sample trips in June, July, and September 2012.

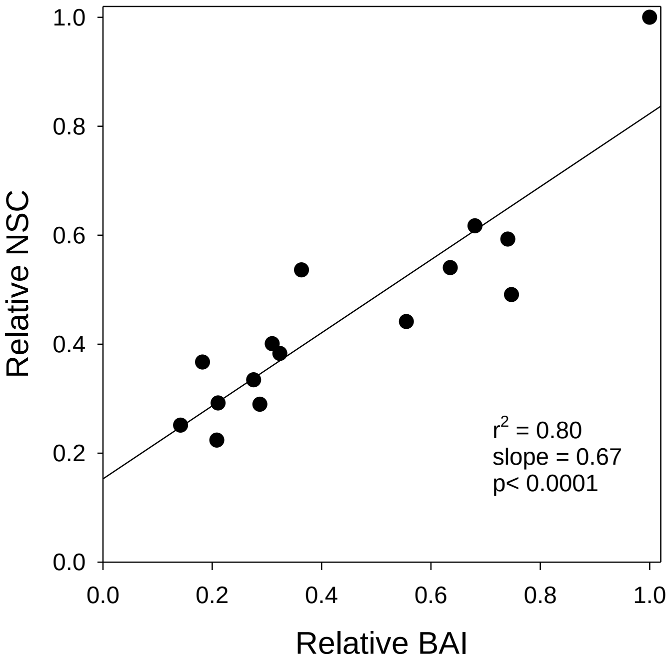


Fig. 2 Scatterplot of relative tree basal area increment (BAI) from 2000-2011 versus mean relative trunk NSC concentration for the three sampling dates (June, July, September 2012) of trees at study site near Tillamook, Oregon. NSC content and BAI were normalized with respect to their maximum values.

It did not appear that the NSC content of one-year-old twigs was affected by disease pressure in the same way as BAI. In contrast, the rankings of trunk NSC content and BAI appeared to be similar. The data suggested that both twig and trunk NSC decreased appreciably over the growing season (see Figure 1).

Discussion

The wide range in disease symptom expression throughout the site will be helpful in identifying the effect of disease on the relationship between growth and NSC abundance/allocation throughout the growing season.

Currently, we have established that trunk NSC abundance varied among trees and was strongly related to mean BAI. This relationship suggests that as disease symptoms increase and BAI concurrently decreases, stem carbohydrate storage is reduced linearly. There were no instances of complete NSC depletion in trunk tissue, which suggests that basal area growth was reduced in favor of maintaining storage carbohydrates, however depleted they may be, or that there was a baseline amount of NSC that was sequestered. There does not appear to be a change in this relationship over the growing season. It is also worth noting that the regression in Figure 2 suggests that growth would reach zero before stem NSC was completely depleted and growth declines more rapidly than NSC when the carbon supply is limited. Thus, it appears that the trees in this study were sacrificing annual growth gain in favor of maintaining a minimum level of NSC.

Stem NSC generally decreased over the growing season, which could be interpreted as the utilization of stored carbohydrates from bud break in June and during shoot extension throughout the summer (Woodruff and Meinzer 2011). Additionally, heavily impacted trees started each season at a disadvantage because their NSC pools in the trunk and branches were smaller.

Although we do not yet have enough information to interpret the lack of a relationship between twig NSC and disease symptom expression, the depletion of twig NSC over the growing season is likely due to the same use of NSC over the season for growth and metabolism that occurs in the stem.

Next Steps

To complete our investigation into the relationship between NSC and growth along a gradient of SNC symptoms over a full growing season, we will extend our data exploration to the rest of the tree measurements, including branch wood and foliage biomass and NSC concentrations, as well as complete a statistical analysis. In addition, we will explore the smaller scale effects of SNC on branch level carbon dynamics within the same tree to better understand the extent to which nonstructural carbon can be mobilized under natural conditions of high demand for carbon and low environmental stresses, as well as identify the potential for branch autonomy.

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Use of tree-ring stable isotopes to quantify Swiss Needle Cast disease severity in Douglas-fir

Brandy Saffell, Oregon State University, Forest Ecosystems and Society

Frederick C. Meinzer, USDA Forest Service, PNW Research Station

Steven L. Voelker, Southern Oregon University, Biology Department

David C. Shaw, Oregon State University, Forest Engineering, Resources, and Management

Barbara Lachenbruch, Oregon State University, Forest Ecosystems and Society

Introduction

Phaeocryptopus gaeumannii was present in the Pacific Northwest before Swiss Needle Cast (SNC) was ever an important disease. The first record of the fungus and SNC appears in the mid-1920s after a severe SNC epidemic of U.S.-imported Douglas-fir in Switzerland (Boyce 1940). It wasn't until the late 1980s that the fungus began causing serious needle loss and growth reductions to Douglas-fir in the United States. Previous research using Douglas-fir tree-ring widths attempted to identify historic SNC epidemics and the cause of the sudden prevalence of the disease in Oregon (Black et al. 2010). Although the study results provided excellent baseline information for understanding the general history and onset of SNC in Oregon, tree-ring widths can be particularly sensitive to numerous confounding environmental variables (e.g. different climate signals, canopy openings, tree injury, etc.) (McCarroll and Loader 2004). These confounding variables could cause the SNC symptom signature in the tree-ring width record to be weak and difficult to isolate. To more accurately quantify past SNC symptom expression in tree-rings, a method is needed that can separate and measure the physiological response of the tree to SNC without significant environmental noise. With this information, it would not only be possible to improve our knowledge of the history of SNC in Oregon, but also to define clearer relationships between SNC symptoms and the climate factors that exacerbate them. As explained below, tree-ring stable isotope signatures should provide an excellent source of such information.

Conceptual approach for using tree-rings to determining SNC infection severity

We are using carbon stable isotope patterns to characterize severity of SNC symptoms. Stable isotopes are non-radioactive and naturally-occurring configurations of elements that differ in their number of neutrons, and therefore atomic mass. The stable isotopes we are discussing here are heavier than the more common isotopes. They are nearly identical chemically, but due to the slight increase in mass, they behave differently in physical, biological, and chemical processes. For example, CO_2 containing heavy carbon (^{13}C) diffuses into the leaf more slowly and therefore will be discriminated against in photosynthesis compared to the most abundant naturally-occurring isotope (^{12}C). Moreover, the primary carboxylating enzyme, ribulose-bisphosphate carboxylase (Rubisco), strongly discriminates against $^{13}CO_2$. Likewise, water molecules containing either heavy oxygen (^{18}O) or heavy hydrogen (D, or deuterium, ^2H) will evaporate less readily and diffuse more slowly once evaporated. Variations in the stable isotope composition of substances such as cellulose in tree-rings are traditionally expressed as delta (δ) values in parts per thousand (‰) with reference to an internationally-recognized standard:

$$\delta = [R_{sample}/R_{standard} - 1] \times 1000$$

where R represents the ratio of the isotopes being studied.

The integration of physical and biochemical processes that determine the $\delta^{13}C$ of plant tissues is shown by the following equation: $\delta^{13}C_{plant} = \delta\ ^{13}C_{air} - a - (b-a)\ C_i / C_a$, where a and b are constants representing isotope fractionation by diffusion into the stomata and by the enzyme ribulose-bisphosphate carboxylase, respectively, and C_i and C_a are the concentration of CO_2 in the leaf-intercellular spaces and in the ambient air, respectively. We know C_a, and we can estimate C_i as: $C_i = C_a - 1.6A/g$, where *A* is the rate of CO_2 assimilation (the photosynthetic rate), *g* is the leaf conductance (stomatal and boundary layer) to water vapor, and 1.6 accounts for the difference in the diffusion coefficients of CO_2 and water vapor in air. Thus, C_i/C_a, and therefore $\delta^{13}C_{plant}$, is a measure of the relative limitation on photosynthesis imposed by stomata. Because C_i/C_a is a ratio, values of $\delta^{13}C_{plant}$ alone do not permit partitioning of variation in C_i/C_a between changes in *A* at constant *g* (e.g. as leaf N content varies), and changes in *g* at constant *A* (e.g. with drought or changing vapor pressure deficit).

Because SNC affects leaf gas exchange in Douglas-fir, there are likely to be changes in $\delta^{13}C$ of carbohydrates in diseased trees. SNC infection starts in newly expanded leaves, but it doesn't affect gas exchange until the pseudothecia start expanding during the fall and through the winter (Stone et al. 2008a). By spring of the year following initial infection, Douglas-fir *A* is reduced via both stomatal limitations (blockage of stomata) and non-stomatal limitations (biochemical effects) (Manter et al. 2000). The physical blockage of stomata will cause a decline in *A*, but a stronger reduction in *g*, such that C_i/C_a should decrease, causing $\delta^{13}C$ to increase (become less negative). This increase in $\delta^{13}C$ should be detectable in the cellulose of Douglas-fir tree-rings.

There are potential limitations to the above hypothesis. Subsequent non-stomatal (e.g. biochemical) reductions in *A* may cause increases in C_i/C_a and thus more negative $\delta^{13}C$ values, though this situation is uncertain and speculative. Additionally, hyphae in the leaf may continue to increase in mass through the summer, causing further decreases in photosynthesis (Manter 2000), which could mean that these needles contribute less to the overall $\delta^{13}C_{plant}$. Another consideration is that in the most extreme cases of infection, nearly all needles on the tree will develop a negative carbon balance (consume more carbon than they fix) and will abscise during the second year of infection (Manter et al. 2003), thus reducing the impact of these needles on $\delta^{13}C_{plant}$. Despite these potential caveats, the effect of the fungus on $\delta^{13}C_{plant}$ should be strong enough to be detected in the wood due to the overwhelming presence and abundance of pseudothecia on diseased trees. As a precaution, we are focusing on the central portion of the tree-ring earlywood and latewood, hereafter referred to as *middlewood*, which will contain cellulose synthesized from sugars produced in spring and early summer. This will likely reduce the influence of abscised needles and increasing fungal presence in late summer.

Finally, variation in tree water status could have an additional, but secondary, influence on $\delta^{13}C$ of cellulose in tree-rings. During dry years, plants will regulate water loss by reducing stomatal conductance, yielding a $\delta^{13}C$ signal in photosynthate that would tend to mimic the signal generated by pseudothecia-blocked stomata. Comparing inter-annual variation in O and C isotopes in tree rings of Douglas-fir and western hemlock thus may allow us to tease apart climatic variables associated with variation in SNC disease severity. To disentangle the impacts of climate and disease on C isotope signals, we are also determining the ratio of heavy to light oxygen ($\delta^{18}O$) in Douglas-fir tree rings and a control species, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). The carbohydrates that become tree ring cellulose carry a signal imparted by the $\delta^{18}O$ of leaf water. Inter-annual variations in the prevailing vapor pressure deficit (VPD) between the leaf interior and ambient air as well as the amount of fog-derived water taken up by roots are expected to cause variation in the $\delta^{18}O$ value of leaf water. Fog is enriched in ^{18}O (the heavy isotope) compared with other precipitation events that recharge the soil water pool so tree rings produced during years with greater fog frequency would be expected to have higher $\delta^{18}O$ values. Douglas-fir needles may be filled with hyphae and stomata can be blocked by pseudothecia. Both of these impediments to normal water flow through infected Douglas-fir needles could influence leaf water $\delta^{18}O$, thus separating this signal from $\delta^{18}O$ in the leaf water and cellulose of western hemlock.

Research goals and broader impact

This research seeks to determine whether tree-ring isotopes can serve as a diagnostic tool for the detection of past SNC infection in Douglas-fir and which climate factors may modify the strength of the signal. We expect to find that the mean $\delta^{13}C$ of tree rings during years of moderate to severe infection will be less negative than the range of $\delta^{13}C$ in years of low to no infection, and thus, render them significantly different and distinguishable within the $\delta^{13}C$ tree-ring record. Previous research shows SNC responds positively to warmer and wetter winter conditions (Rosso and Hansen 2003; Stone et al. 2008b). We therefore expect to find less negative tree ring $\delta^{13}C$ (i.e. greater infection severity) following winters with above average precipitation and temperatures.

The results of this study will improve knowledge of the disease distribution and severity, as well as the ecology and epidemiology of *P. gaeumannii*, ultimately aiding foresters in selecting sites where disease severity will be minimal. If a diagnostic signal of SNC can be identified in the tree-ring stable isotope record, the wood produced in earlier years (e.g. up to 100 years ago, or more) could be studied to better understand the historical context in which the disease developed. In addition, having information about how to use stable isotopes to identify similar pathogens in the tree-ring record will aid future, related studies.

Methods

We are quantifying the impact of SNC on tree-ring $\delta^{13}C$ by examining infected and uninfected trees growing under the same conditions. In practice this is usually very difficult, but from 1996 to 2000, the Oregon Department of Forestry annually applied Bravo fungicide (Chlorothalonil), which reduces fungal infection, to Douglas-firs with SNC at a site near Beaver, Oregon (Hansen et al. 2000). This experimental site should provide an exceptional opportunity to quantify the strength and the timing of the $\delta^{13}C$ signature imprinted by SNC in tree-rings. We sampled trees from the fungicide-treated site in Beaver, Oregon, which is an area known to have severe SNC symptoms. We determined the site severity index using the standard SNC sampling method (Dave Shaw, personal communication). We collected four increment cores (5 mm diameter) from six trees each at the treated and untreated plots. We also collected four cores from each of six trees in a nearby western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) stand to use as a baseline of climate impacts on relative stable isotope values without SNC infection.

To ensure accurate tree-ring dating, we measured the core ring-widths with the program Measure J2X and cross-dated them with COFECHA (Holmes 1983; Grissino-Mayer 2001). Each ring was separated into middlewood and latewood with a scalpel and α-cellulose was isolated following Leavitt and Danzer (1993). Middlewood was determined as the portion of the ring that includes the latter 75% of earlywood and 25% of attached latewood. The $\delta^{13}C$ and $\delta^{18}O$ of the tree-ring cellulose was determined using a stable isotope ratio mass spectrometer (IRMS).

Additionally, we collected wood and foliage from the terminal branches of six trees at a severely SNC-diseased site near Tillamook, OR, to characterize the $\delta^{13}C$ signal closer to the source of carbohydrate synthesis in the tree canopy. The branches were separated into growth internodes from 2012-2009, and then separated into wood and foliage. The tissues were oven-dried and ground to a fine powder, packaged as whole tissue into tin capsules, and analyzed for $\delta^{13}C$ in an IRMS.

Preliminary Results

The average severity index for the site near Beaver was two years of needle retention for both the treated and untreated plots (data not shown).

The average basal area increment (BAI, cm^2) of the treated and untreated plots was similar from 1993 to 1996, but one year after treatment began (1997), BAI in the treated plot was significantly greater than in the untreated plot each year until 2000 (see Figure 1). After 2000, the average BAI of the treated trees steadily decreased until the treated and untreated plots resumed similar annual growth in 2004.

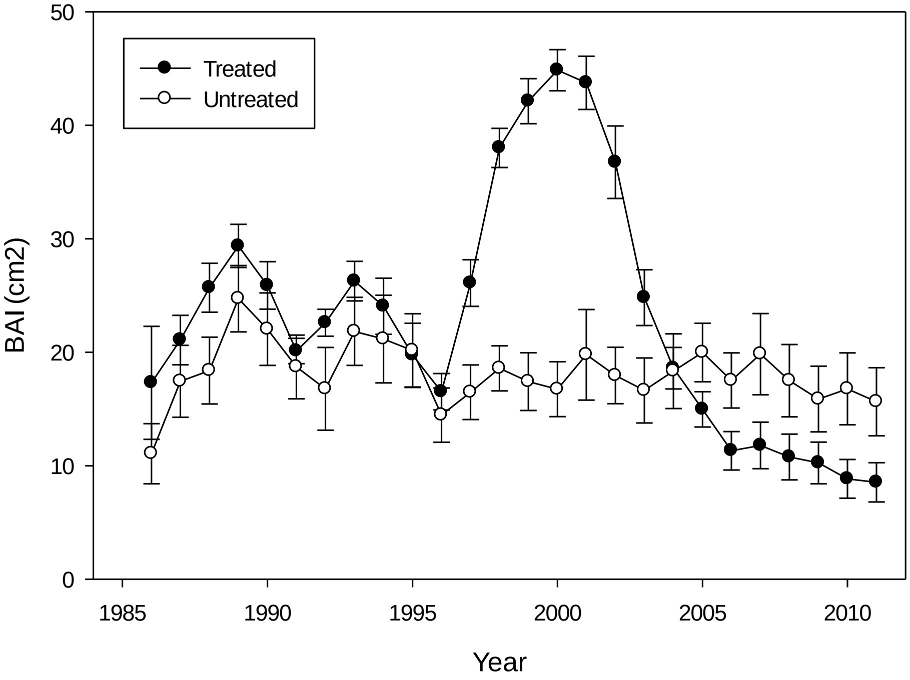

Fig. 1 Average basal area increment (BAI, cm^2) of trees in the treated (sprayed with Bravo fungicide 1996-2000; n=8) and untreated plots (unsprayed 1996-2000; n=7). Vertical lines represent error bars

Figure 2 shows that the average δ^{13}C of branch wood was generally about 2.5‰ greater than foliage δ^{13}C, regardless of tissue age. Both tissues showed increases in δ^{13}C with age such that the average δ^{13}C value of three-year-old tissue was nearly 2.0‰ greater than the value in new, current-year tissue.

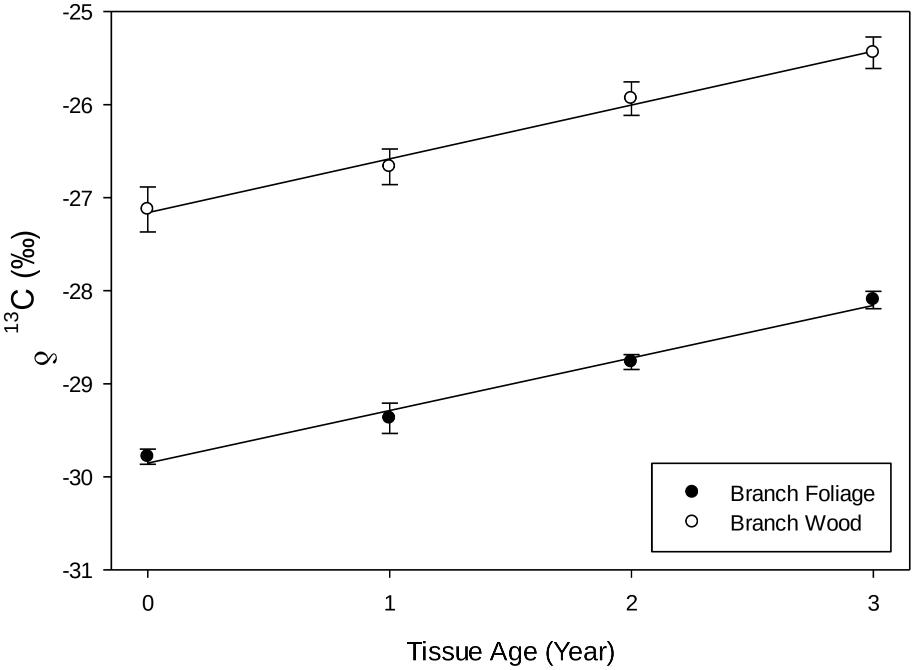

Fig. 2 Average $\delta^{13}C$ of foliage (ages 0-2: n=6, age 3: n=3) and wood (all ages: n=6) tissues from branches of SNC-diseased Douglas-fir trees in Tillamook, OR. The tissue ages range from zero (current year) to three years. The regressions are significant at $p<0.01$.

The preliminary results on the $\delta^{13}C$ of tree-rings (see Figure 3) are means of two trees from each plot type. The final analysis will compare annual $\delta^{13}C$ between plots from 1989 to 2011 for four additional trees in each treatment. Due to similar trends in $\delta^{13}C$ values of latewood and middlewood, we decided to only analyze the middlewood of the rest of the sample set (data not shown). In the years prior to the first Bravo fungicide treatment in 1996, there was no clear difference between the average tree-ring $\delta^{13}C$ values of the treated and untreated plots. In contrast, subsequent treatment years appear to have more negative $\delta^{13}C$ values compared to the untreated plot. Furthermore, treatment effects on tree-ring $\delta^{13}C$ appear to have lagged the fungicide treatment for another three years (2001-2003). By 2004, the $\delta^{13}C$ of treated and untreated plots was nearly identical.

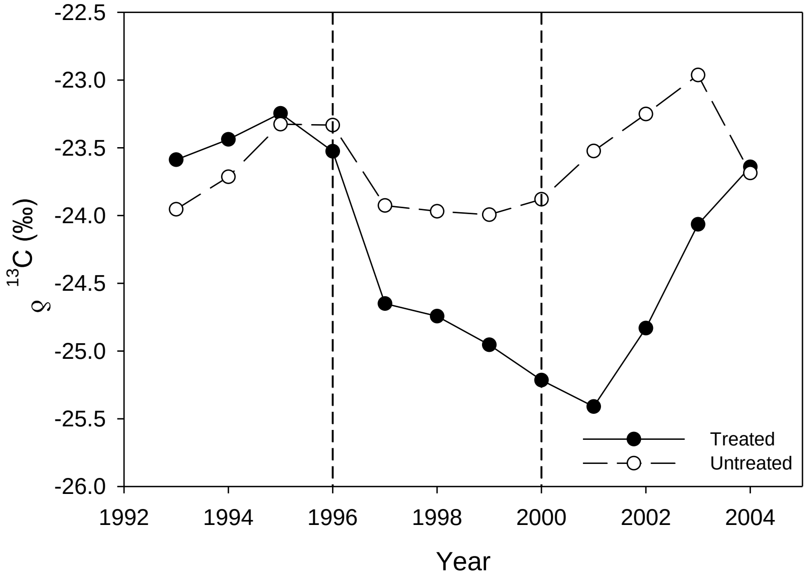

Fig. 3 Middlewodd $\delta^{13}C$ of tree-ring cellulose of SNC-diseased Douglas-fir in Beaver, Oregon. Treated plots (n=2) were sprayed with Bravo fungicide each year from 1996-2000 (indicated by dashed vertical lines), while untreated plots (n=2) were not. Standard error is not indicated due to the limited sample size.

To date, there are insufficient data to determine whether there was a treatment effect on $\delta^{18}O$ values of cellulose from middlewood (Figure 4). Further analyses will be conducted when we receive the data from the remaining four trees sampled in each plot.

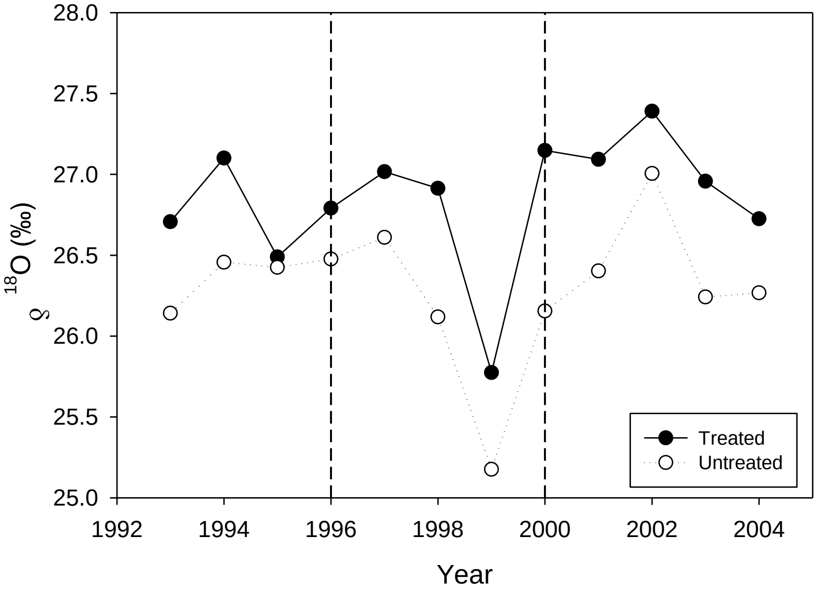

Fig. 4 Average $\delta^{18}O$ of cellulose from tree-rings of SNC-diseased Douglas-fir in Beaver, Oregon. Treated plots (n=2) were sprayed with Bravo fungicide each year from 1996-2000 (indicated by dashed vertical lines), while untreated plots (n=2) were not. Standard error is not indicated due to the limited sample size.

Discussion

On SNC-diseased Douglas-fir, reduction in the fungal load by BRAVO fungicide results in much greater tree-ring widths (Johnson et al. 2003). Our results indicate that the effect on BAI lags the initial treatment by one year but is effective for at least two years following the last treatment. These results are consistent with those of Black and colleagues (2010), who also showed SNC negatively affects tree-ring growth. The apparent one-year lag in tree growth response to Bravo treatment is likely due to the temporal nature of the pathogen life cycle. Because *P. gaeumannii* requires one full year to grow and reproduce within new foliage, the difference in fungal loads, and thus stomatal blockage and reduced photosynthate, between sprayed and unsprayed plots would require one year to manifest.

The branch wood and foliage $\delta^{13}C$ data confirm that *P. gaeumannii* substantially impedes diffusion of CO_2 through the stomata, lowering C_i/C_a, which results in the synthesis of carbohydrates enriched in ^{13}C. The present year growth, 2012, had no pseudothecia-blocked stomata, whereas successively older needles should have more and more pseudothecia until they reach a threshold pseudothecia density at which they abscise. This is likely why the branch wood and foliage tissues become more enriched in ^{13}C with time since initial infection. The branch wood and foliage results further imply that the isotopic signal generated is dominated by increased limitations on diffusion of CO_2 through the stomata rather than increased biochemical limitations on photosynthesis because the latter should lead to increasingly negative $\delta^{13}C$ values with increasing tissue age.

With regard to tree-ring $\delta^{13}C$, the preliminary data suggest that there is a clear difference between trees with and without SNC. Thus, it appears that the effects of the disease on the isotopic signature of carbohydrates synthesized in the leaves can indeed be detected downstream in the cellulose incorporated into the trunk.

Next Steps

We will employ repeated measures analysis of variance on the middlewood $\delta^{13}C$ and latewood $\delta^{18}O$ time-series from both treatment groups and among species with tree as a random factor (SAS Proc Mixed). Simple linear regression models will be employed to compare the relationships among these de-trended ring-widths and their $\delta^{13}C$/ $\delta^{18}O$ signatures as influenced by treatment and period (i.e. pre-spray, spray and post-spray). Differences in slopes or shifts among groups with a common slope will be tested with SMATR software (Warton et al. 2006).

Once we have developed a tree-ring stable isotope record of Swiss Needle Cast severity, we plan to compare the annual $\delta^{13}C$ and $\delta^{18}O$ signatures to records of different climate factors, such as average annual temperature, mean temperatures for each season, total annual and seasonal precipitation, and seasonal fog occurrence. The stable isotope values from co-occurring western hemlock trees will be used to generate a baseline of the impact of climate variables in the absence of SNC infection to compare back to the Douglas-fir stable isotope values, thus enabling the separation of the relative impacts of disease and climate on tree-ring $\delta^{13}C$ and $\delta^{18}O$ in Douglas-fir.

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Response of Ectomycorrhizae to Soil Nitrogen Amendments and SNC Disease Three Years After Treatment, 2012 Update

Daniel Luoma and Joyce Eberhart
Dept. of Forest Ecosystems and Society, College of Forestry, Oregon State University

Abstract

We studied ten sites across a gradient of Swiss Needle Cast disease and measured ectomycorrhizal root density and species richness. Mean root density varied by about 7x among sites, while mean ectomycorrhizal species richness varied by about 4x.

Some normally common ectomycorrhiza types were reduced in frequency on sites highly impacted by Swiss Needle Cast disease. The variable responses of ectomycorrhizal fungi to carbon availability and soil nutrient status provides a context for understanding the strong relationship between ectomycorrhizal richness and needle retention, and why root density exhibits a less consistent relationship to needle retention. We confirmed our previous hypothesis that knowledge of ectomycorrhizal fungal community structure would reveal responses associated with particular fertilizer treatments.

Three years after treatment, the nitrogen (urea) treatment decreased feeder-root density by 62% (p = 0.008), and decreased ectomycorrhiza type richness by 33% (p = 0.047). However, the richness effects varied by block.

For control plots, ectomycorrhizal fungus species richness was significantly correlated with root density; $R^2 = 0.82$, $p = 0.0003$. For urea plots, ectomycorrhizal species richness was not correlated with root density; $R^2 = 0.09$, $p = 0.39$.

For control plots, ectomycorrhizal species richness was significantly correlated with Douglas-fir needle retention; $R^2 = 0.76$, $p = 0.001$. For urea plots, ectomycorrhizal species richness was not correlated with Douglas-fir needle retention; $R^2 = 0.09$, $p = 0.43$.

For control plots, ectomycorrhizal root density was significantly correlated with Douglas-fir needle retention; $R^2 = 0.59$, $p = 0.01$. For urea plots, ectomycorrhizal root density was not correlated with Douglas-fir needle retention; $R^2 = 0.006$, $p = 0.84$.

We speculate that our observations demonstrate a threshold of root density below which mean richness stabilizes at about two ectomycorrhizal types per 350 cc soil core volume.

Introduction

Ectomycorrhizae and Silvicultural Manipulations

Ectomycorrhizal symbioses are formed on about 8000 plant species (Dahlberg 2001), and the current estimate of the number of ectomycorrhizal fungus (EMF) species is 6000 (Molina et al. 1992). Most of the dominant and economically important timber species in the Pacific Northwest are ectomycorrhiza (EM) dependent, including all members of the pine, oak, and birch plant families (Smith and Read 2008). Douglas-fir has about 2000 EMF symbionts throughout its range (Trappe 1977), and will not grow in soil without ectomycorrhizal fungi (Trappe and Strand 1969).

Ectomycorrhizal fungus diversity is an important attribute of forested ecosystems; for instance, stabilizing below-ground processes after disturbances (Perry et al. 1989). Seedlings associated with a high diversity of EMF may be better adapted to disturbance as compared to seedlings with less diversity (Simard et al. 1997). In addition, high EMF diversity seems to increase trees' competitive abilities. A laboratory study supported this hypothesis by documenting that *Pinus patula* seedlings inoculated with two species of EMF grew taller and put on more biomass than seedlings inoculated with only one EMF species (Sudhakara and Natarajan 1997).

Several small studies have suggested a correlation between Swiss needle cast (SNC) disease severity and the nutrient status of both soil and Douglas-fir foliage. Although preliminary fertilization trials have not found evidence of nutritional amelioration of SNC, it is still plausible that imbalanced nutrition may contribute to the susceptibility of Douglas-fir to SNC. Research and experience in agriculture suggests that nutrients are not as available to plants if the soil microbial community is not in a stable and healthy condition (Berg and Smalla 2009). Ectomycorrhiza (EM) communities are particularly influential with respect to nutrient availability and tree nutrition (Smith and Read 2008), so may be influential in predisposition of Douglas-fir to SNC.

Previous Results

In 2006, we determined levels of ectomycorrhizae in forest stands with moderate to high levels of SNC disease (Luoma and Eberhart 2006). In that pilot study, the levels of EM diversity found indicated that the below-ground ecosystem was strongly affected by SNC, by the previous removal of mature trees during timber harvest, by post-harvest silvicultural practices, or by a combination of all three. Comparison of EM diversity in naturally regenerated young stands following stand-replacing disturbances may help separate harvest or natural disturbance effects from those of post-harvest silvicultural treatments.

However, there was also indication that some EM fungi may be "stress tolerators" (*sensu* Grime 1979). Common Douglas-fir EM types, such as *Cenococcum* and *Rhizopogon*, were less widespread in SNC stands than they were found to be in other studies (Eberhart et al. 1996, Luoma et al. 2006, Luoma and Eberhart 2007). Because the trees strongly affected by SNC were mycorrhizal, albeit at low densities, we hypothesized that certain EM fungi had become more predominant on the remaining roots and were filling the important functional roles that EM play in tree nutrition. Studies were undertaken to examine and test the hypothesis that "stress tolerant" EM fungi are important for sustaining Douglas-fir in the face of SNC disease (Luoma and Eberhart 2008)

Rather than a few EM species dominating because they are particularly tolerant of a reduced carbon supply on highly impacted SNC sites, Luoma and Eberhart (2008) hypothesized that they were observing a "survival of the survivors" scenario. They found that stand-level aggregate species richness (exhibiting an approximate 50% reduction) was not impacted as severely as species richness at the level of the individual soil core (exhibiting an 80% reduction).

The highly patchy soil environment may provide opportunities for particular EM species to persist due to each species' unique adaptive advantages in a given location. In addition, the prestress abundance of particular EM species could induce a founder effect that favors EM species that were already locally dominant (at the scale of the soil core). Luoma and Eberhart (2008) demonstrated the potential ecological value conferred by the existence of a high number of EMF that can form mycorrhizae with Douglas-fir. As the stress of reduced carbon flow to the roots asserts it influence, many EMF are available to fulfill the role of "stress-tolerator" in the heterogeneous soil environment.

Luoma and Eberhart (2009) studied a Kinsey blend fertilizer treatment and found no effects, two years after treatment, on either feeder-root density (p = 0.84) or ectomycorrhiza type richness (p = 0.96). The effect of block was significant for both variables (p = 0.02 and 0.009, respectively). Mean root density varied by nearly 8x among sites while mean EM species richness varied by about 3x. That study also found: 1) ectomycorrhiza species richness was significantly correlated with root density; $R^2 = 0.75$, $p = 0.01$; 2) ectomycorrhizal root density was not significantly correlated with Douglas-fir needle retention; $R^2 = 0.41$, $p = 0.12$; and 3) ectomycorrhiza species richness was significantly correlated with Douglas-fir needle retention; $R^2 = 0.70$, $p = 0.02$.

Here, we present results (at the three-year post-treatment point) from the "Beyond Nitrogen" fertilization study. We measured ectomycorrhizal root density and EMF species richness at ten sites across a gradient of SNC disease. Our findings provide an essential component to assess functional fertilizer effects on SNC disease because ectomycorrhizae are the organs through which any nutritional benefits of fertilization are conferred to Douglas-fir trees.

Methods

Ten blocks of the "Beyond Nitrogen" study (Mainwaring et al. 2006, 2007) were sampled (Table 1). The blocks varied by degree of SNC disease symptoms, with average stand-level foliage retention used to quantify disease severity. Ectomycorrhizal roots of Douglas-fir trees from two treatments were obtained:

1) Unfertilized control
2) Nitrogen (202 lbs./acre (230 kg/ha) as urea, Mainwaring et al. 2007)

Table 1. Study sites (blocks) with mean needle retention (2009) of sampled trees.

Land manager	Location	Block code	Retention (yrs.)
Cambell (Menasha[1])	Menasha - north	MNN	1.66
Cambell (Menasha[1])	Menasha - south	MNS	1.92
Cascade Timber	Sweethome	CT	2.60
Hampton	Grand Ronde	HAGR	2.00
Hampton	Knappa	HAK	2.10
Giustina L&T	Pleasant Hill	GIUS	3.00
Oregon Dept. Forestry	Elk City	ODF	2.18
Oregon State University	McDonald Forest	OSU	3.04
Starker	Burnt Woods	STR	2.47
Stimson (Green Diamond[1])	Hemlock	GDH	1.65

[1] Land management at start of study

For the nitrogen treatment, one 350 cc soil core was taken from beneath the canopy of five randomly chosen treatment trees in each block. Seven of the blocks had pre-treatment sampling in 2007. In the three previously unsampled blocks, five randomly selected control trees were also sampled. Five of the trees in five blocks were sampled from the control treatment in 2009. A total of 100 soil cores were used (10 trees/block x 10 blocks) for this analysis. When possible, soil cores were obtained about 15 cm from the marked 2007 soil core location. In a few instances, the location of the previous core could not be determined, in which case the new core was located the same distance from the base of the tree (1m) and on the side of the tree from which the nearest adjacent trees were at the greatest distance, following the same procedures used in previous samples (Luoma and Eberhart 2009).

Methods for measurement of EM were the same as those used in gathering the pre-treatment data (Luoma and Eberhart 2007). Roots from the soil cores were extracted by wet-sieve washing the sample. The contents of the sieve were spread evenly, with enough water to cover the bottom of a 38 x 17 x 2 cm tray that was divided into 36 compartments by an inserted Plexiglas partition (Eberhart et al., 1996). Roots were examined with a stereomicroscope at 15-30X magnification. Each EM type encountered was classified by morphological characteristics, similar to those described in Ingleby et al. (1990) and Goodman et al. (1996), including color, texture, and presence/absence of rhizomorphs and emanating hyphae. Morphotype identities were determined by comparison to the EM character database maintained by J. Eberhart. The total number of ectomycorrhiza types per soil core and total number of mycorrhizal root tips in each core were recorded for ten soil cores from each site. Representative samples of the predominant mycorrhiza types were saved in CTAB buffer for potential molecular analysis of the fungal DNA.

Feeder root density (total number of EM tips per soil core) and species richness (number of EM types per soil core) were used as response variables. The data were used to test for treatment effects and to test for gradient responses to SNC disease. ANOVA was used to test for effects of the nitrogen treatment across ten blocks.

Linear regression was used to examine gradient responses in feeder root density and EM species richness to among-block variation in SNC disease (average tree-level foliage retention rounded to the hundredth of a year). 2009 needle retention data were provided by D.

Mainwaring and were obtained following the methodology described in Mainwaring and Maguire (2008). Mean years needle retention did not require transformation. Linear regression was also used to measure the association between feeder root density and species richness. When necessary, to better meet the assumptions of normality and constant variance, we transformed the dependent variables (Sabin and Stafford 1990). To test for fertilizer treatment effects, feeder root density and EM richness were square-root transformed, as was the case when testing for among-block variation in the response variables and for the linear regression analysis.

Results and Discussion

Three years after treatment, across 10 blocks, the nitrogen (urea) treatment decreased feeder-root density by 62% (control mean = 284 EM root tips/soil core, N mean = 109 EM root tips/soil core; p = 0.008, Fig. 1.), and decreased ectomycorrhiza type richness by 33% (control mean = 3.7 species/soil core, N mean = 2.5 species/soil core p = 0.047). However, the effects varied by block (Fig. 2).

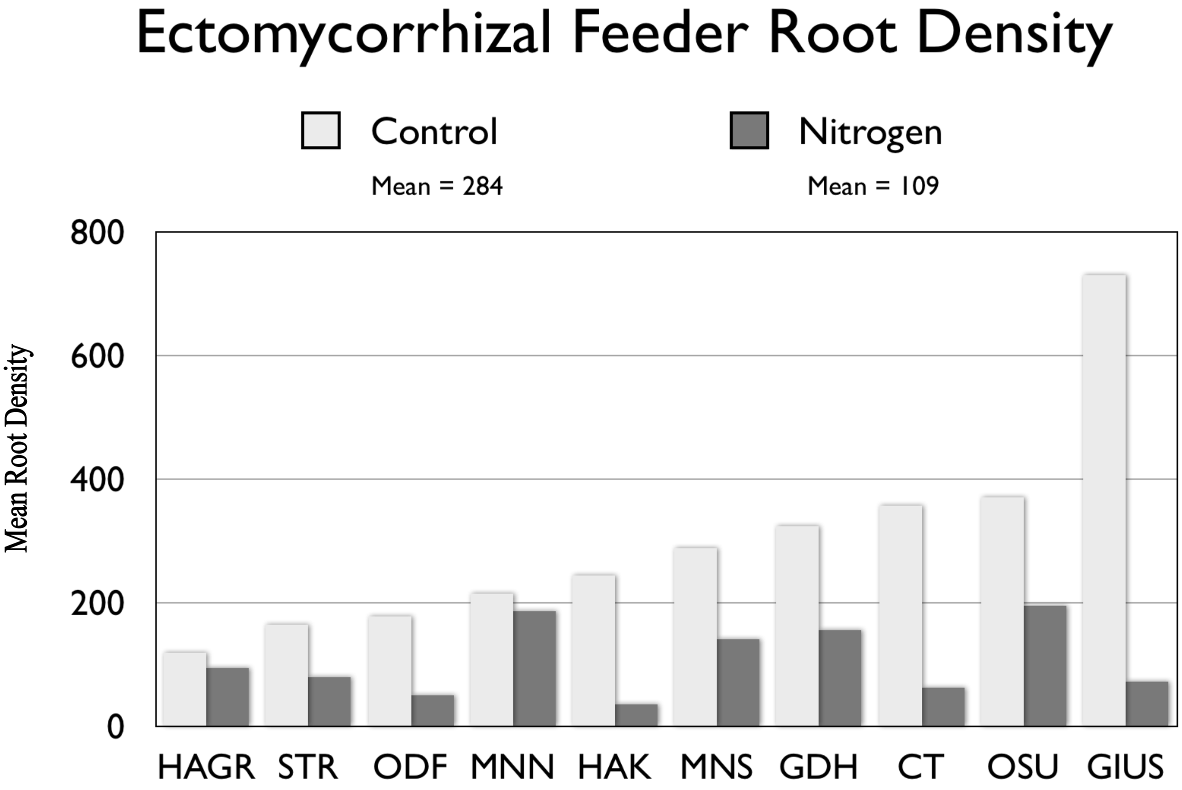

Figure 1. Variation in feeder root density (mean # of ectomycorrhizal root tips/soil core) by treatment across study sites (blocks). Three years after treatment, across nine blocks, the nitrogen treatment decreased mean feeder-root density by 62% (p = 0.0001). Site codes are provided in Table 1.

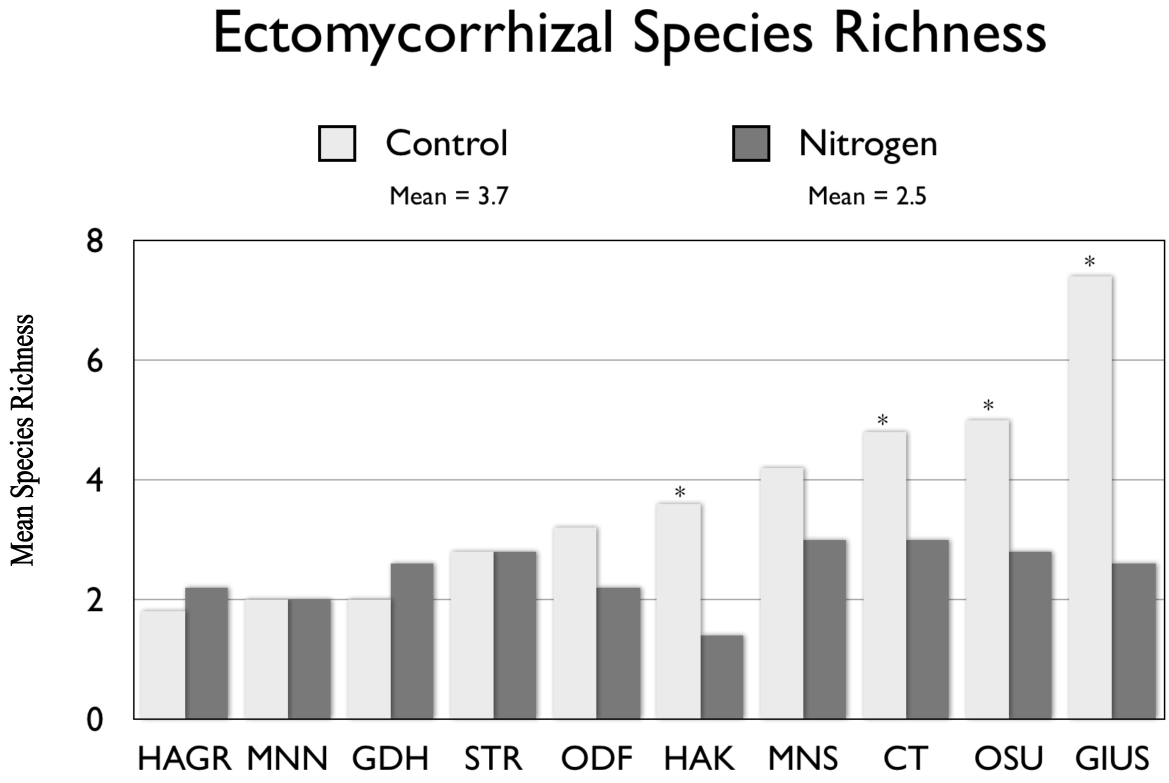

*Figure 2. Variation in EMF species richness (mean # of ectomycorrhiza morhpotypes/soil core) by treatment across study sites (blocks). Three years after treatment, the nitrogen treatment decreased mean species richness by 33% (p = 0.047). However, the effects varied by block; sites with significant differences are indicated by a *. Site codes are provided in Table 1.*

The one-time application of N (as urea) in our study, at a rate of 230 kg/ha, is at the high end of application rates for which EM responses have been reported. The reduction in ectomycorrhizae found here closely mirrors the results of Nilsson and Wallander (2003) who found that EM fungi produced about 50% less mycelium in the soil after N fertilization of 100 kg/ha/yr (as ammonium sulfate) for ten years. Kårén and Nylund (1997) found a 49% reduction in EM root biomass associated with N fertilization of 100 kg/ha/yr (as ammonium sulfate) for six years prior to sampling. Conversely, Jonnson et al. (2000) found that moderate nitrogen (as ammonium nitrate) additions of 35 Kg/ha/yr for four years had little effect on EM root tip density.

For the control treatment, ectomycorrhizal fungus species richness was significantly correlated with root density; $R^2 = 0.82$, $p = 0.003$ (Fig. 3). For the nitrogen treatment, ectomycorrhizal species richness was not correlated with root density; $R^2 = 0.02$, $p = 0.76$.

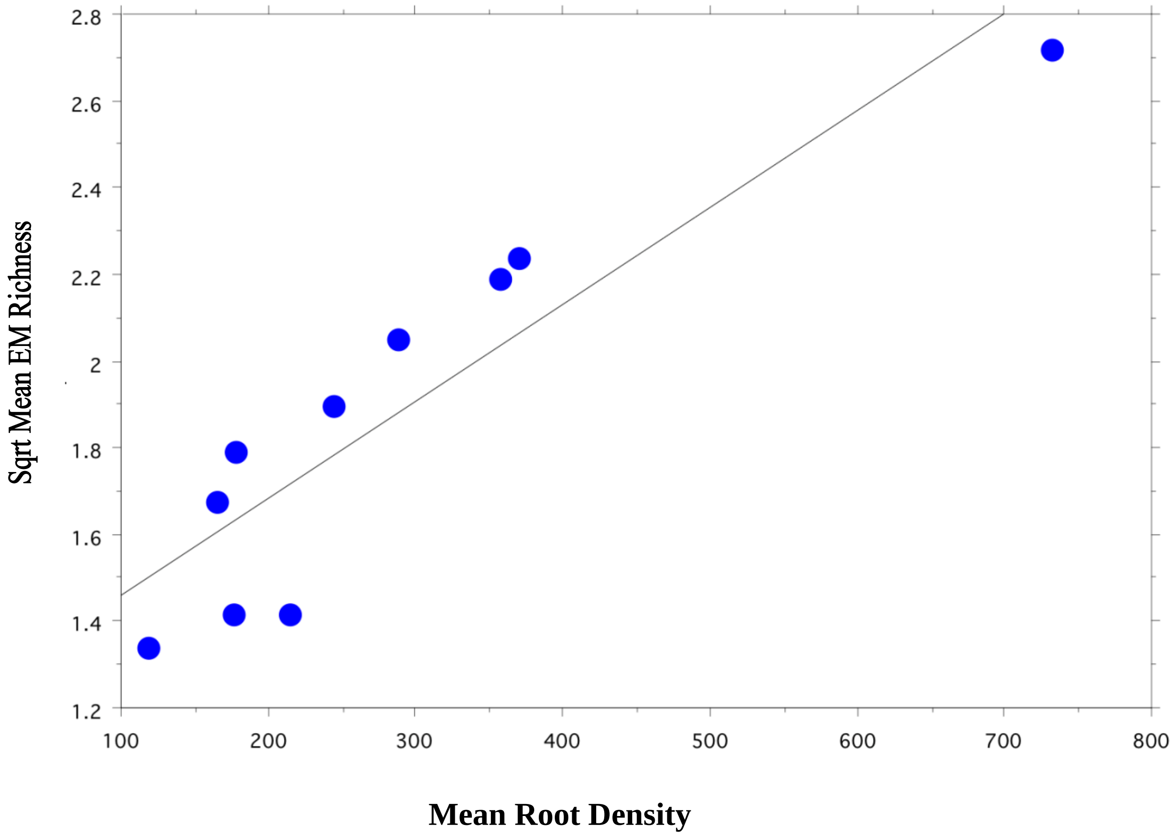

Figure 3. Control treatment regression of mean ectomycorrhiza species richness (square-root transformed) against mean root-tip density (# of EM tips/soil core), $Y = 1.237 + .002 * X$; $R^2 = 0.82$ ($p = 0.0003$, $n = 5$).

For control plots, the regression relationship between EM richness and root density remained similar to past values, even though two highly impacted SNC sites were added to the analysis (2007: $R^2 = 0.65$, 2009: $R^2 = 0.75$, 2010: $R^2 = 0.74$). The nitrogen treatment eliminated that correlation. Mean root densities under the nitrogen treatment trees ranged from 40 to 200 EM tips/soil core and species richness ranged from two to seven EM types/soil core. Though there is a strong correlation between root tip density and EM species richness over a range of densities, including mean values as high as 1200/soil core (Luoma et al. 2006, Luoma and Eberhart 2009), at the low root densities imposed by the nitrogen treatment, mean EM species richness fell to a low value (2.5/soil core), with no correlation over the range of root densities. We speculate that the data show a threshold effect at about 200 EM tips/soil core (< 1 tip/cc soil volume), below which EM species richness stabilizes (Figs. 1 and 2). The apparent stability may simply reflect the physical limit of EM richness to drop below 1, as long as live EM roots are present.

For control plots, ectomycorrhizal root density was significantly correlated with Douglas-fir needle retention; $R^2 = 0.59$, $p = 0.01$ (Fig. 4). For urea plots, ectomycorrhizal root density was not correlated with Douglas-fir needle retention; $R^2 = 0.006$, $p = 0.84$.

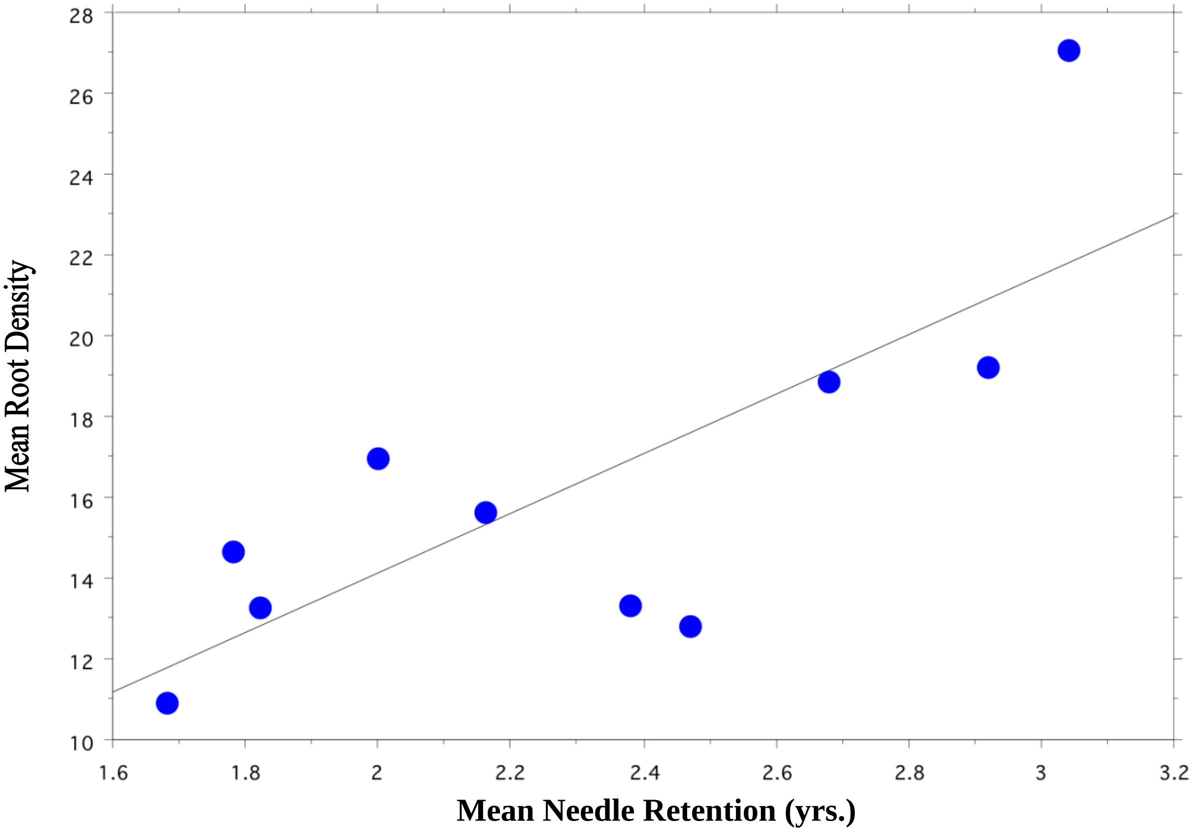

Figure 4. Control treatment regression plot of mean ectomycorrhiza root density (square-root transformed) against mean years needle retention, $Y = 0.592 + 7.358 * X$; $R^2 = 0.59$ *(*$p = 0.01$, $n = 5$*).*

For control plots, ectomycorrhizal species richness was significantly correlated with Douglas-fir needle retention; $R^2 = 0.76$, $p = 0.001$ (Fig. 5). For urea plots, ectomycorrhizal species richness was not correlated with Douglas-fir needle retention; $R^2 = 0.15$, $p = 0.40$.

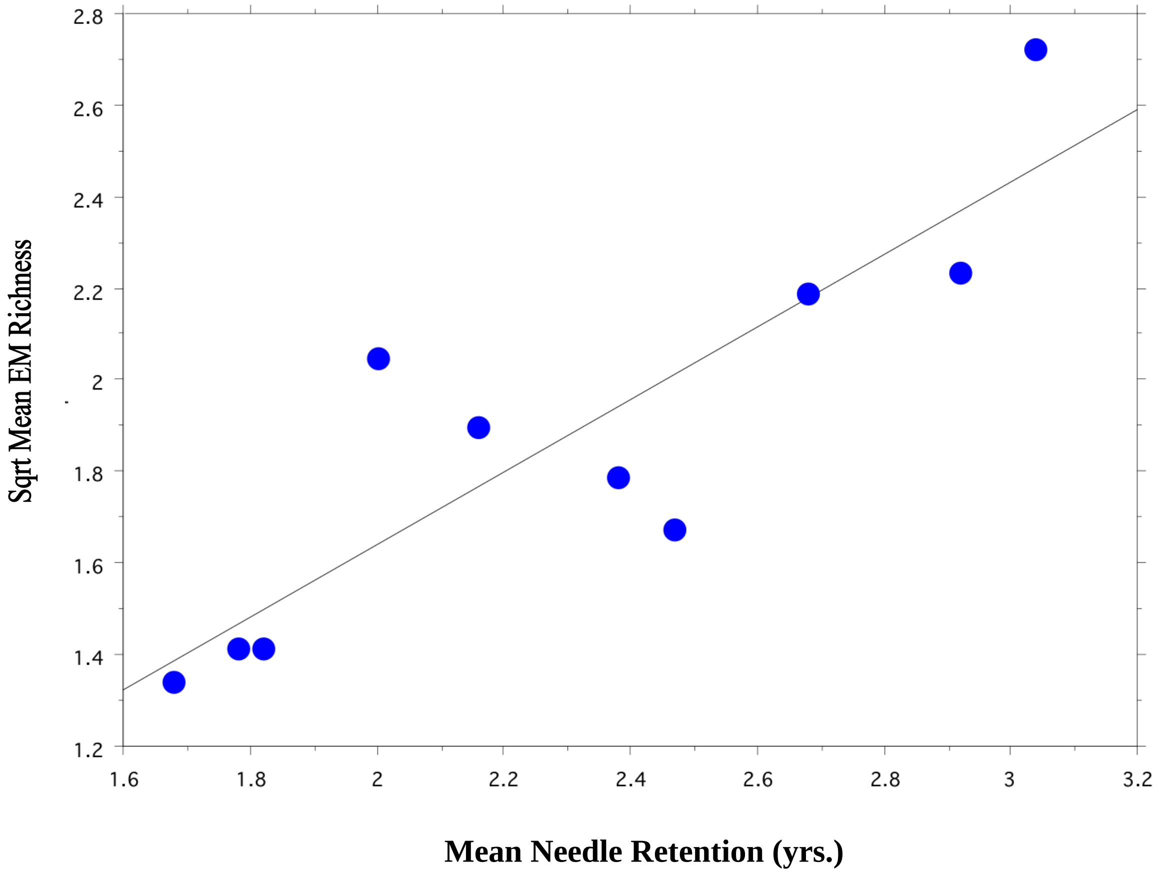

Figure 5. Control treatment regression plot of mean ectomycorrhiza root density (square-root transformed) against mean years needle retention, $Y = 0.061 + 0.79 * X$; $R^2 = 0.76$ ($p = 0.001$, $n = 5$ in each block).

Although EM type (species) richness was significantly related to needle retention in the control treatment samples (Fig. 5), the strength of the relationship was far less than we found in 2007 ($R^2 = 0.90$) or 2008 ($R^2 = 0.93$). This may well be related to the blocks having fewer samples per treatment than in the past sampling efforts. In addition, the MNS site was something of an outlier with higher than expected EM species richness, given the level of SNC disease on the site. The correlation between root density (EM habitat availability) and species richness helps explain the lack of a significant regression between EM richness and needle retention in the nitrogen treatment plots. Low root densities associated with nitrogen fertilization across the range of retention (Fig. 2) limited the opportunities for EM fungus species to colonize roots. There was a striking difference in the correlation coefficients for root density vs. needle retention between the control and N treatments. For the control treatment, the correlation coefficient was

0.59 while the N treatment had a correlation of 0.001. This suggests stronger absolute changes in response to nitrogen at higher root densities (see also Fig. 1).

Fertilizer effects on ectomycorrhizal fungi are varied and complex. Arnebrant and Soderstrom (1992) found that a one-time fertilization with 600 kg nitrogen ha^{-1}, 13 years prior to study, produced no difference in the total number of ectomycorrhizal root tips. However, yearly application of 30-80 kg nitrogen ha^{-1} over a period of 15 years, was associated with 20% fewer mycorrhizal roots. Other aspects of fertilization effects on EM were examined by Nilsson and Wallander (2003). They found that the addition of phosphorus ameliorated negative effects of nitrogen addition alone on mycelia growth of EM fungi.

The carbon sink strength of EM fungi varies and is affected by nutrient additions. In a study of four EM fungi, Bidartondo et al. (2001) found that response to calcium phosphate addition (as apatite) was reflected in biomass accumulation, while nitrogen addition (as ammonium) was associated with increased respiratory activity. They also noted that fungi with relatively low carbon sink strength may be poor competitors when carbon is limited. We have shown that the presence of *Cenococcum* is reduced on highly impacted SNC sites (Luoma and Eberhart 2008), which, in light of Bidartondo et al.'s (2001) results, indicates that *Cenococcum* may be poorly adapted to compete for a greatly reduced carbon supply.

The variable responses of EM fungi to carbon availability and soil nutrient status provides a context for understanding the strong relationship between EM richness and needle retention, and illuminates why root density, *per se*, exhibits a less consistent relationship to needle retention. Our finding of mass proliferations of single-species clusters of mycorrhizae provides a good example of how those different responses can be manifested in the soil. Mycorrhizae are a strong carbon sink for recent photosynthate (Norton et al. 1990). Reduced carbon to the roots should result in a shrinking pool of potential EM symbionts that can successfully maintain the symbiosis.

The response variables that we measured were significantly affected by the nitrogen treatment. This strongly demonstrated that characteristics of the EM community can be used to monitor forest health and are useful in predictive models. We confirmed our previous hypothesis that knowledge of EMF community structure would reveal responses associated with particular fertilizer treatments (Luoma and Eberhart 2009).

Acknowledgements

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Six-year growth response of young Douglas-fir to nitrogen, calcium, phosphorus, and blended fertilization treatments in Oregon and Washington

Doug Mainwaring, Oregon State University
Doug Maguire, Oregon State University
Steve Perakis, USGS-FRESC

Abstract

Management of forest nutrition in Douglas-fir plantations has predominantly addressed nitrogen limitations, yet growth of Douglas-fir is often unresponsive to nitrogen fertilization. High soil nitrogen availability and harvesting of second and third generation stands has raised the potential for other nutrient limitations, and nutrient imbalances have been hypothesized to predispose young Douglas-fir to Swiss needle cast. Six fertilizer treatments were tested for their ability to improve the growth of dominant and co-dominant trees within young Douglas-fir plantations in western Oregon and Washington. Treatments included a control and applications of urea, lime, calcium chloride, or mono-sodium phosphate on 16 experimental installations. Two additional site-specific blends (Fenn and Kinsey) were applied at 12 of the 16 the installations (One of these sites has been subsequently harvested). On 10 of the remaining 15 sites thus far measured this fall, stem volume growth responded marginally to the Kinsey treatment in the second 3-yr period after treatment. On this subset of sites, there is no evidence of a positive response to the other treatments in the second period following fertilization. Nevertheless, because some of the as-of-yet unmeasured sites were influential responders during the first three-yr remeasurement, anything other than site-level conclusions are premature.

Introduction

The three-year remeasurement of the Beyond N field trials indicated that dominant/codominant trees exhibited a marginal positive stem volume response to nitrogen, lime, and phosphorus fertilizers, but were unresponsive to applied blended fertilizers (Mainwaring et al. 2010). Though the initiation of the study was partially motivated by an interest in exploring whether these fertilizer treatments might induce improvements in foliage retention or tree growth within Swiss needle cast-infected stands, there was no evidence that this occurred. Further evidence that these treatments did not improve the condition of infected trees came from a study which found that pseudothecial density within the needles of treated trees didn't vary by fertilizer treatment (Mulvey et al. 2012).

Methods

Study sites

Sixteen study sites were distributed across a range in elevation, aspect, and SNC disease severity in the Oregon and Washington Coast Ranges and west slope of the Cascade Mountains (43.28° to 46.60° N and 122.05° to 124.25° W; Fig. 1). The GDE site has been subsequently harvested as part of the State Highway 20 construction project. Target stands were 20 years of age, contained 750 tph, and received no previous thinning or fertilization treatments (Table 1).

Figure 2. Location of the 16 study sites in OR and WA

Sites received either seven treatments (twelve sites) or five of the original seven treatments (four sites) (Table 1). The five fertilization treatments common to all 16 sites included the following fertilizers and rates (Table 2): 1) untreated control with no fertilizer; 2) nitrogen (225 kg N ha^{-1} as urea); 3) calcium (1020 kg Ca ha^{-1} as lime, intended to provide calcium and increase soil pH); 4) calcium (105 kg Ca ha^{-1} as CaCl$_2$, intended to provide calcium with minimal influence on soil pH), and 5) phosphorus (580 kg P ha^{-1} as monosodium phosphate). Sites with seven treatments received these five core treatments and two additional site-specific blends. The Kinsey blend was based on an analysis of soil chemistry and targeted a specific base cation saturation ratio (McLean et al. 1983). Attaining this ratio typically necessitated a multi-year application regime. The Fenn blend was based on foliar chemistry and entailed a single application of a blended fertilizer (George Fenn, personal communication). The Kinsey regime called for addition of N, P, S, B, Cu and Ca (as lime) on all 12 sites; dolomitic lime on 11 of the sites; Zn and Fe on nine of the sites; Mg on eight of the sites; K on six of the sites; and Mn on one of the sites (Table 3). The Fenn blend called for addition of nitrogen on all 12 sites; K, Mg, and S on 11 sites; Ca on ten sites; and Zn on two sites (Table 4).

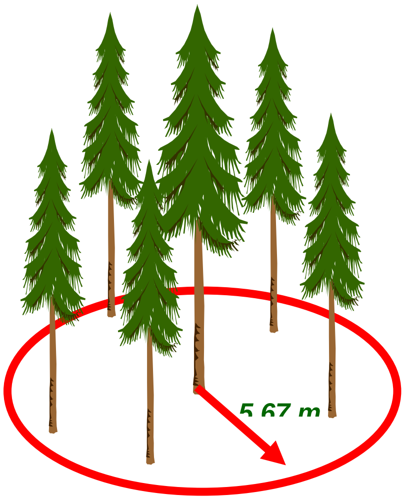

Figure 1. Schematic of the individual tree plot

Treatments were ground applied on fixed-area plots (0.01 ha; radius=5.67 m) centered on an undamaged, dominant or co-dominant "measurement" tree (Fig. 2). Suitable measurement trees were selected on a 20 m grid, skipping grid points if no suitable subject tree was available. Treatments were randomly assigned to ten trees per treatment per site, and fertilizer treatments were applied during February-April 2007. The Kinsey regime was spread prescriptively over two years, with non-lime materials applied during February-April 2007 and lime applied during the winter of 2007-2008.

Measurements

The following dimensions were recorded for all measurement trees prior to the 2007 growing season, and after the 2009 and 2012 growing seasons: dbh (nearest 0.1 cm), height (nearest 0.1 m), height to lowest live branch (nearest 0.1 m), breast-height sapwood width (nearest 1 mm), and diameter at 5.5 m of height (nearest 0.1 cm). All trees within the treated fixed-area plots were also measured for initial dbh (nearest 0.1 cm). To standardize foliage sampling, the southernmost branch in the fifth whorl from the tip of the tree was identified and the largest 4-yr-old lateral was removed from this branch on each tree for estimating foliage retention and analyzing foliar chemistry. The samples for foliar chemistry were a composite sample of 1-yr foliage from trees receiving the same treatment at a given site.

Two soil cores of mineral soil only (10 cm) were collected from opposite sides of each sample tree, perpendicular to the slope. Soil cores collected for all trees receiving the same treatment were pooled and fully mixed, and a small quantity was subsampled for chemical analysis. Foliar and soil sampling were repeated in the fall of 2007 and 2009, after the end of the first and third growing seasons since treatment.

For this report all sites were measured with the exception of GDE (harvested), HAK, MNN, MNS, WE, and WW.

Table 1. Average tree and stand attributes for the 16 installations comprising the Douglas-fir fertilization trials.

	Tree attributes						**Plot attributes**	
Plot	**Quadratic mean dbh (cm)**	**Height (m)**	**Crown ratio**	**Foliage retention (yrs)**	**Breast height age (years)**	**Bruce's site index(m @ 50 yrs)**	**Douglas-fir trees per ha**	**Douglas-fir basal area (m^2/ha)**
CTC	27.9	23.1	0.57	3.38	23	41.8	977	35.4
GDE	39.1	28.1	0.51	2.77	27.1	46	512	43.4
GDH	29.2	21.1	0.64	1.62	19.8	41.3	724	32.6
GPH	23.4	17.2	0.64	3.64	15	47.5	921	24.9
HAGR	27.2	16.6	0.75	2.22	15.9	46.5	683	27.9
HAK	32	23.9	0.6	2.36	21.8	46.9	630	37.3
LRT	36.8	22.6	0.65	3.35	21.1	43.1	435	36.3
MNN	27.4	17.8	0.7	2.22	13.3	54.1	782	31.4
MNS	29.5	20.9	0.61	2.66	20	46.6	768	33.9
ODF	25.9	16.9	0.69	2.34	14.7	48.9	877	30.2
OSU	25.9	18	0.67	3.31	14.8	46.9	819	32.6
PB	26.4	21.5	0.47	3.41	20.4	45.1	1186	36.5
STR	29.2	20.2	0.65	2.71	17.7	48.7	754	35.8
WE	19.6	12.9	0.71	2.13	13	44.1	1544	31.4
WF	35.1	20.2	0.79	3.65	20	42.7	476	39.7
WW	29.5	23	0.59	2.28	28.4	36.2	708	35.4

Table 2. Materials and rates of application for seven treatments in the fertilization trials.

Treatment	**Material**	**Material application rate (kg/ha)**	**Elemental application rate (kg/ha)**
Control	-	0	0
Nitrogen	Urea: $(NH_2)_2CO$	493	225
Lime	$CaCO_3$	2915	1020
Calcium chloride	$CaCl_2$	291	105
Phosphorus	Mono-sodium phosphate: NaH_2PO_4	2240	580
Kinsey	see Table 3	see Table 3	
Fenn	see Table 4	see Table 4	

Table 3. Materials and rates of application for the Kinsey fertilization regime.

Material	WF	CTC	HAGR	STR	GDE	GDH	PB	OSU	ODF	MNN	MNS	HAK	Mean
Fertilizer application rates (kg/ha)													
Mono-ammonium phosphate	255	255	255		255	255	255	255	255	255	255	255	234
K_2SO_4	204	509	127			127	178	433					132
Sulfur	97	107	92	97	92	97	97	97	92	87	97	81	94
Boron	15	15	15	15	10		15	15	10		5	7	10
$ZnSO_4$	20		20	20	15	20	10	10	20	20			13
$CuSO_4$	20	10	10	20	31	20	20	20	25	25	25	25	21
$FeSO_4$		407	331		407		407	433	407	407	407	407	301
Potassium magnesium sulfate	407		305			305	764		407	330	407	407	278
$MnSO_4$						102							9
$MgSO_4$					305								25
Calcium lime	356	4939	1935	2851	1222	1222	967	2138	2291	967	2291	1527	1892
Dolomitic lime	1222	4226	2749	2546	3055	3157			2189	3259	1731	2138	2627
Elemental application rates(kg/ha)													
N	134	31	31	0	31	31	31	31	31	31	31	31	28
P	69	69	69	0	69	69	69	69	69	69	69	69	63
K	166	228	113	0	0	113	220	194	74	60	74	74	110
S	224	279	250	97	261	209	381	265	269	247	269	255	250
Ca	135	1877	735	1083	464	464	367	812	871	367	871	580	719
Mg	204	549	391	331	459	444	84	0	329	460	270	323	320
Mn	0	0	0	0	0	29	0	0	0	0	0	0	3
B	2	2	2	2	1	0	2	2	1	0	1	1	2
Zn	7	0	7	7	5	7	4	4	7	7	0	0	5
Cu	5	2	2	5	7	5	5	5	6	6	6	6	5
Fe	0	85	70	0	85	0	85	91	85	85	85	85	63

Table 4. Materials and rates of application for the Fenn blended fertilization.

Material	WF	CTC	HAGR	STR	GDE	GDH	PB	OSU	ODF	MNN	MNS	HAK	Mean
Fertilizer application rates (kg/ha)													
ESN (slow release N)	534	33	190	155	334	334	190	67	67	601	785	190	290
Potassium magnesium sulfate	637		382	382	764	764	382	255	255	448	240	382	
Gypsum			280	117	700	700	280	351	351	84	534	280	408
Ammonium sulfate		467	47				47					47	51
ZnSO4										307	157		
Elemental application rates (kg/ha)													
N	203	111	82	59	127	127	82	25	25	228	298	82	121
K	117	0	70	70	140	140	70	47	47	82	44	70	75
S	140	112	148	106	301	301	148	123	123	176	185	148	168
Ca	0	0	64	27	161	161	64	81	81	19	123	64	70
Mg	70	0	42	42	84	84	42	28	28	49	26	42	45
Zn	0	0	0	0	0	0	0	0	0	124	64	0	17

Analysis

Response to fertilization was based on differences in stem volume growth (Bruce and Demars 1974) during 1) the second three-year period (3yr), and 2) the entire period following fertilization (6yr). Treatment effects were tested by analysis of covariance under a generalized randomized complete block design. Covariates included within the analysis included those related to initial tree size and local stand density. Tests were considered statistically significant at α=0.05, and variables were included in the final models at this same α-level. In some cases, where noted, variables with marginal significance ($0.05< \alpha <0.10$) were retained in the models. Treatment effects on volume growth were first tested at the regional level. Significant treatment effects were further explored by testing for volume growth differences within site.

All sites were included to test for urea, lime, calcium chloride, and phosphorus fertilization effects, but fewer sites were available for testing the Kinsey regime and Fenn blend. Replication within sites allowed for identification of site-specific treatment effects.

Results and Discussion

When data from all 2012-measured sites were analyzed as a generalized randomized complete block experiment with initial diameter and plot-level basal area as covariates, site was a significant factor but neither treatment nor site*treatment interactions were significant. Nevertheless, across all measured sites, the Kinsey treatment was associated with marginal increases in 3-yr stem volume response (3yr: p=0.095 (6.4%)), suggesting that trees may be responding to the lime-heavy blend. When analyzed on a site-by-site basis, significant or marginal response to the Kinsey blend was apparent at only one site (ODF, 3-yr: p=0.024; 6-yr: p=0.070). The ODF site is relatively coastal, exhibiting symptoms of SNC (foliage retention: 2.34 yrs), and had one of the lowest soil calcium concentration within the datasets (241 ppm). Trees at the ODF site also responded positively to urea (p=0.0018), calcium chloride (p=0.092), and the Fenn blend (p=0.0021) during the second-three year period, though none of the four treatments were associated with a significant response during the first three-year period.

Other significant positive site-level responses over the six year period of the study include urea and lime at CTC (p=0.035 and 0.022 respectively), urea and Fenn at ODF (p=0.025 and 0.018 respectively), and urea at GPH (p=0.077). Fenn at GDH was associated with a negative 6-yr stem volume growth response (p=0.004).

The obvious similarity between the Kinsey and Fenn treatments at the ODF site is added calcium: total elemental calcium added in the two treatments was 871 and 81 kg/ha, respectively. However, the calcium was added in different forms, lime from the Kinsey blend altering soil pH and gypsum from the Fenn not altering soil pH. Further complicating the explanation of similar responses from the two blends at ODF is the fact that each received roughly similar additions of nitrogen, sulfur, potassium, and magnesium (tables 3,4). The lime treatment provided a similar amount of calcium as the Kinsey treatment (1020 kg/ha), but didn't include the other macro-nutrients common to the two blends. While the trees receiving the lime treatment exhibited a greater average volume growth in the second 3-yr period than control trees, the difference was not significant.

When the first three-year measurement was reported, it was acknowledged that the relatively slow incorporation of lime meant that the lime-heavy treatments may need additional time for a true test of their worth. If these preliminary results are not washed out by the inclusion of data from the additional sites, an argument can be made for future monitoring of lime-based treatments.

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Climatic influences on needle cohort survival mediated by Swiss needle cast in coastal Douglas-fir

Junhui Zhao, Douglas A. Maguire, Douglas B. Mainwaring
Department of Forest Engineering, Resources and Management, College of Forestry, Oregon State University

Alan Kanaskie
Oregon Department of Forestry

Abstract

Swiss needle cast (SNC) severity in Douglas-fir (*Pseudotsuga menziesii*) has been shown to vary spatially and temporally in response to climatic factors both within its native range and in regions where it has been planted as an exotic species. Survival models were developed for different Douglas-fir needle cohorts to enhance our understanding of how climatic influences on needle longevity are mediated by SNC in the Oregon Coast Range. The climate-based models were based on repeated measurement of 100 plots between 1998 and 2005 coupled with downscaled PRISM climate data. Potential predictors of needle survival by annual cohort were selected from numerous climatic variables at annual, seasonal, and monthly scales. Needle survival probability was positively associated with maximum summer temperature, and negatively associated with minimum winter temperature and spring precipitation. Seasonal climate variables associated with needle longevity are consistent with current epidemiological understanding of *Phaeocryptopus gaeumannii*, as well as with previous analyses of climatic influences on SNC severity as measured by average years of foliage retention and frequency of fungal fruiting bodies, or pseudothecia, in stomates.

Key Words: cohort survival, needle longevity, climatic effects, survival probability.

Introduction

Needles of most conifers can live for many years, and within a species needle longevity can vary tremendously (Reich et al. 1994). Coastal Douglas-fir has been observed to hold needles for up to seven years in western Oregon and Washington (Mitchell 1974) and 10 years in British Columbia (Silver 1962). Variation in needle longevity is related to many factors, including latitude (Reich et al. 1996, Xiao 2003), climate (Xiao 2003, Coop and Stone 2007), site fertility (Balster and Marshall 2000, Niinemets and Lukjanova 2003), and insect and disease history (Hansen et al. 2000, Kurkela et al. 2005).

As part of an effort to monitor SNC disease levels, estimate growth impacts, and investigate potential silvicultural mitigation of impacted stands, a network of permanent fixed-area plots was installed in north coastal Oregon in 1998. Although many different indices have been used to rank stands for symptom severity, average foliage retention (the number of annual needle cohorts remaining on a tree) has been the surrogate of choice for describing SNC intensity due to its relative objectivity, operational ease of estimation, and its correlation with tree growth (Maguire et al. 2002, Maguire et al. 2011).

Across the age range, management intensity, and site conditions sampled in the permanent plot network, Douglas-fir foliage retention ranged from a maximum of approximately four years in healthy stands to as low as one year in the most severely infected stands (Maguire et al. 2002, Maguire et al. 2011). Due to the significant positive correlation between tree growth and foliage retention in infected stands, foliage retention has been used to estimate regional volume growth losses from SNC (Maguire et al. 2002, Mainwaring et al. 2005, Maguire et al. 2011), and has also been incorporated into regional growth models (Garber et al. 2007) and applied in financial analyses (Latta and Adams 2010).

In the effort to create hazard rating maps for SNC in the Coast Ranges of Oregon and Washington, quantitative links between foliage retention and climate variables have been established using varying methodologies (Rosso and Hansen 2003, Manter et al. 2005, Coop and Stone 2007, Latta et al. 2009, Zhao et al. 2011). In each of these analyses, tree-level foliage retention is calculated as the summed proportions of needles surviving in each annual cohort. This foliage retention is generally interpreted as number of annual cohorts with 100% survival plus the surviving fraction of the oldest cohort that is experiencing needle abscission. Older foliage is generally cast before younger foliage, but this pattern is not universal because: 1) only new emerging foliage can be infected by hyphae growing across the surface of the needles and into stomates; and 2) annual variation in climatic conditions creates annual variability in infection success or intensity. As a result, some younger annual cohorts may start to lose foliage before older cohorts. Zhao et al. (2011) analyzed the influence of local climatic factors on spatial and temporal variation on SNC as measured by average foliage retention. Modeling the effect of climatic factors on individual needle cohorts may further advance our understanding of mechanisms behind infection and mycelial development, and subsequent intensification of SNC. The objectives of this study were: 1) to identify climate variables that account for variability in survival patterns of annual cohorts of Douglas-fir needles; 2) to develop a needle survival model that explains observed variation in needle longevity by specific climatic conditions that prevailed during year of needle formation; and 3) to explore implied survival curves for needle cohorts formed under the full range of climatic conditions observed over the last 10 years.

Method

Field Work

Plots were distributed across a range of SNC severity, stand density, aspect, and slope (Table 1). The study sites ranged from 44.53° to 46.23° N latitude and from 123.38° to 124.00°W longitude (Fig. 1). Elevation ranged from 48 to 914 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 80% of the total typically occurring from October to March.

Measurements

Data for this analysis were compiled from two ongoing studies established to investigate growth losses under the influence of SNC: the Growth Impact Study (GIS) and the Precommercial Thinning study (PCT). The GIS plots were established in 1998 to monitor SNC symptoms and tree growth in 77 randomly selected 10- to 30-yr-old Douglas-fir plantations within 18 miles of the Pacific coast in northwestern Oregon (Maguire et al. 2002, Maguire et al. 2011). The PCT plots were established in 23 stands in 1998 and to test the effect of thinning and initial SNC severity on subsequent symptom development and tree growth (Mainwaring et al., *review*). Only control plots from the PCT study were included in this analysis.

Just prior to budbreak in each spring (April-May), foliage retention was recorded using two different methods on ten dominant or codominant trees on each plot. The first method involved estimating the average number of annual needle cohorts held by the tree, and has been referred to in past analyses as foliage retention (Hansen et al. 2000, Maguire et al. 2002). The second approach yielded the data used in this analysis and called for estimating separately the percentage of surviving needles from each of the four youngest annual cohorts. Specifically, cohort retention was scored on each of the four most recent shoot age classes on secondary laterals. This retention score was recorded as 0, 1, ..., or 9, with 0 representing 0-10%, 1 representing 11-20%, . . . , and 9 representing 91-100%. These measurements were generally repeated on the same trees on each plot from 1998-2005; however, if a tree died or was badly damaged, a tree similar in size was chosen as a replacement.

Climate data

Climate data corresponding to the year that each needle cohort emerged was calculated with the software ClimateWNA v4.60 (Wang et al. 2006). ClimateWNA extracts and downscales PRISM (Daly et al. 2002) monthly data (2.5 x 2.5 arcmin) for the reference period (1961-1990), and calculates annual, seasonal and monthly climate variables for specific locations based on latitude, longitude, and elevation for western North America. This program also downscales and integrates historical climate data (1901-2009) (Mitchell and Jones 2005, Mbogga et al. 2009). The output included both measurable climate variables and derived climatic indices (Hamann and Wang 2005). In total, ClimateWNA can produce 85 climate variables, including 48 monthly, 16 seasonal and 21 annual variables (Table 2).

Statistical Analysis

Annual cohort retention scores were expressed as the midpoint of each interval of percent retention, i.e., 5%, 15%. . . , and 95%. We first generated the observed life-table survival and hazard probabilities (Lawless 1982) to obtain descriptive information using PROC LIFETEST in SAS version 9.2 (SAS Institute Inc. 2009). A proportional hazards model (Lawless 1982) was first fitted to the data with PROC PHREG in SAS version 9.2 to select best subsets of climate variables for predicting needle longevity of individual cohorts. Climate variables at different scales (annual, seasonal and monthly climate variables) were tested as potential predictors, and only those pertaining to the year of foliage emergence and first year of foliage development were considered as predictors for each corresponding foliage cohort. The criterion to determine "best" subsets was based on the highest global score chi-square statistic (Lawless 1982). Preliminary analysis suggested that physiographic and stand-level related variables were not influential predictors.

The final needle survival model was generated with PROC LIFEREG in SAS version 9.2. This method uses maximum likelihood to fit parametric regression models to the cohort survival data (Lawless 1982, Allison 2010). This procedure considers the scale and shape of the distribution of failure times (time to needle abscission) as conditional on specified covariates.

The relationship between needle longevity and potential covariates was assessed by accelerated failure time analysis. The response variable was average needle longevity for each plot expressed as 0.5, 1, 2, 3, or 4 years. Assuming that each cohort started with 100 total needles, the number of needles with a lifetime of ***n*** years was calculated as the difference between the % cohort survival at age ***n*** and the % cohort survival at age ***n+1***, yielding a value between 0 and 100. This number was weighted by the number of needles in each age class. Because needles were not monitored past four years to determine their full lifetimes, right-censoring was specified in PROC LIFEREG. We tested whether a normal, log-normal, Weibull, Gamma, exponential, or log-logistic function provided the best fit to the needle longevity and survival data and selected the function that gave the lowest AIC (indicating goodness-of-fit), the fewest number of parameters, and best fit to individual populations. The selected model was then assessed by examining the survival probability plot from a modified Kaplan-Meier method that adjusts for covariates. If the specified model is adequate, the graph of the transformed survival estimates against the log of time should appear as a straight line (Allison 2010).

Results

Survival and hazard probabilities

The overall average needle longevity was 2.45 years, with stand deviation of 1.17 years. The majority of plots had needle survival curves that indicated moderate declines in needle retention over time (plots 2 and 7 in Fig. 2), with the most healthy plots retaining needles for a long time (plot 107 in Fig. 2), and the most severely affected plots showing rapid decline in needle retention (plot 99 in Fig. 2).The distribution of survival probabilities in different age classes demonstrated the declining survival rates with increasing needle age (Fig. 3). For ages 1 and 4, the majority of survival probabilities are 95% and 5%, respectively. The average probabilities of survival to ages 1-4 years were 0.99, 0.73, 0.42 and 0.19, respectively (Table 3). Corresponding probabilities of abscission were 0.01, 0.30, 0.55 and 0.73, respectively (Table 3). In short, most needles survived the first two years, but were likely to die shortly afterwards.

Best climate predictors

The climate predictors that appeared in the best proportional hazards models varied somewhat among the three temporal resolutions (Table 4). Based on variables identified in previous epidemiological research (Capitano 1999, Rosso and Hansen 2003, Manter et al. 2005), and on statistical scores (global chi-square statistic), models based on seasonal climate variables (models 4-6 in table 3), were judged most suitable. Model 5 included maximum temperature in summer (Tmax_sm), minimum temperature in winter (Tmin_wt), and precipitation in spring (PPT_sp), so was selected as the optimal subset because it had the best combination of few predictors and high accuracy (high score).

Needle longevity model

The relative performance of the normal, log-normal, Weibull, Gamma, exponential, and log-logistic models differed considerably (Table 5). Gamma and lognormal distributions had the lowest AIC, but the Gamma distribution also has an additional parameter to estimate. In addition, the equation using the Gamma function is more complicated, making it difficult to judge the shape of the survival curve from the estimated parameters (Allison 2010). Therefore, we chose the lognormal distribution as the preferred model. The estimated scale parameter was 0.5591 with 95% confidence limits of 0.5552 and 0.5630 (Table 6), suggesting that the rate of needle loss is increasing with time. All covariates (Table 4) were significantly related to the probability of needle loss (all $p<0.0001$), and the probability plot indicated close conformity to the specified model (Fig. 4).

In order to view differences in the survival curve for needles formed under different climatic conditions, survival probabilities were predicted from the final model based on minimum and maximum values of the covariates represented in this dataset (maximum PPT_sp, Tmax_sm, and Tmin_wt of 1281 mm, 25.6°C, and 5.8°C, respectively; minimum PPT_sp, Tmax_sm, and Tmin_wt of 275 mm, 17.1°C, and -2.2°C, respectively). The highest survival probabilities occurred for a cohort formed in a year with low PPT_sp, high Tmax_sm, and low Tmin_wt, with survival probabilities exceeding 90% through year four (Fig. 5). The lowest survival probabilities occurred for a cohort formed in a year with high PPT_sp, low Tmax_sm, and high Tmin_wt, with survival probabilities dropping below 20% by year four.

Discussion

Swiss Needle Cast (SNC) can be sufficiently severe that foliage retention reaches slightly less than one year in populations where the maximum foliage retention would otherwise be approximately four years (Hansen et al. 2000, Maguire et al. 2002). In general, needle loss progresses from the oldest to the youngest needles, but it is not uncommon for a younger needle cohort to start losing needles before an older cohort. Presumably this sequence is a result of environmental conditions that are more favorable for infection of new foliage during the year that the younger cohort was formed. Survival analysis provided a methodology to describe differential rates of survival for specific needle cohorts, and to test the effects of weather conditions specific to the year in which each cohort emerged and developed. In our analysis of Douglas-fir needle dynamics, patterns in needle longevity and survival probability were first assessed by nonparametric estimation of empirical survival rates and hazard probabilities, indicating that survival probability declines rapidly after two years in the population sampled.

The semi-parametric proportional hazards models illustrated that a relatively small set of climatic variables describing conditions during year of foliage emergence could explain a significant amount of variation in cohort survival. These key variables were then introduced into alternative parametric models, identifying the lognormal distribution as best and providing a model that could be compared to previous work analyzing the spatial and temporal variability in foliage retention (Manter et al. 2005, Stone et al. 2007, Zhao et al. 2011).

The climate variables with greatest efficacy for predicting survival of Douglas-fir needle cohorts were consistent with the strongest variables for predicting spatial and temporal patterns in average foliage retention (Zhao et al. 2011). In general both cohort survival rates and average foliage retention declined as winter temperatures and spring precipitation increased, and increased as summer temperatures increased (Zhao et al. 2011 and results presented above). Similar climatic variables have also been shown to influence indices of SNC infection intensity based on frequency of stomatal occlusion by pseudothecia (Manter et al. 2005, Stone et al. 2007).T he covariates for describing needle cohort survival patterns were selected to represent an optimal combination of strong predictive ability and consistency with biological mechanisms known to influence SNC epidemiology. As a group, the monthly climate variables accounted for the greatest amount of variation in needle survival patterns, and represented some of the factors previously hypothesized to influence SNC severity. Annual climate variables also accounted on average for a greater proportion of the variability in needle survival than did seasonal climate variables.

Numerous SNC hazard maps have been developed for Douglas-fir stands in the Oregon Coast Ranges (Manter et al. 2005, Coop and Stone 2007, Latta 2009, Zhao et al. *In prep*). The hazard rating models predict foliage retention as the average number of annual needle cohorts, but do not reflect the survival rate of any specific cohort. For some applications, including refinement of growth losses and improved understanding of the climatic drivers of SNC epidemiology, it may be more important to accurately simulate the proportion of surviving foliage in each annual cohort. With respect to growth impacts, needle cohorts have been shown to experience declining net photosynthetic rates and resource use efficiency with age (Warren 2006, Ethier 2006). Although the oldest foliage on an individual SNC-infected Douglas-fir tends to be lost first, this pattern is not universal. At sites experiencing moderate levels of infection, annual variation in SNC infection pressure can result in a given cohort losing foliage before an older cohort that was formed during a year that was less conducive to *Phaeocryptopus* infection (Mainwaring et al. 2008). This variability in cohort survival and associated stomatal occlusion complicate the usual patterns in photosynthetic efficiency and introduce some additional variation in growth that has not been accounted for by correlating growth with average foliation retention (e.g., Maguire et al. 2011).

The ability to predict survival rates of individual needle cohorts or age classes over time may be particularly useful for refining mechanistic or hybrid models that simulate ecophsyiological processes, total carbon fixation, and stem growth and yield (e.g., Mäkela et al. 2000, Schwam and Ek 2004, Weiskittel et al. 2010). Such models combine conventional empirical data with mechanistic elements such as climate- and soil-driven water availability, water uptake and evapotranspiration, nutrient uptake, foliar nutrient dynamics, and net photosynthesis. This hybridization allows the models to react to changes in environmental conditions including various climatic factors, and possibly improve predicted responses of trees and stands to silvicultural treatment and foliage loss from insects or disease (Monserud 2003). Given the apparent influence of climate on foliar longevity, and obvious links between foliar longevity and carbon fixation, the ability to predict the survival of individual cohorts may prove valuable in forecasting future growth.

Care must be taken in application of the cohort survival models beyond the geographic bounds of the SNC plot network. During an earlier effort to produce a climate-based prediction model, a dataset was compiled that included the data used in this analysis and additional data collected in the southern and central Coast Ranges and in the western Cascades of Oregon. In the initial analysis, ordinary least squares regression produced a model that significantly underpredicted foliage retention at nearly every site outside the geographic range of the sites used in the cohort analysis (Latta et al. 2009). Although this bias was corrected by accounting for spatial autocorrelation, such techniques do not account for the factors which cause foliage retention to vary between sites.

Overestimation of disease severity outside north coastal Oregon suggests subtle differences in environmental conditions that are not captured as well by the variables that were effective for the north coast, but genotypic differences in the host and abundance of fungal spores also cannot be totally dismissed (e.g., Johnson 2002, Hood and Kimberly 2005). It is possible that subtle differences in climate that are not represented by the monthly, seasonal, or annual climatic variables from ClimateWNA create conditions that are not as conducive to SNC intensification, or that biases in geographic interpolation of climatevariables imply predisposing climatic conditions that do not actually occur in these areas. Alternatively, stands experiencing similar climatic regimes but much lighter spore loads than stands at the SNC epicenter in north coastal Oregon may be protected to some degree by lower disease pressure. Where this disease pressure is absent, the same climate variables may not lead to the same declines in needle longevity.

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Table 1. Initial (1998) attributes of Douglas-fir control plots included in the SNCC pre-commercial thinning (PCT) study and Growth Impact (GIS) Study.

Variable	Units	***PCT Study***			***GIS Study***		
		mean (stdev)	Minimum	Maximum	Mean (stdev)	Minimum	Maximum
Douglas-fir tree density	trees ha^{-1}	1020.8 (313.3)	629.9	2001.0	628.1 (290.7)	86.5	1630.2
Douglas-fir basal area	m^{2}ha^{-1}	15.76 (6.32)	3.92	27.05	17.62 (8.59)	0.62	38.71
Douglas-fir breast height age	yrs	10.9 (2.4)	5.0	15.5	20.0 (5.6)	11.0	32.0
Douglas-fir QMD	cm	14.1 (3.1)	7.2	19.7	18.6 (6.2)	3.8	34.0
Douglas-fir top height	m	11.7 (2.1)	7.8	15.6	26.2 (8.4)	5.8	44.6
Douglas-fir site index	m at 50 yrs	43.0 (6.7)	32.1	62.5	44.9 (7.6)	14.6	61.7
Basal area of other conifers	m^{2}ha^{-1}	1.75 (6.14)	0.00	29.62	2.76 (5.24)	0.00	24.03
Basal area of broadleaved species	m^{2}ha^{-1}	1.21 (1.14)	0.00	3.97	1.05 (2.03)	0.00	13.40
Total tree density	trees ha^{-1}	1496.6 (950.2)	629.9	5101.0	848.4 (413.7)	259.4	2037.8
Total plot basal area	m^{2}ha^{-1}	18.72 (8.79)	3.92	60.64	21.43 (10.17)	0.66	48.65
Foliage retention	years	2.4 (0.5)	1.3	3.3	2.3 (0.4)	1.1	3.1

Table 2. Climatic variables tested as predictors of Douglas-fir needle cohort survival.

Group		***Predictor***	***Definition***
Annual variables	*Direct variables*	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 Sept.) precipitation (mm)
		AHM	annual heat:moisture index (MAT+10)/(MAP/1000))
		SHM	summer heat:moisture index ((MWMT)/(MSP/1000))
	Derived variables	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, se_{xy}=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.(prev. yr) - Feb.), spring (Mar. - May), summer (Jun. - Aug.), and autumn (Sep. - Nov.).
	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)

Table 3. Life table analysis of Douglas-fir needle survival in different age classes.

Age Interval	*Number Failed*	*Number Censored*	*Effective Sample Size*	*Survival*		*Hazard*	
				probability	**(SE)**	**probability**	**(SE)**
0-1	625	0	60661	1.0000	0.0000	0.0104	0.0004
1-2	15644	0	60036	0.9897	0.0004	0.2996	0.0024
2-3	17766	6651	41066.5	0.7318	0.0018	0.5520	0.0040
3-4	9180	5690	17130	0.4152	0.0021	0.7321	0.0071
4-	0	5105	2552.5	0.1927	0.0019		

Table 4. Selected models for predicting Douglas-fir needle cohort survival from climatic variables. Bold type indicates negative effects and regular type indicates positive effects.

No	*Climate variables*	*Number of predictors*	*Predictors*	*Score*
1	Annual	2	**TD** MSP	6131.7829
2	Annual	3	MSP NFFD **eFFP**	7631.4501
3	Annual	4	**TD** MSP NFFD **eFFP**	8428.1364
4	Seasonal	2	Tmin_wt PPT_sp	5929.6470
5	Seasonal	3	Tmin_wt **Tmax_sm** PPT_sp	6780.4181
6	Seasonal	4	Tave_wt Tmin_sm **Tave_sp** PPT_sp	7680.2884
7	Monthly	2	Tave02 **Tmax03**	9123.6956
8	Monthly	3	PPT03 Tave02 **Tave09**	9828.2675
9	Monthly	4	Tave02 **Tave09 Tmax03** PPT10	10469.6083

Table 5. Goodness-of-fit statistics of different distributions fitted to Douglas-fir needle survival data.

Distribution	*2 Log Likelihood*	*AIC*	*AICC*	*BIC*
Exponential	132023.9	132031.9	132031.9	132054.7
Normal	157245.0	157255.0	157255.0	157283.5
Lognormal	99508.83	99518.83	99518.86	99547.36
LLogistic	100475.4	100485.4	100485.4	100513.9
Logistic	157402.6	157412.6	157412.6	157441.1
Weibull	105373.5	105383.5	105383.5	105412.0
Gamma	99358.9	99370.9	99370.9	99405.1

Table 6. Parameter estimates and statistical tests for the lognormal regression regression model fitted to Douglas-fir needle survival data.

Parameter	*DF*	*Estimate*	*Standard Error*	*95% Confidence Limits*		*Chi-Square*	*Pr > ChiSq*
Intercept	1	-0.4170	0.0371	-0.4898	-0.3442	126.13	<.0001
Tmin_wt	1	-0.1582	0.0020	-0.1621	-0.1543	6327.82	<.0001
Tmax_sm	1	0.0931	0.0016	0.0899	0.0964	3211.51	<.0001
PPT_sp	1	-0.0006	0.0000	-0.0007	-0.0006	1548.46	<.0001
Scale	1	0.5591	0.0020	0.5552	0.5630		

Figure 1. Location of 100 permanent plots on which Douglas-fir needle survival was monitored from 1998 to 2003. Locations are indicated by county in northwestern Oregon.

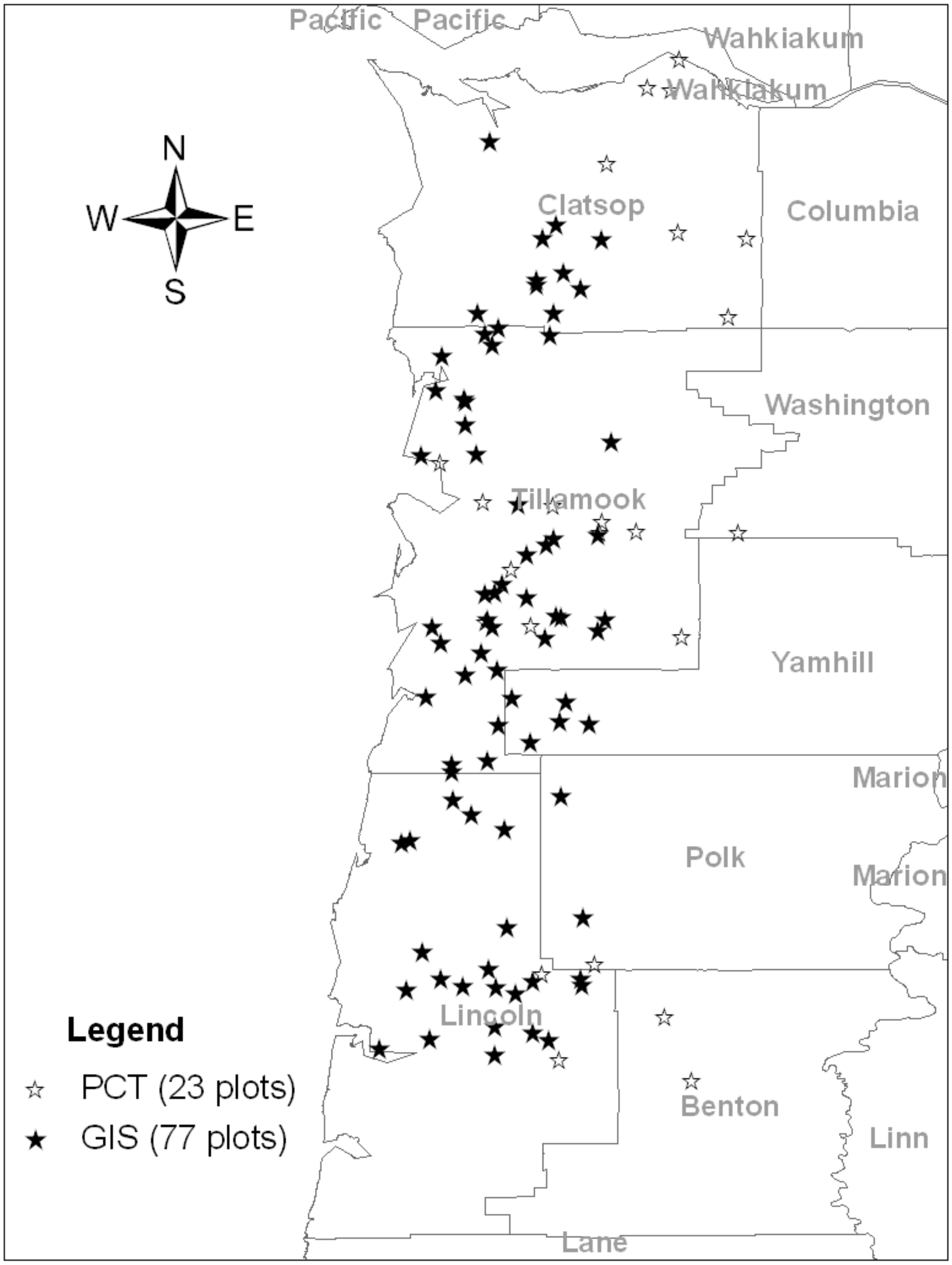


Figure 2. Empirical needle survival curves for two average plots (2 and 7), a relatively healthy plot (107), and a severely impacted plot (99).

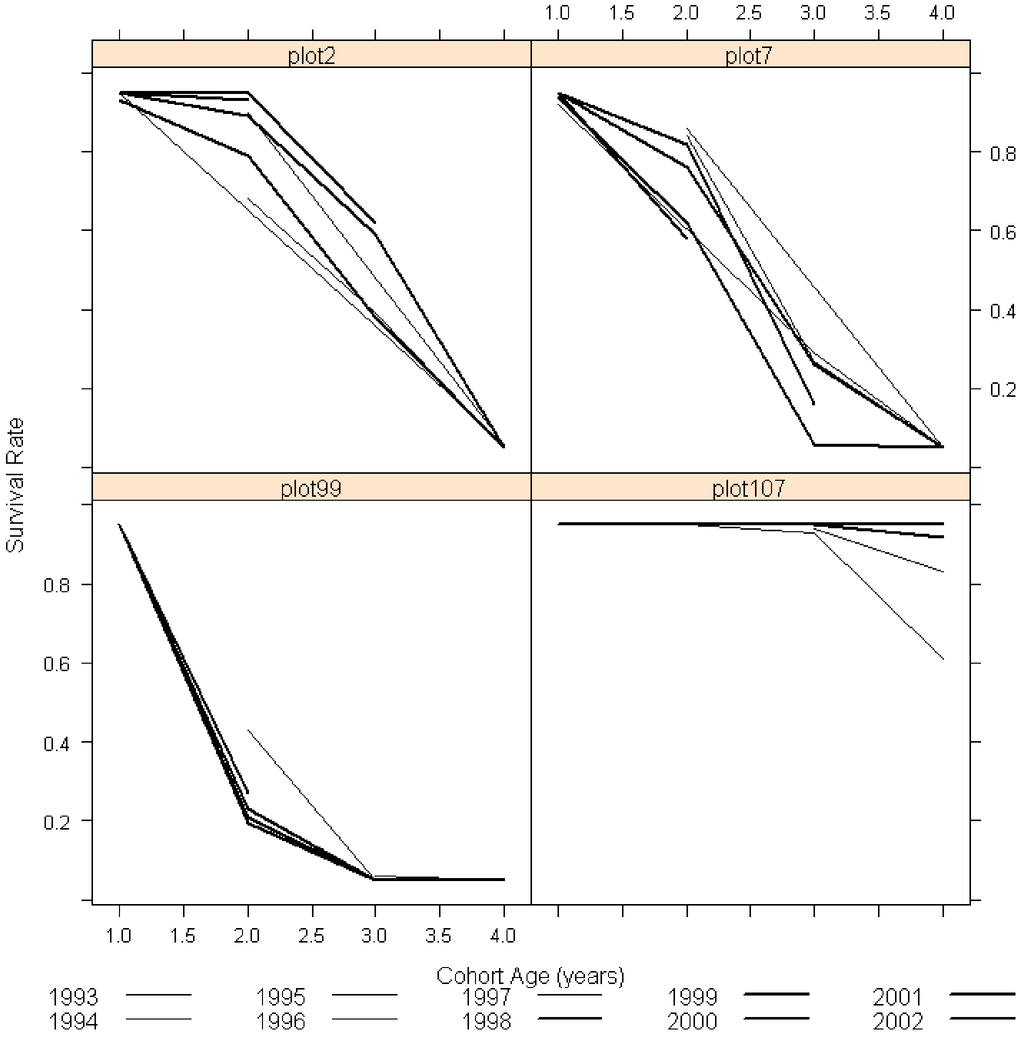


Figure 3. Survival probability of Douglas-fir needles by age class.

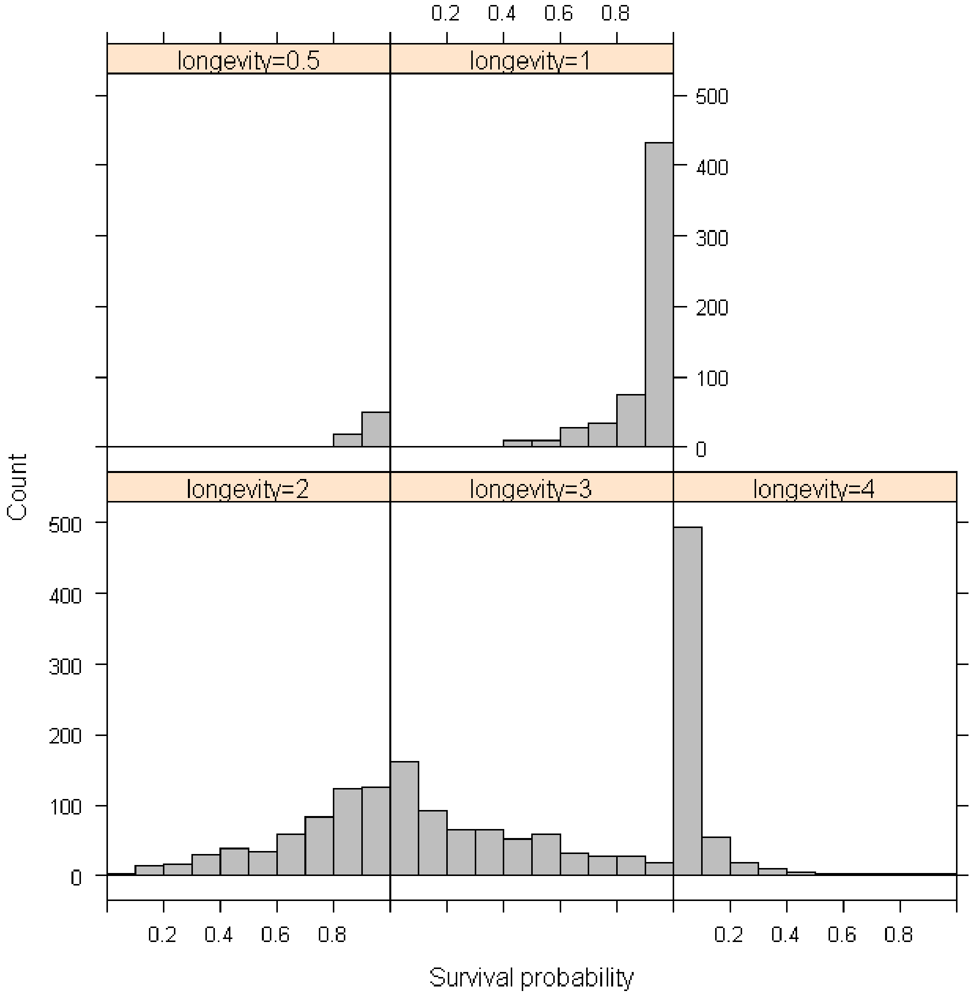


Figure 4. Lognormal probability plot for Douglas-fir needle longevity data.

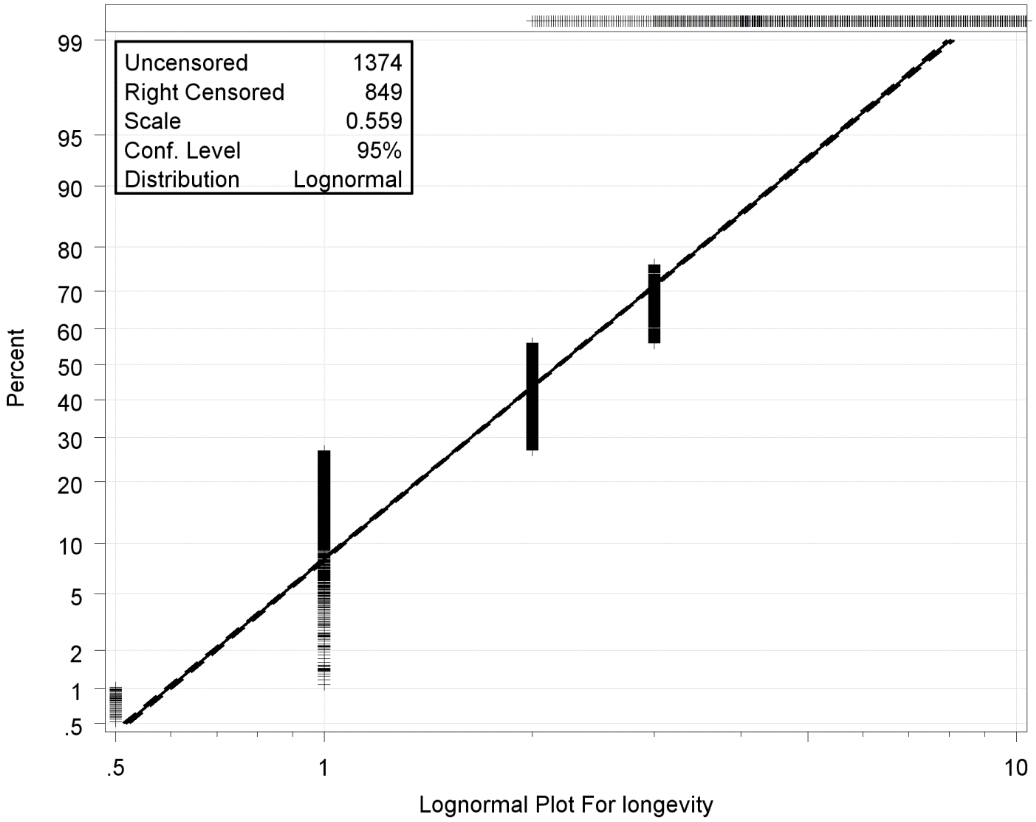
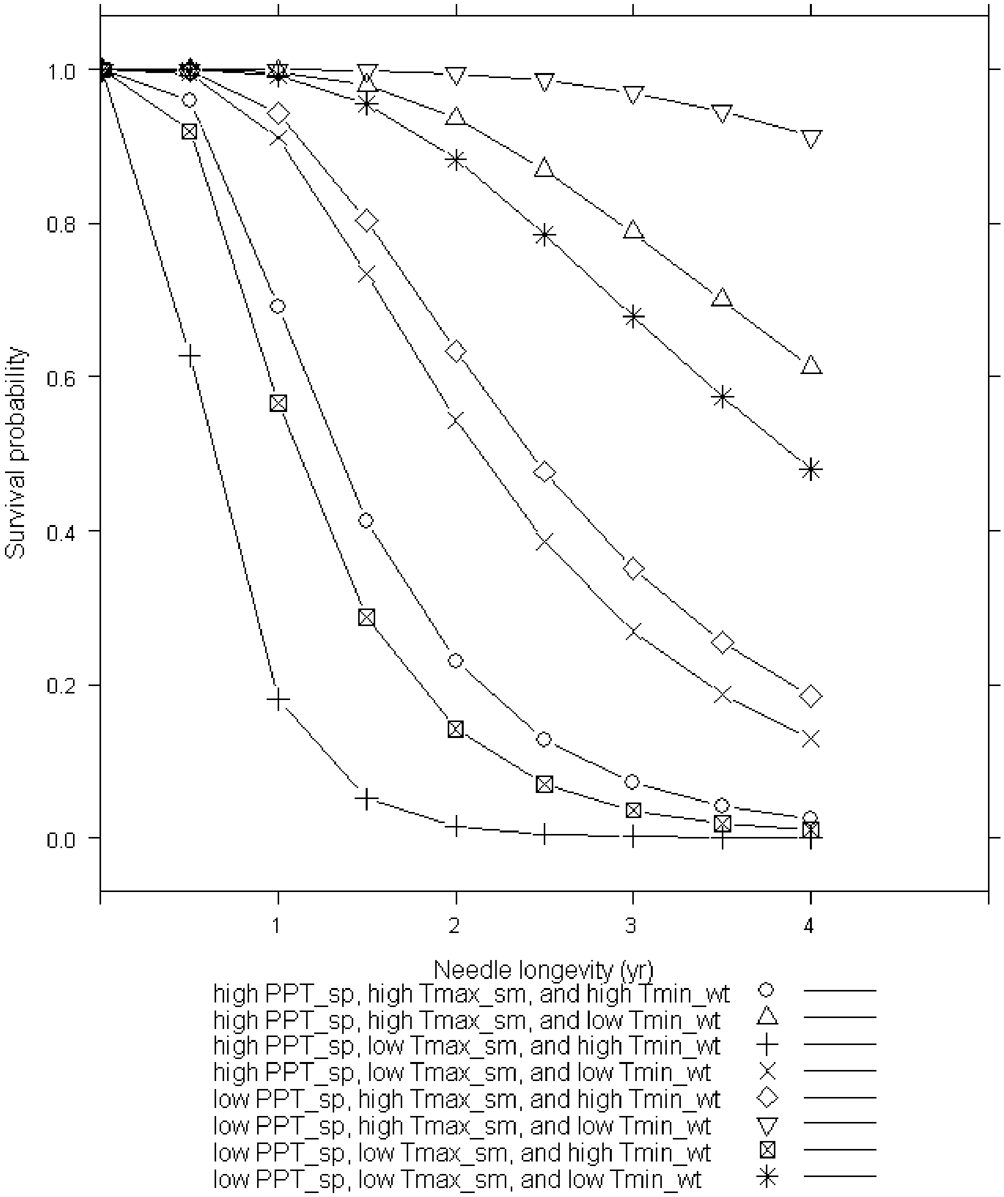


Figure 5 Predicted survival curves for Douglas-fir needles initiated under different climatic conditions (high and low PPT_sp=1281 mm and 275 mm, respectively; high and low Tmax_sm=25.6°C and 17.1°C, respectively; and high and low Tmin_wt=5.8°C and -2.2°C, respectively).



Thinning mixed-species stands of Douglas-fir and western hemlock in the presence of Swiss needle cast: Guidelines based on relative basal area growth of individual trees

Junhui Zhao, Douglas A. Maguire, Douglas B. Mainwaring,
Department of Forest Engineering, Resources and Management, College of Forestry, Oregon State University

Jon Wehage
Stimson Lumber Company, Tillamook, Oregon

Alan Kanaskie
Oregon Department of Forestry

Abstract

In coastal forests of the Pacific Northwest, young coniferous plantations typically contain a mixture of planted and natural Douglas-fir and western hemlock. Swiss needle cast (SNC) inhibits the growth of Douglas-fir to varying degrees in these stands, depending on SNC severity. In addition to the value differential between Douglas-fir and western hemlock, foresters must account for differences in growth potential (tree size, competitive position, disease pressure) when selecting trees for retention during thinning operations. Diameter increment models for Douglas-fir and western hemlock were developed from permanent plot data collected for a SNC growth impact study. Predictor variables represent tree size, competitive position, site quality, and SNC severity. SNC severity was indexed by foliage retention, defined as the number of annual needle cohorts held by a tree. Foliage retention was positively correlated with Douglas-fir diameter increment and negatively correlated with western hemlock diameter increment. Charts developed from the diameter growth models provide a field tool for assessing the relative basal area growth of adjacent Douglas-fir and western hemlock of a given initial diameter in a stand of given SNC severity. In a stand with severe SNC (foliage retention=1.5 years) the basal area growth of a 6-inch western hemlock tree will exceed the basal area growth of any Douglas-fir tree up to 9 inches in dbh. In a relatively healthy stand (foliage retention=3.0 years) the basal area growth of 6-inch Douglas-fir and western hemlock trees will be approximately equivalent.
Key Words: Relative growth, basal area increment, foliage retention, disease severity, thinning guidelines.

Introduction

Young Douglas-fir plantations (≤40 yr) are tremendously important to the economic and environmental health of Oregon and Washington due to their extent and productivity (Campbell et al. 2004, Gray et al. 2005). Over the past 20 years, coastal forests in this region have been suffering from an epidemic of Swiss needle cast (SNC), a foliar disease of Douglas-fir caused by the Ascomycete *Phaeocryptopus gaeumannii* (Hansen et al. 2000). Productivity of Douglas-fir in affected stands has diminished considerably, with volume growth losses reaching as high as 50% due to premature needle abscission and disruption of photosynthesis in surviving foliage (Hansen et al. 2000, Manter et al. 2000, Maguire et al. 2011). Annual aerial surveys of three million acres of coastal forests conducted by the Oregon Department of Forestry indicate that the area of symptomatic forest (stands with visible chlorosis) has been fluctuating annually but has also been gradually increasing since 1996. The SNC-affected area reported in 2011 was 444,228 acres, the highest total since the aerial survey began (Kanaskie and McWilliams 2011). The extent of discoloration is particularly significant given the relatively aggressive conversion of both merchantable and non-merchantable Douglas-fir stands to non-susceptible species in the most severely impacted areas.

Pre-commercial thinning (PCT) is commonly used in stands where high stand density limits individual tree growth required to achieve management objectives or reduces vigor to a level that leaves trees more susceptible to insects and disease (Mitchell et al. 1983). PCT was among the earliest silvicultural treatments applied in severely SNC-impacted stands to test for possible beneficial or detrimental effects on residual tree growth and foliage retention (Kanaskie et al. 1998). Results from a commercial thinning study indicate that infected stands respond positively to thinning (Mainwaring et al. 2005, Mainwaring et al. in review), but consistent with unthinned stands (Maguire et al. 2011), Douglas-fir growth remains lower than its potential in absence of SNC. With continued increase in affected area of coastal Douglas-fir, land managers are not currently emphasizing Douglas-fir as much as they have in the recent past in coastal Oregon. Specifically, silvicultural strategies have shifted to interplanting with non-susceptible species and preferential retention of the latter during PCT.

Due to its historically greater value, Douglas-fir continues to be an important component of planted stands. Increasing proportions of Douglas-fir are generally planted from west to east within the Coast Ranges of Oregon, with western hemlock most commonly planted as the substitute species (Beth Fitch, *pers. comm*). Natural regeneration of western hemlock contributes to this planned shift in species composition by increasing with proximity to the coast, presumably due to higher precipitation and lower summer temperatures (Schrader 1998). The abundance of natural regeneration of hemlock generally increases along the gradient of increasing SNC severity in Douglas-fir. Although prolific natural regeneration often makes density control in these stands necessary, the resulting mix of Douglas-fir and hemlock also provides an opportunity for manipulating species composition to match the anticipated relative growth performance of the two species at any one location.

In the absence of SNC, a larger planted Douglas-fir would be retained during thinning in preference to a smaller western hemlock, given the equal or greater growth potential of Douglas-fir and its higher market value. However, the current negative growth impact of SNC should be accounted for in determining the best species mix for coastal stands. With appropriate diameter increment equations, expected growth rates of the two species can be assessed by considering SNC intensity, stand structure, site quality, and relative size.

Individual-tree diameter increment models are routinely applied to simulate the growth dynamics among trees in stands of varying structure and among sites of varying quality (Wykoff 1990; Monserud and Sterba 1996; Trasobares et al. 2004). Diameter or basal area growth is fundamental to these growth models (Cao 2000; Westfall 2006), in part because it is a dimension that is relatively easy to measure with high precision and in part because it is widely used for predicting future tree volume or biomass, as well as probability of survival (Yang et al, 2009). The aims of the present study were: 1) to develop distance-independent individual-tree diameter growth models for young Douglas-fir and western hemlock trees growing in mixed-species stand across a gradient in SNC severity; 2) to compute the implied relative basal area growth of Douglas-fir and western hemlock trees of varying initial diameter as a function of foliage retention; and 3) to develop a field chart to help managers select trees for removal and retention during thinning of mixed Douglas-fir and hemlock stands .

Methods

The target population for the SNCC Growth Impact Study (GIS) initiated in 1998 was defined as 10- to 30-yr-old Douglas-fir plantations in north coastal Oregon (Maguire et al. 2002, Maguire et al., 2011) (http://www.cof.orst.edu/coops/sncc/). A list of all 10- to 30-yr-old Douglas-fir stands was first compiled in 1996 within a geographic area bounded by Astoria to the north (N46°11',W123°50'), Newport to the south (N44°38', W124°04'), the Pacific Coast to the west (W124°05'), and the crest of the Oregon Coast Ranges to the east (W123°30'). A set of 76 stands was randomly selected from the target population, so were distributed across a wide range of SNC severity. 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 non-viable.

Field work

Permanent plots were established in each of the 76 selected stands in the late winter/early spring of 1998. GIS plots were square, 0.2 acres (0.08 ha) in area (93.3 ft or 28.45 m to a side), and centered on the fifth point of an ODF (Oregon Department of Forestry) transect established in spring 1997 (retrospective plots reported by Maguire et al. (2002) were centered on the third point). On each measurement plot, all trees with diameter at breast height (dbh, nearest 0.04 inch or 0.1 cm) greater than 1.6 inches (4 cm) were tagged at a height of 4.5 ft (1.37 m), and at least 40 Douglas-fir were measured for total height (nearest 0.03 ft or 0.01 m) and height to crown base (nearest 0.03 ft or 0.01 m) at time of plot establishment. After two, four, six, and ten growing seasons, all trees were remeasured for dbh, and all undamaged trees from the original height subsample were remeasured for total height and height to crown base. Some plots contained a significant amount of western hemlock, as well as various broadleaved species, most commonly cascara (*Rhamnus purshiana*), red alder, and red elderberry (*Sambucus racemosa*). Other conifers that occurred less frequently included Sitka spruce, western red cedar (*Thuja plicata*), noble fir (*Abies nobilis*), and grand fir (*Abies grandis*). Other hardwood species includes bitter cherry (*Prunus emarginata*) and bigleaf maple (*Acer macrophyllum*).

Ten dominant or codominant trees on each GIS plot were also scored for SNC at time of plot establishment in 1998, and just prior to bud break in years 1999-2004. Needle retention of individual trees was visually estimated by first dividing the live crown into thirds, with the base of the live crown defined as the lowest live branch. Secondary or lateral branches on a primary or main branch were then examined in the center of each third, and the average number of needle age classes present at time of sampling was estimated to the nearest 0.5 yr in 1998 and to the nearest 0.1 yr in subsequent years (Maguire et al. 2002). Needle retention of individual trees was estimated by averaging across the crown thirds. The GIS modeling data consisted of 13,416 observations from 3,708 Douglas-fir trees in 76 plots and 2,695 observations from 856 western hemlock trees in 40 plots.

Model development

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 (Weiskittel et al., 2007; Maguire et al., 2011). The natural logarithm of periodic annual increment in tree diameter was modeled as a function of tree size, competitive position, site attributes and SNC severity. The tested explanatory variables include the following:

1. Tree size variables: dbh (all species); crown ratio (CR) and height to crown base (HCB) for Douglas-fir only. Logarithmic, inverse, and squared transformations of these variables were also tested.
2. Competition variables: number of stems, N (stems/acre); average diameter of largest 40 trees by dbh, D40 (inches); average height of largest 40 trees by dbh, H40 (feet); quadratic mean diameter of all trees, QMD (inches); arithmetic mean diameter of all trees, MDBH (inches); stand age, Age (year); basal area, BA (feet^2/acre); crown competition factor, CCF (Krajicek et al. 1961); stand density index, SDI; and Bruce's site index (Bruce 1981), SI (feet); relative diameter defined as the ratio between subject tree breast height diameter and average diameter of largest 40 trees, (dbh/D40); basal area of trees larger than the subject tree, BAL (feet^2/acre); and crown competition factor in trees larger than the subject tree (CCFL). Various transformations of these variables were also tested. Crown competition factor (CCF, Krajicek et al., 1961) was calulated for each plot and inventory year with species-specific maximum crown width estimated from equations developed by Paine and Hann (1982) and Bechtold (2004). Reineke's (1933) SDI was computed as the competitive equivalent of a varying number of trees per ac with a quadratric mean diameter of 10 inches (multiply by 0.144 for metric equivalent).
3. Site characteristics: elevation (ELEV, feet), slope (SL, %), longitude (LNG, °), latitude (LAT, °), aspect (ASP, °), and various transformations of slope and aspect (Stage et al. 2007).
4. SNC severity: the number of years of retained foliage (FR). Squared, logarithmic, and inverse transformations of foliage retention and the natural logarithm of foliage retention minus a constant (0.1 to 1.0 in 0.1 increments) were also tested.

Various linear and nonlinear models were fitted to the data to model periodic annual diameter growth of Douglas-fir and western hemlock. Linear diameter increment models were tested in the first stage of model fitting. Potential predictor variables at the tree-level and stand-level were selected based on the available data and their biological significance to tree growth (Wykoff 1990, Zhao et al. 2004). A random plot effect was also tested in the models to account for the repeated measurements across the four growth periods. The linear model was estimated using the maximum likelihood procedures in PROC REG and PROC MIXED in SAS version 9.2 (SAS Institute, 2008).

At the second stage, nonlinear diameter increment models were tested using the predictors identified with the linear diameter increment models. The nonlinear model was estimated using maximum likelihood by PROC NLMIXED in SAS version 9.2 (SAS Institute, 2008). Final models were chosen on the basis of statistical significance of parameter estimates (α= 0.05), residual analysis, Akaike's information criterion (AIC), and biological interpretability.

The models were evaluated quantitatively by examining the magnitude and distribution of residuals on all possible combinations of variables to detect any obvious dependencies or patterns that indicate systematic bias. The following fit index was also computed as an analog to R^2:

$$[3] \quad FI = 1 - \frac{\sum_{i=0}^{n}\left(\Delta\mathrm{dbh} - \widehat{\Delta\mathrm{dbh}}\right)^2}{\sum_{i=0}^{n}\left(\Delta\mathrm{dbh} - \overline{\Delta\mathrm{dbh}}\right)^2}$$

Trends in diameter growth implied by the fitted models over initial tree diameter and SNC intensity were graphically assessed for their behavior by setting other predictor variables to their average across the entire dataset.

Thinning guidelines

Basal area growth implied by the models was computed assuming that the subject stand had 400 trees/acre (988 trees/ha), including 250 Douglas-fir/ac (618/ha) and 150 western hemlock/ac (371/ha). Western hemlock trees ranged in diameter from 2 to 12 inches (5.1 to 30.5 cm), and Douglas-fir trees ranged in diameter from 0 to 5 inches (0 to 12.7cm) larger than the western hemlock. For simplicity, all Douglas-fir trees were assumed to have equal dbh and all western hemlock trees were likewise assumed to have equal diameters but 0 to 5 inches (0 to 12.7cm) smaller than Douglas-fir. Crown ratio of Douglas-fir was set to the mean value of 0.7 for the entire dataset. The ratio of basal area growth of the Douglas-fir and western hemlock trees was computed as a function of foliage retention and the difference between the diameters of the two species. This basal area growth ratio was finally plotted on the diameter difference between the two species for different SNC intensities as measured by foliage retention. For a given foliage retention, the diameter difference between the two species at which the growth ratio equals one (or some other value of the forester's choice) implies a diameter difference threshold that can be applied to choose between adjacent trees of these two species during a thinning.

Results

A large range of tree sizes was available for both species, with western hemlock exhibiting a greater diameter range (Table 1). The following final diameter increment equation for Douglas-fir included variables representing initial tree size, competition, and SNC severity:

$$[1] \quad \Delta\mathrm{DBH}_{\mathrm{DF}} = \exp\left(\alpha_0 + \alpha_1 * \mathrm{CCFL} + \alpha_2 * \log\left(\frac{\mathrm{CR}+\mathbf{0.2}}{\mathbf{1.2}}\right) + \alpha_3 * \frac{\mathrm{DBH}}{\mathrm{D40}} + \frac{\alpha_4}{\mathrm{FR}} + \alpha_5 * \frac{\mathrm{BAL}}{\mathrm{BA}} + \frac{\alpha_6}{\mathrm{DBH}} + \delta_1\right) + \varepsilon_1,$$

where ΔDBH_{DF} = Periodic annual diameter growth of Douglas-fir tree (inches/yr)
CCFL = Crown competition factor in trees with larger dbh than subject tree (%)
CR = Crown ratio (proportion)
DBH = Initial tree diameter (inches)
D40 = Mean diameter of 40 largest trees per acre by diameter (inches)
FR = Plot mean foliage retention (years)
BAL = Basal area in trees with larger dbh than subject tree (ft^2/ac)
BA = Total stand basal area (ft^2/ac)
α_k = Parameter to be estimated from the data
δ_1 = Random plot effect with $\delta \sim N(0,\sigma_{\delta 1}^2)$
ε_1 = Random error with $\varepsilon \sim N(0,\sigma_{\varepsilon 1}^2)$

All parameter estimates were significantly different from zero at α=0.05, the fit index was 0.733, and the model AIC was -22907. Residual plots indicated that the model provided a good fit to the data.

The following final model describing western hemlock diameter increment had fewer predictor variables, but also included variables representing tree size, competition, and SNC severity:

$$[2] \quad \Delta DBH_{WH} = \exp(\beta_0 + \beta_1 * \frac{BAL}{DBH} + \beta_2 * FR + \beta_3 * H40 + \delta_2) + \varepsilon_2$$

where ΔDBH_{WH} = Periodic annual diameter growth of western hemlock tree (inches/yr)
H40 = Mean diameter of 40 largest trees per acre by diameter (inches)
β_k = Parameter to be estimated from the data
δ_2 = Random plot effect with $\delta \sim N(0,\sigma_{\delta 2}^2)$
ε_2 = Random error with $\varepsilon \sim N(0,\sigma_{\varepsilon 2}^2)$
and all other variables are defined above.

All parameter estimates were significantly different from zero at α=0.05, the fit index was 0.766, and the model AIC was -3965. Residual plots indicated that the model provided a good fit to the data.

SNC severity was negatively correlated with Douglas-fir diameter increment, but positively correlated with western hemlock diameter increment. Douglas-fir diameter increment under severe SNC (foliage retention of 1 year) was only 40.4% of that expected in a comparable uninfected stand (Fig. 1). In contrast, western hemlock growing in the same mixed species stand grew 85% more in diameter where foliage retention in Douglas-fir was only one year.

As indicated in the Methods sections, the graphs constructed for depicting the basal area growth ratios as a function of initial tree diameter and foliage retention relied on some assumptions that simplified the wide range in possible stand structures (specifically the diameter and height distributions by species). These assumptions allowed an approximate assessment of relative basal area growth of Douglas-fir and western hemlock trees in stands with two potential layers, a Douglas-fir component with equal diameters and heights and an equal or smaller western hemlock component with equal diameters (and implied equal heights). When constructing the field charts, compatibility between D40 in the Douglas-fir diameter growth model (equation [1]) and H40 in the western hemlock diameter growth model (equation [2]) was ensured by fitting the following equation to the GIS dataset:

$$[3] \quad H40 = 4.5 + \gamma_1 * exp(\gamma_2/D40 + \gamma_3/BA) + \delta_3 + \epsilon_3,$$

where γ_k = Parameter to be estimated from the data
δ_3 = Random plot effect with $\delta \sim N(0,\sigma_{\delta 3}^2)$
ε_3 = Random error with $\varepsilon \sim N(0,\sigma_{\varepsilon 3}^{\ 2})$

The Douglas-fir and western hemlock diameter growth models implied that, as SNC severity increased, the diameter of western hemlock trees that can be expected to match or exceed the basal area growth of Douglas-fir becomes smaller (Fig. 2). Under the assumptions made to generate the charts (Fig. 2), basal area growth of individual Douglas-fir trees in a healthy stand (foliage retention of about 3.5 years) would exceed that of western hemlock with equal or smaller initial diameter if the latter was ≥8 inches. If initial western hemlock dbh was <8 inches, then even in healthy stands Douglas-fir would have to have an initial dbh 1-1½ inches greater than western hemlock to achieve equal basal area growth. With increasing SNC severity (declining foliage retention), basal area growth of individual western hemlock trees increases relative to that of Douglas-fir with equivalent initial diameter. In stands with the most severe SNC, (foliage retention about 1.5 years or less), basal area growth of individual western hemlock trees exceeds that of Douglas-fir trees with dbh as much as 2-3½ inches larger (Fig. 2).

Discussion

In the last 20 years SNC has emerged as sufficiently influential in the Oregon Coast Ranges that land managers can no longer plant or tend Douglas-fir without considering SNC effects on Douglas-fir growth, on its ability to compete against other species, and even on survival of Douglas-fir to commercial size. Although it has been estimated that Douglas-fir remained financially competitive with other local conifer species even with as much as a 50% volume growth loss (Elwood and Mainwaring 2004, *unpublished*), this conclusion relies on assumptions about relative value. Furthermore, knowledge that SNC is at least influenced if not controlled by climate factors (Manter et al. 2005, Zhao et al. 2011), coupled with anticipated changes in future PNW climates, suggests that the current epidemic may not just be a short term anomaly (Stone et al. 2008). Although research has identified Douglas-fir families that exhibit tolerance to SNC (Johnson 2002, Temel et al. 2005), the enhanced performance of such families are believed to be practical in areas of only moderate infection, not where disease intensity is high (Filip et al. 2000). Managers must consider including greater proportions of non-susceptible species on forestland within areas of higher SNC risk (Filip et al. 2000).

Western hemlock generally has slower juvenile height growth than Douglas-fir, but its shade tolerance allows it to persist in stands where the two species are associated (Tesch 1995). In healthy even-aged stands, growth rates of the two species tend to diverge as western hemlock becomes overtopped by Douglas-fir (Wierman and Oliver 1979; Figs. 1 and 2). In healthy stands with a foliage retention of 3.5, the basal area growth ratio of trees of the same size (i=0) declines as tree diameter increases from 2 to 12 inches. This is almost certainly due more to natural differentiation patterns of the species mix than to potential species performance in absence of overtopping. Not surprisingly, as foliage retention declines with increasing SNC severity, combined Douglas-fir growth decline and increasing canopy light transmittance improve the relative performance of hemlock.

At foliage retention of 1.5 years, the most severe SNC depicted in this analysis, western hemlock outproduces individual Douglas-fir trees that are 2-3 inches larger in diameter depending in part on the initial diameter of the hemlock (Fig. 2). This difference would almost certainly be larger at lower foliage retention, although where foliage retention has remained at such low levels, optimal selection of residual trees in a thinning operation becomes considerably more obvious. To illustrate general application of the graphs, assume that an 8-in western hemlock tree was growing next to a Douglas-fir tree in a stand with foliage retention of 2.0 years. In this case, the Douglas-fir tree would have to be 11 inches in diameter to produce the same basal area increment as the western hemlock. This conclusion, of course, is a consequence of the assumptions made to generate the field guides, as well as observed growth patterns in the SNCC Growth Impact Study. Other factors that would enter into the decision include the relative stand-level productivity of the two species (partly reflected in diameter growth differences at a given stand density), the relative value of the two species, and other stand management objectives besides timber production or maximization of economic return.

Under a stand management objective of maximizing economic return, conclusions from the analysis and graphs developed in this study would have to be further modified to the degree that market values of Douglas-fir and western hemlock diverge. In the third quarter of 2011, the delivered price for Number 2 Douglas-fir and western hemlock sawlogs in NW Oregon was \$530/mbf and \$455/mbf, respectively, or a difference of \$75/mbf. These prices during the same period five years earlier (and ten years earlier) were \$580/mbf and \$385/mbf, or a difference of \$95 (http://www.oregon.gov/ODF/STATE_FORESTS/TIMBER_SALES/logpage.shtml). During pre-commercial thinning operations, currently log prices are not as important as long-term projections, but the improved markets for western hemlock during the last two years underscores the appeal of considering the relative growth potential of individual trees and corresponding stand-level differences in potential productivity (e.g., McArdle et al. (1961) versus Barnes (1962)), in addition to current value differentials.

Conclusion

The foliar losses of Douglas-fir imposed by SNC reduce Douglas-fir crown density and diameter increment, thereby enhancing diameter increment of western hemlock, the most common associate of Douglas-fir in coastal forests of Oregon. Application of Douglas-fir and western hemlock diameter increment models indicates that the relative basal area growth of the two species in young, mixed stands varies directly with foliage retention. When thinning in mixed stands where foliage retention is as low as 1.5 yrs, western hemlock trees will grow more in basal area than Douglas-fir tree that are 2-3 inches larger in diameter. These results can be useful for forest managers who can prescribe “D+x” thinning where x represents the diameter advantage that Douglas-fir must have over an adjacent western hemlock to be selected as the leave tree. In this approach, “x” would be selected as a function of SNC intensity as measured by foliage retention.

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Table 1. Summary of tree and stand characteristics in Swiss Needle Cast Cooperative database for modeling individual-tree diameter growth of Douglas-fir and western hemlock in the Oregon Coast Ranges.

	Douglas-fir (13416 observations)				Western hemlock (2695 observations)			
Variable	Mean	Std Dev	Min	Max	Mean	Std Dev	Min	Max
Dbh (inch)	8.03	3.22	0.04	22.56	6.32	3.57	2.28	40.71
CR	0.74	0.16	0.02	1.00	0.82	0.13	0.23	1.00
BAL (ft^2/acre)	70.31	45.31	0.00	227.13	98.03	60.22	0.00	233.40
CCFL (ft^2/acre)	93.66	58.25	0.00	310.20	129.29	74.50	0.00	324.11
ΔDBH (inch/yr)	0.13	0.10	0.00	0.62	0.14	0.11	0.00	0.60
Age (yr)	22.20	5.77	11.00	38.00	22.17	6.96	11.00	38.00
FR(yr)	2.38	0.44	1.01	3.85	2.33	0.43	1.29	3.28
BA (acre)	117.99	47.00	2.90	233.90	134.42	55.11	16.01	233.90
CCF (ft^2/acre)	176.62	59.29	20.63	336.86	194.44	63.31	39.93	324.69
D40 (inch)	11.10	3.03	2.30	19.29	11.69	3.60	4.23	18.81
H40 (feet)	54.90	14.89	14.13	112.00	56.69	15.82	20.75	89.48
TPA (trees/acre)	389.91	169.52	101.01	1166.67	507.26	228.95	166.67	1166.67
QMD (inch)	7.74	2.30	1.51	14.28	7.26	2.18	3.32	12.89
SDI (inch)	234.80	84.00	11.11	459.28	273.86	98.89	43.53	459.28

Table 2. Parameter estimates and their standard errors for the Douglas-fir and western hemlock diameter growth models (equations [1] and [2]).

		Douglas-fir		Western hemlock	
Parameter	Variable	Estimate	Standard Error	Estimate	Standard Error
α_0	Intercept	-1.5203	0.0801		
α_1	CCFL	-0.00524	0.0002		
α_2	(CR+0.2)/1.2	1.4058	0.0408		
α_3	DBH/D40	1.4153	0.0465		
α_4	1/FR	-1.2079	0.1366		
α_5	BAL/BA	0.7286	0.0372		
α_6	1/DBH	0.08365	0.0033		
σ_δ^2		0.04425	0.0040	0.07247	0.0107
β_0	Intercept			0.7162	0.1943
β_1	BAL/DBH			-0.04010	0.0009
β_2	FR			-0.2044	0.0633
β_3	H40			-0.0134	0.0018

Table 3. Parameter estimates and their standard errors for the relationship between mean diameter and mean height of the 40 largest (by diameter) trees per acre in the SNCC growth impact database (equation [3]).

Parameter	Estimate	Standard Error
γ_1	183.78	7.8417
γ_2	-15.4372	0.7076
γ_3	8.2973	1.6048
σ_δ^2	50.5173	9.3193

Figure 1. Diameter increment of Douglas-fir and western hemlock for a given initial diameter and SNC severity (foliage retention) in a stand with average total basal area. Douglas-fir CCFL and BAL were set to zero, Douglas-fir D40 and CR were set at the the GIS database average, western hemlock BAL was set at total Douglas-fir basal area, and H40 in the western hemlock equation was estimated from equation [3].

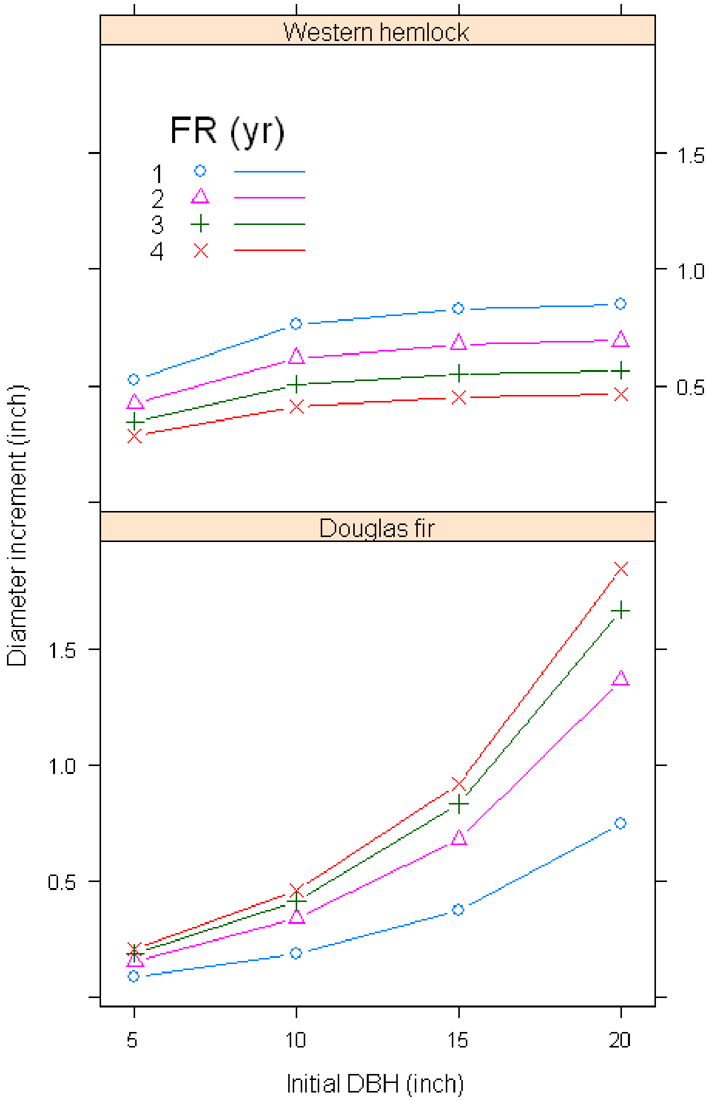
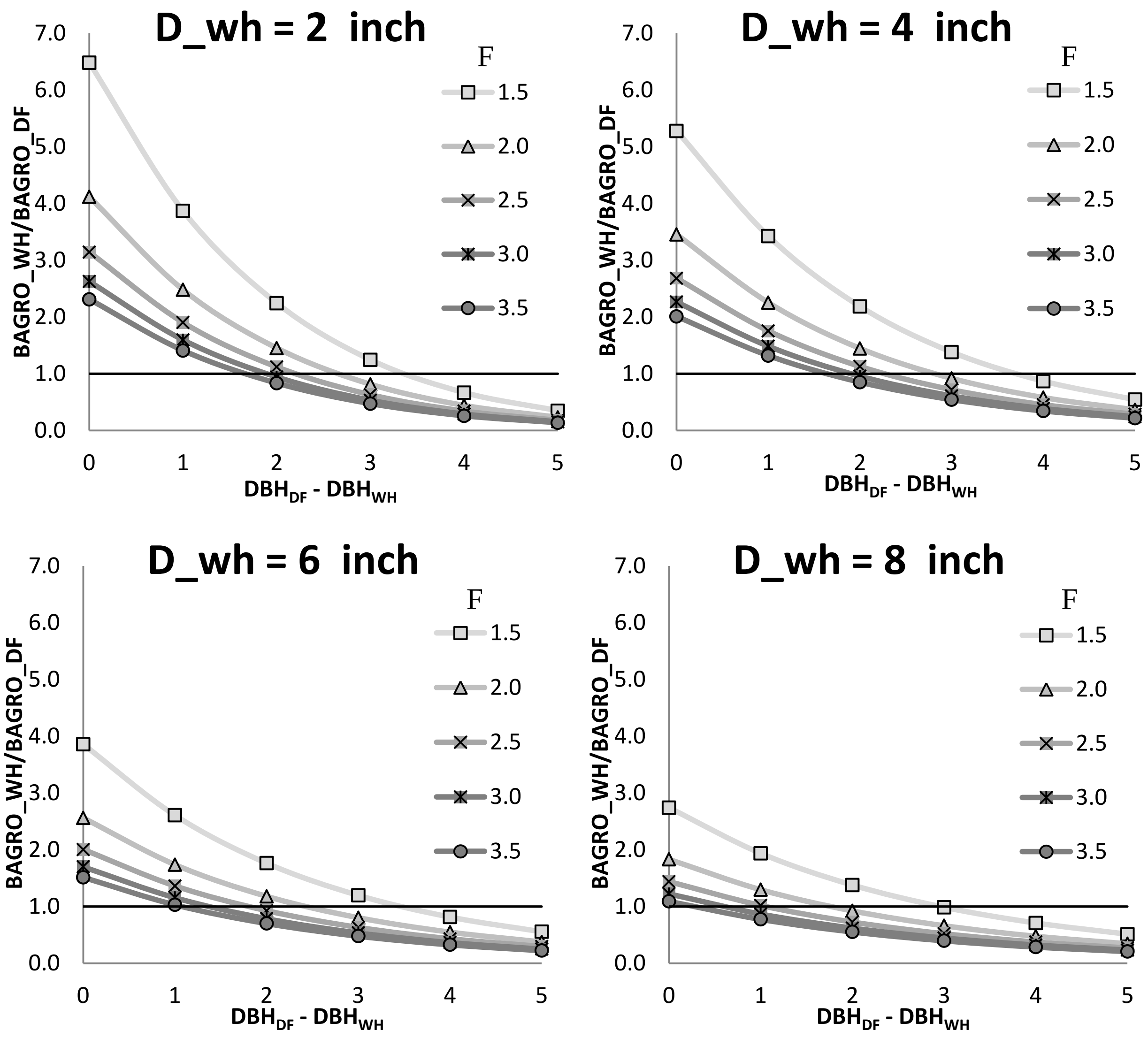
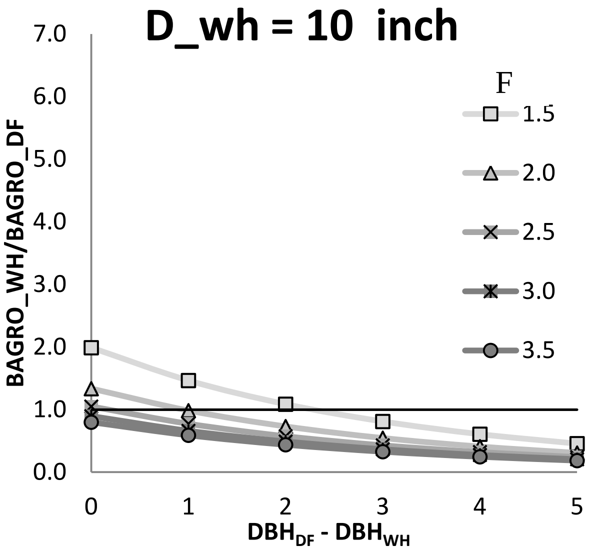
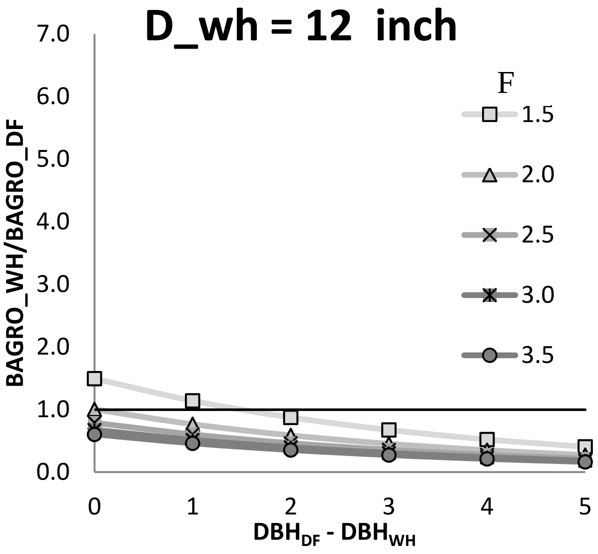


Figure 2. Ratio of western hemlock to Douglas-fir basal area growth (BAGRO_WH/BAGRO_DF) as a function of size differential (DBH_{DF} - DBH_{WH}) between Douglas-fir and western hemlock (assuming Douglas-fir is larger) under different initial diameters of western hemlock (D_WH) and SNC severity (foliage retention).




D_wh = 10 inch
BAGRO_WH/BAGRO_DF
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
0
1
2
3
4
5
DBH$_{DF}$ - DBH$_{WH}$
F
1.5
2.0
2.5
3.0
3.5


D_wh = 12 inch
BAGRO_WH/BAGRO_DF
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
0
1
2
3
4
5
DBH$_{DF}$ - DBH$_{WH}$
F
1.5
2.0
2.5
3.0
3.5

Western hemlock growth response to declining Douglas-fir across a gradient in SNC intensity

Junhui Zhao, Douglas A. Maguire, Douglas B. Mainwaring,
Department of Forest Engineering, Resources and Management, College of Forestry, Oregon State University

Alan Kanaskie
Oregon Department of Forestry

Abstract

Western hemlock is major commercial tree species in coastal forests of Oregon and Washington, and is associated with Douglas-fir in mixed-species stands. Growth of Douglas fir in these coastal forests has been negatively affected by Swiss needle cast (SNC), a foliar disease causing premature foliage loss on infected Douglas-fir trees. The effect of SNC on stand dynamics in mixed Douglas-fir-western hemlock stands was assessed by constructing a diameter increment model for western hemlock that quantified its growth acceleration in response to decline in Douglas-fir caused by increasing SNC severity. Both foliage retention and the change in foliage retention on Douglas-fir were negatively correlated with diameter increment of western hemlock. Compared with relatively healthy stands having foliage retention of 3.5 yrs, western hemlock trees in severely impacted stands (foliage retention = 1.5 yr) averaged 45% greater diameter growth. Western hemlock surpasses Douglas-fir in mixed stands subject to severe SNC and provides an economically viable alternative species in mixed or pure stands.
Key Words: SNC, western hemlock, stand dynamics, foliage retention, diameter increment, mixed-species stands.

Introduction

Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) is a major commercial tree species in coastal forests of the northwestern United States and Canada (Packee 1990). This native conifer exhibits rapid growth and accumulates large stem volumes due to its relative shade tolerance and longevity. In mixed stands, western hemlock most commonly grows with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), Sitka spruce (*Picea sitchensis*), western redcedar (*Thuja occidentalis*), grand fir (*Abies grandis*), and/or red alder (*Alnus rubra*). Because Douglas-fir has historically been of greater economic value than hemlock or any other associated species, it has been grown as a preferred species in coastal forests of the Pacific Northwest. The proportion of Douglas-fir planted in the *Picea sitchensis* coastal fog belt has increased over the last forty years, and may be a contributing factor to the current epidemic of Swiss needle cast (SNC), a foliar disease of Douglas-fir (Hanson et al. 2000). In some areas of severe SNC, Douglas-fir plantations have failed, and in other areas this species can drop out of the stand due to superior growth and overtopping by associated species. With the continued prevalence of SNC and the increasing relative economic value of western hemlock, interest in the latter species has increased among private and public landowners within the coastal belt of the Oregon Coast Ranges.

Numerous silvicultural strategies have been considered as a means of mitigating the growth losses suffered by Douglas-fir in the presence of SNC, including thinning (Mainwaring et al. 2005), fertilization (Mainwaring et al. 2005), use of genetically tolerant trees (Johnson 2002, Temel et al. 2005), and fungicidal treatment (Mainwaring et al. 2002, Mainwaring et al. 2009). Although these strategies may all helped mitigate growth losses, support for conversion to a non-susceptible species such as western hemlock has gained momentum due to declining value differential, continued growth losses in Douglas-fir (Maguire et al. 2011), and an expanding area with visible SNC symptoms (even after accounting for thousands of harvested and converted acres; Kanaskie and McWilliams 2011).

In healthy mixed stands of Douglas-fir and western hemlock, Douglas-fir generally exhibits greater height growth and over time and becomes the dominant species within an even-aged, stratified stand (Wierman and Oliver 1979). Because western hemlock is shade tolerant, it can persist and grow in both dominant and sub-dominant canopy layers. In SNC-impacted stands that suffer significant Douglas-fir foliar loss (foliage retention =1.5 yrs), Douglas-fir LAI has been found to drop by 31% relative to healthy stands (Weiskittel and Maguire 2007). This degree of Douglas-fir foliar loss in mixed stands is advantageous to western hemlock in two ways: 1) greater light penetration through the upper canopy enhances light availability to the subordinate species; and 2) loss of foliage results in diminished diameter growth (Zhao et al. in review), height growth (Garber et al. 2007), and crown expansion of Douglas-fir (Weiskittel 2003), thereby reducing its ability to compete with non-susceptible species. The objectives of this study were: 1) to test the hypothesis that western hemlock accelerates its diameter growth in response to increasing SNC severity in mixed-species stands; and 2) to quantify the release effect of SNC on western hemlock diameter growth in mixed stands. In pursuit of these two objectives, a diameter increment model for western hemlock (Hann et al. 2003) was modified and fitted to data from the growth impact study implemented by the Swiss Needle Cast Cooperative (SNCC: http://sncc.forestry.oregonstate.edu/). Swiss needle cast effects were accounted for by including two additional covariates, Douglas-fir foliage retention and change in foliage retention over the growth period. Results from this study were intended to describe the change in stand dynamics imposed by SNC and to assist silvicultural decision-making in mixed stands of Douglas-fir and western hemlock experiencing a range in SNC severity.

Methods

Data for this analysis came from the SNCC Growth Impact Study. The target population was the collection of 10- to 30-yr-old Douglas-fir plantations in north coastal Oregon (Maguire et al., 2011). Plots were distributed across a range of SNC severity with the objective of estimating current growth impacts on the target population and monitoring change in disease symptoms and the relationship between disease symptoms and growth loss.

Field work

A list of all 10- to 30-yr-old Douglas-fir stands was first compiled in 1996, with geographic bounds defined by Astoria to the north (N46°11',W123°50'), Newport to the south (N44°38', W124°04'), the Pacific Coast to the west (W124°05'), and the crest of the Oregon

Coast Ranges to the east (W123°30'). A set of 76 stands was randomly selected from this list and square, 0.08-ha permanent plots were established in the late winter/early spring of 1998. 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. After two, four, and six growing seasons, all trees were remeasured for dbh, and all undamaged trees from the original height subsample were remeasured for total height and height to crown base. Some plots contained a significant amount of western hemlock (*Tsuga heterophylla*), as well as various broadleaved species, most commonly cascara (*Rhamnus purshiana*), red alder (*Alnus rubra*), and red elderberry (*Sambucus racemosa*). Other conifers that occurred less frequently included Sitka spruce (*Picea sitchensis*), western red cedar (*Thuja plicata*), noble fir (*Abies procera*), and grand fir (*Abies grandis*). Other hardwood species includes bitter cherry (*Prunus emarginata*) and bigleaf maple (*Acer macrophyllum*).

Ten dominant or codominant trees on each plot were also scored for SNC at time of plot establishment in 1998, and just prior to bud break in years 1999-2003. Needle retention of individual trees was visually estimated by first dividing the live crown into thirds, with the base of the live crown defined as the lowest live branch. Secondary or lateral branches on a primary or main branch were then examined in the center of each third, and the average number of needle age classes present at time of sampling was estimated to the nearest 0.5 yr (Maguire et al. 2002). The needle retention of the tree was then estimated by averaging these values across the crown thirds. Plot level foliage retention was averaged using all foliage retention from all 10 trees in the plot.

Statistical Analysis

Periodic annual diameter increment of western hemlock was calculated for all tagged western hemlock trees that survived at least one growth period. Predictor variables represented initial tree size, relative position of the tree in the stand, stand density, stand age/size, site quality, and SNC severity (Tables 1 and 2). Transformations were also tested for all variables, including the natural logarithm, square, and inverse transformation.

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

The sampling scheme has a distinct hierarchical structure (multiple measurements within trees, and within plots), therefore violating the assumption that error terms were independent and uncorrelated. Alternative diameter increment models were fitted to the western hemlock data with PROC NLMIXED in SAS 9.2 (SAS Institute Inc., 2008), with plot as the random effect. The plot effect was tested by adding a random plot term to each of the parameters, and also an additive term to the whole model. Final models were chosen on the basis of residual analysis, Akaike's information criterion (AIC) and biological interpretability. Variables retained in the final model were all significant at $\alpha=0.05$ level. The models were evaluated quantitatively by examining the magnitude and distribution of residuals for all possible combinations of variables. The aim was to detect any obvious dependencies or patterns that indicate systematic discrepancies. The accuracy of the model was assessed by the residual variation represented by the MSE and a form of the coefficient of multiple determination computed as follows:

$$R2 = 1 - \frac{\sum_{i=0}^{n}\left(\Delta \mathrm{dbh} - \widehat{\Delta \mathrm{dbh}}\right)^2}{\sum_{i=0}^{n}\left(\Delta \mathrm{dbh} - \overline{\Delta \mathrm{dbh}}\right)^2}$$

where Δdbh is the observed periodic annual diameter increment, $\widehat{\Delta \mathrm{dbh}}$ is the predicted periodic annual diameter increment, $\overline{\Delta \mathrm{dbh}}$ is the average value of observed periodic annual diameter increment, n is number of observations.

The hypothesis representing the first objective of this analysis was met by testing the effect of foliage retention and change in foliage retention on western hemlock diameter growth in the final mixed-effects model. The second objective was met by constructing graphs that depicted western hemlock growth as a function of initial foliage retention and annual change in foliage retention.

Results

The initial DBH of western hemlock within this dataset had a large range (5.7 -103.4 cm), though most trees varied from 10 to 40 cm. Diameter increment varied between 0.0 and 2.5 cm/yr (Fig. 1). The periodic annual change in foliage retention varied from -0.38 to 0.47 yrs/yr, though most plots changed by and increase or decrease of only 0.1 yr (Fig. 2). The final diameter increment equation for western hemlock included variables representing initial tree size, stand density, and SNC severity:

[1]

$$\begin{array}{l}
\Delta \mathrm{dbh} = \exp(0.3002 + u - 0.1379*(BAL/\ln(DBH)) - 0.00122*SDI - 7.1361*DBH^{-1} \\
\qquad\qquad (0.2588)\ (0.02716)\ \ (0.01408) \qquad\qquad (0.000127) \qquad (0.5242) \\
\qquad + 0.8842*FR^{-1} - 0.4703*\ln(\Delta FR+1) + 0.005554*CCFL + 0.203*SI - \\
\qquad\quad (0.2451) \qquad (0.07425) \qquad\qquad (0.000842) \qquad\quad (0.004200) \\
\qquad 0.00201*DBH*FR \\
\qquad\ (0.000993)
\end{array}$$

with $u \sim normal(0, 0.09474)$.

Diameter at breast height, SI, and CCFL were positively correlated with western hemlock diameter increment. Conversely, as social position of the tree in the stand declined (increasing BAL) and as total stand density increased, western hemlock diameter growth declined. The null hypothesis that foliage retention has no effect on western hemlock growth was rejected; in fact, diameter growth of this species increased with lower initial foliage retention in Douglas-fir, and with a further decline in foliage retention over the growth period (ΔFR). Likewise, the positive effect of increasing initial diameter on hemlock diameter growth was damped by increasing foliage retention on Douglas-fir, further indicating that hemlock diameter growth benefited from increasing SNC severity. The residual analysis represented by observed plotted on predicted diameter growth (Fig. 3) indicated that the models provided a good fit to the data. The western hemlock diameter increment model explained approximately 73% of the variation of diameter growth ($R^2 = 0.726$). The residual variance of the model was 0.09347, with standard error of 0.002793.

In the course of applying the model for graphical summary, only fixed effects can be assessed. Graphs were produced from the final model by assuming a SI of 44 m and an SDI of 600. Diameter growth response was evaluated over a range in initial western hemlock dbh from 10 to 40 cm, in Douglas-fir foliage retention from 1.5-3.5 yrs, and in periodic annual change in Douglas-fir foliage retention from -0.4 to 0.5 yr (Fig. 4).

In a healthy stand (foliage retention = 3.5 yr), the diameter increment of a tree with a dbh =10, 20, 30, and 40 cm averaged 0.57, 1.00, 1.13, and 1.17 cm/yr. As foliage retention decreased, diameter increment of western hemlock increased. For western hemlock trees covering an initial diameter range of 10-40 cm on plots with foliage retention of 3.0, 2.5, 2.0, and 1.5 yr, the diameter increment of western hemlock would increase relative to a healthy stand by 5.4-8.6%, 12.9-19.9%, 24.6-36.4%, and 45.8-64.5%, respectively (Fig. 5). For a given foliage retention, western hemlock diameter increment would also be affected by whether the Douglas-fir foliage retention changed over the growth period in question. For a given initial foliage retention, the hemlock diameter increment decreased by an average of 4.4%, 8.2%, 11.6%, 14.6% and 17.4% if the foliage retention increased by 0.1, 0.2, 0.3, 0.4, and 0.5 yr; conversely, the increase in hemlock diameter increment averaged 5.1%, 11.1%, 18.3% and 27.2% if Douglas-fir foliage retention decreased by 0.1, 0.2, 0.3, and 0.4 yr.

Discussion

Swiss needle cast has had a strong influence on stand dynamics of mixed stands of Douglas-fir and western hemlock. As would be expected, the diminishing canopy density of Douglas-fir stands with severe SNC provide considerably more light to natural or planted western hemlock than would be the case in stands with very low SNC severity. Likewise, the Douglas-fir growth reductions leave more resources available for western hemlock growth.

The relationships represented within the diameter increment model were similar to those found in other diameter growth models that have been fitted to more comprehensive databases; for example, the tree size and stand variables all have the expected correlations with diameter increment. The interaction term of foliage retention and initial western hemlock diameter reflects the greater capacity of a larger tree to respond to an increase in resources. Among the variables representing competition, BAL/ln(DBH) showed the expected negative correlation with diameter increment, while diameter increment unexpectedly increased with increasing CCFL. This result may be a consequence of collinearity between CCFL and species composition. Because CCF is influenced by species composition through their crown widths at a given dbh, CCF and CCFL may in part indicated species composition. Western hemlock usually has a smaller crown width than a Douglas-fir when dbh is less than 50 cm, but a larger crown width when diameter exceeds 50 cm (Hann 1997). Red alder, another common associate of western hemlock in coastal stands (and within this dataset), also tends to have wider crowns than hemlock (Hann 1997). Because most of the trees in this dataset have a diameter less than 50 cm, larger CCFLs may have implied a higher proportions of Douglas-fir or red alder in the overtopping stand component. Douglas-fir with severe SNC and red alder under most conditions have sparser crowns, and therefore may have promoted greater diameter growth in hemlock trees occupying lower crown classes.

The phenomenon of increased growth of non-host trees following defoliation of host-tree neighbors has been recorded following other pest outbreaks. Tulip-tree and ash exhibited increased diameter increment following defoliation of species more susceptible to Gypsy moth in the NE United States (Muzika and Leibhold 1999). The effect of western spruce budworm defoliation on diameter growth of non-host species in the Rocky Mountains depended on species, pre-outbreak stand structure, and the degree and duration of defoliation (Hadley and Veblen 1993). Ponderosa pine was especially responsive to severe or extended outbreaks. These previous observations in other forest systems suggest that the significant response of western hemlock diameter growth to Douglas-fir defoliation can be partly explained by the gradual and long-term nature of the current SNC outbreak.

Studies looking at the effects of defoliation by pests within other forest types have found other evidence of shifting stand dynamics besides changes in relative diameter growth (Moore and Hatch 1981, Hadley and Veblen 1993). Relative height growth between species, for example, has shifted in target Douglas-fir stands of north coastal Oregon. Height of naturally regenerated western hemlock has in some cases surpassed that of planted Douglas-fir over the last 10 years, as exhibited by the change in relative position of height-diameter curves from plots that contained substantial numbers of both species (Fig. 6).

This analysis of individual tree growth on SNCC growth impact plots revealed the correlation between enhanced western hemlock growth and low Douglas-fir foliage retention. However, the gradient of increasing foliage retention on Douglas-fir found in the Oregon Coast Range also parallels a gradient of declining hemlock abundance (Schrader 1998, Ohmann and Spies 1998), and to some extent a gradient in declining productivity (Meurisse 1976), suggesting that some caution must be exercised in interpreting cause and effect. Site factors related to the decreasing abundance of hemlock on a west to east transect are likely the warmer summer temperatures, lower precipitation, and increasing vapor pressure deficits associated with distance from the coast (Taylor and Hannan 1999), and are manifest in the poor performance of hemlock seedlings relative to Douglas-fir under such conditions (Livingston and Black 1987). Western hemlock site productivity in the northern Oregon Coast Range has also been found to be negatively correlated with elevation (Meurisse 1976), a trend that is difficult to separate from all the other environmental factors that vary with distance from coast. The elevational effect itself is largely climatic, although chemical and physical soil characteristics may also involved (Meurisse 1972).

Even in the absence of Swiss needle cast, an improvement in hemlock growth relative to Douglas-fir would be expected nearer the coast. Although Douglas-fir generally exhibits greater height growth than western hemlock on the same site, this is not always the case (Steinbrenner 1976, Nigh 1995). In the presence of SNC, Douglas-fir also suffers height growth loss (Maguire et al. 2002), so the more competitive height growth of western hemlock is likely to be magnified with increasing foliage loss associated with proximity to the coast. Ultimately, the increase in diameter and height growth of western hemlock growth relative to Douglas-fir with severe SNC may not be entirely attributable to lower canopy needle density under low Douglas-fir foliage retention. Testing these effects separately would be difficult because the geographic distribution of the disease is not independent of gradients in various climatic factors to which the growth of western hemlock responds even in pure stands.

In forests managed for timber production along the Pacific coast, harvested stands are generally replanted to Douglas-fir or western hemlock (Briggs 2007), with the favored species depending on site, market, and disease conditions. It would be improper to apply this diameter increment model to stands that do not match the target population for the SNC growth impact study, i.e., 10-30-yr-old stands with at least 90% Douglas-fir basal area in 1996. However, due to severe impact of SNC on Douglas-fir growth in some of these stands (Maguire et al. 2011), and the high fedundity of western hemlock (Packee 1990) on wetter sites occupied by this population, the shifts in stand dynamics are important for making silvicultural decisions, particularly residual stand structure (including composition) after thinning. The information provided by this analysis of western hemlock growth in Douglas-fir stands of varying Swiss needle cast intensity should help prioritize stands and trees for silvicultural treatment.

Acknowledgements

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Table 1 Statistics of tree level variables

Variable	**Definition**	**Unit**	**N**	**Mean**	**Std Dev**	**Minimum**	**Maximum**
Dbh	Diameter at breast height (1.37m)	cm	2288	14.90	8.79	5.70	103.4
ht	Total tree height	m	2288	14.96	5.46	5.38	35.08
BAL	Basal area in larger trees	m^2/ha	2288	21.11	12.93	0.00	50.53
CCFL	Crown competition factor in larger trees	m^2/ha	2288	126.56	72.33	0.00	320.87
Δdbh	Annual increment of dbh	cm/yr	2288	0.82	0.58	0.00	3.05

Table 2 Statistics of plot level variables

Variable	Definition	unit	N	Mean	Std Dev	Minimum	Maximum
SI	Bruce's (1981) 50 years Site index	m	116	43.63	6.88	25.40	63.10
FR	Foliage retention	years	116	2.28	0.43	1.29	3.28
Δ FR	Annual change of foliage retention	years	116	0.00	0.15	-0.38	0.47
Age	Stand age	years	116	22.38	6.10	11.00	36.00
D100	Average diameter of the largest 100 trees per hectare by dbh	cm	116	29.53	8.02	10.74	46.99
H100	Average height of the largest 100 trees per hectare by dbh	m	116	16.90	4.45	6.32	27.27
BA	Stand basal area per hectare	m^2	116	28.26	10.60	3.64	50.66
CCF	Crown competition factor calculated following Paine and Hann (1982)	m^2	116	179.32	55.05	39.53	321.44
TPH	trees per hectare	trees/ha	116	1009.19	416.57	407.55	2852.85
QMD	Quadratic mean diameter	cm	116	19.50	5.16	8.43	31.41
SDI	Stand density index		116	613.48	203.75	107.53	1113.96
DFBA	Douglas-fir basal area per hectare	m^2	116	20.04	9.20	1.54	40.26
OCBA	Other coniferous tree basal area per hectare	m^2	116	6.87	7.45	0.04	32.64
HWBA	Hardwood basal area per hectare	m^2	116	1.35	2.60	0.00	16.29
pctDFBA	Percent Douglas-fir basal area	%	116	0.71	0.24	0.14	1.00
QMDwh / QMDdf	Ratio of quadratic mean diameter of western hemlock by quadratic mean diameter of Douglas-fir	cm	116	0.85	0.41	0.26	2.83

Figure 1. Relationship between periodic annual diameter increment (PAI) and initial tree diameter at breast height (dbh) for western hemlock.

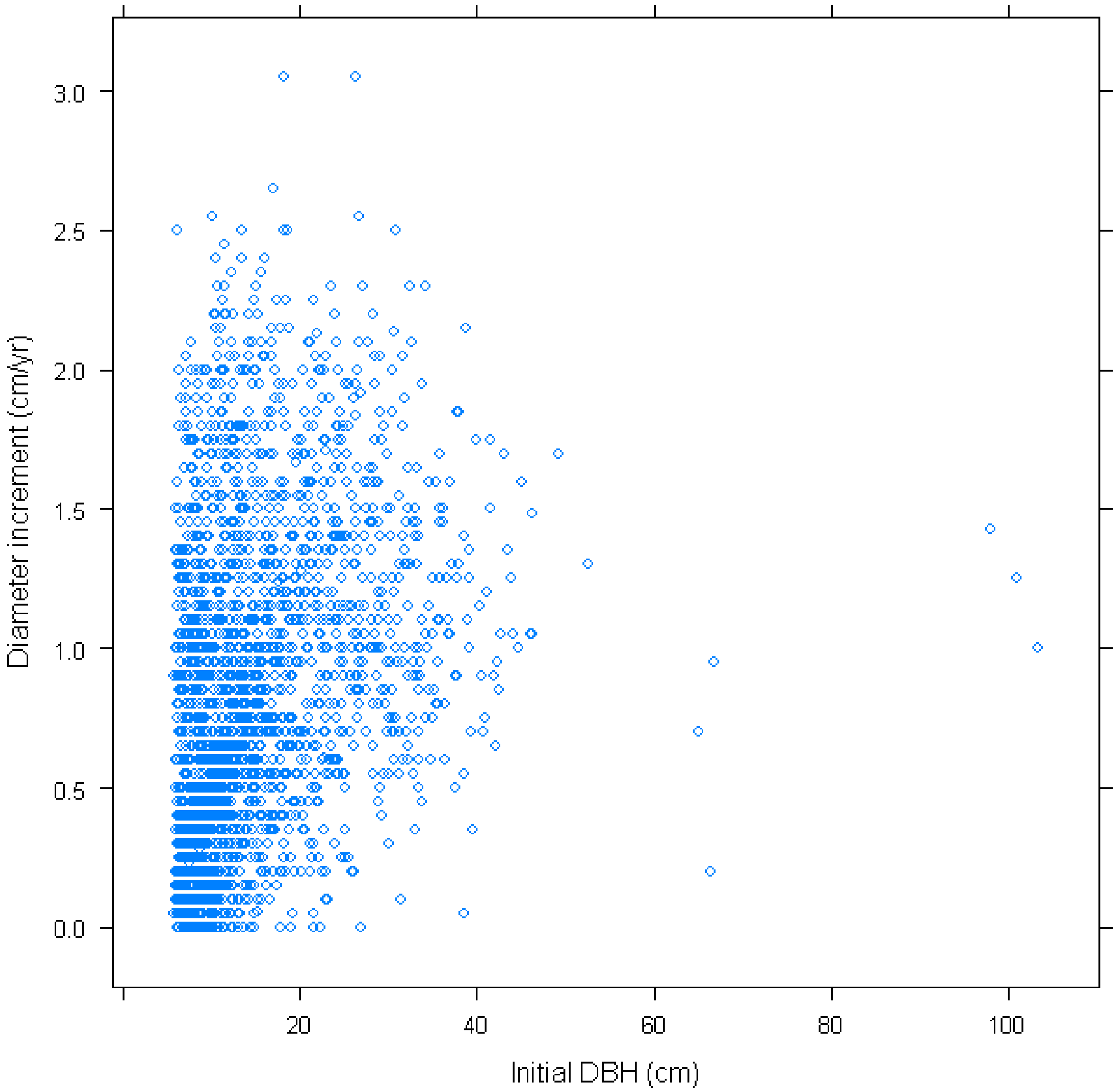


Figure 2. Frequency histograms of periodic annual change in foliage retention for individual western hemlock trees.

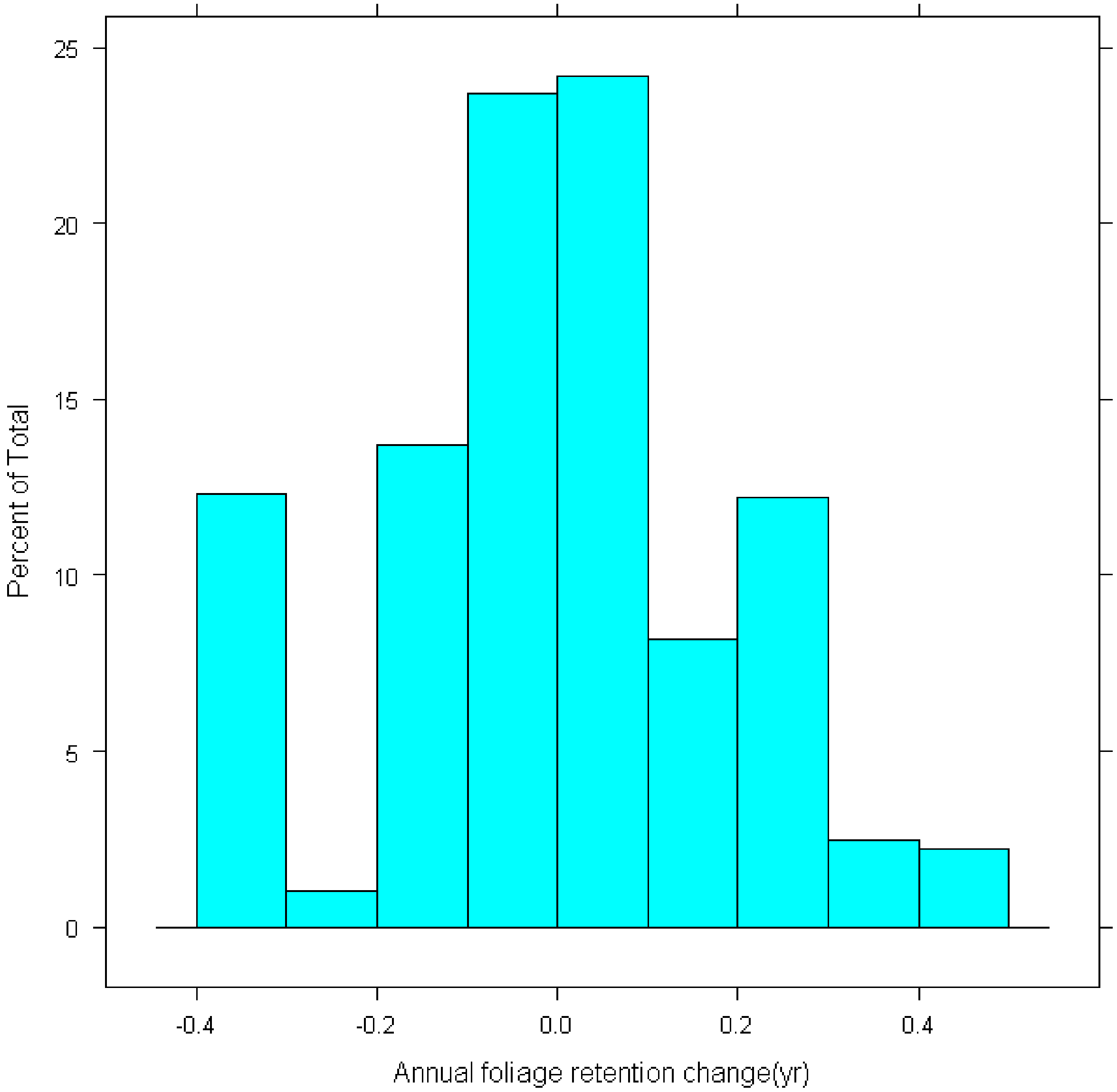


Figure 3. Observed diameter increment versus predicted diameter increment for western hemlock using equation [1].

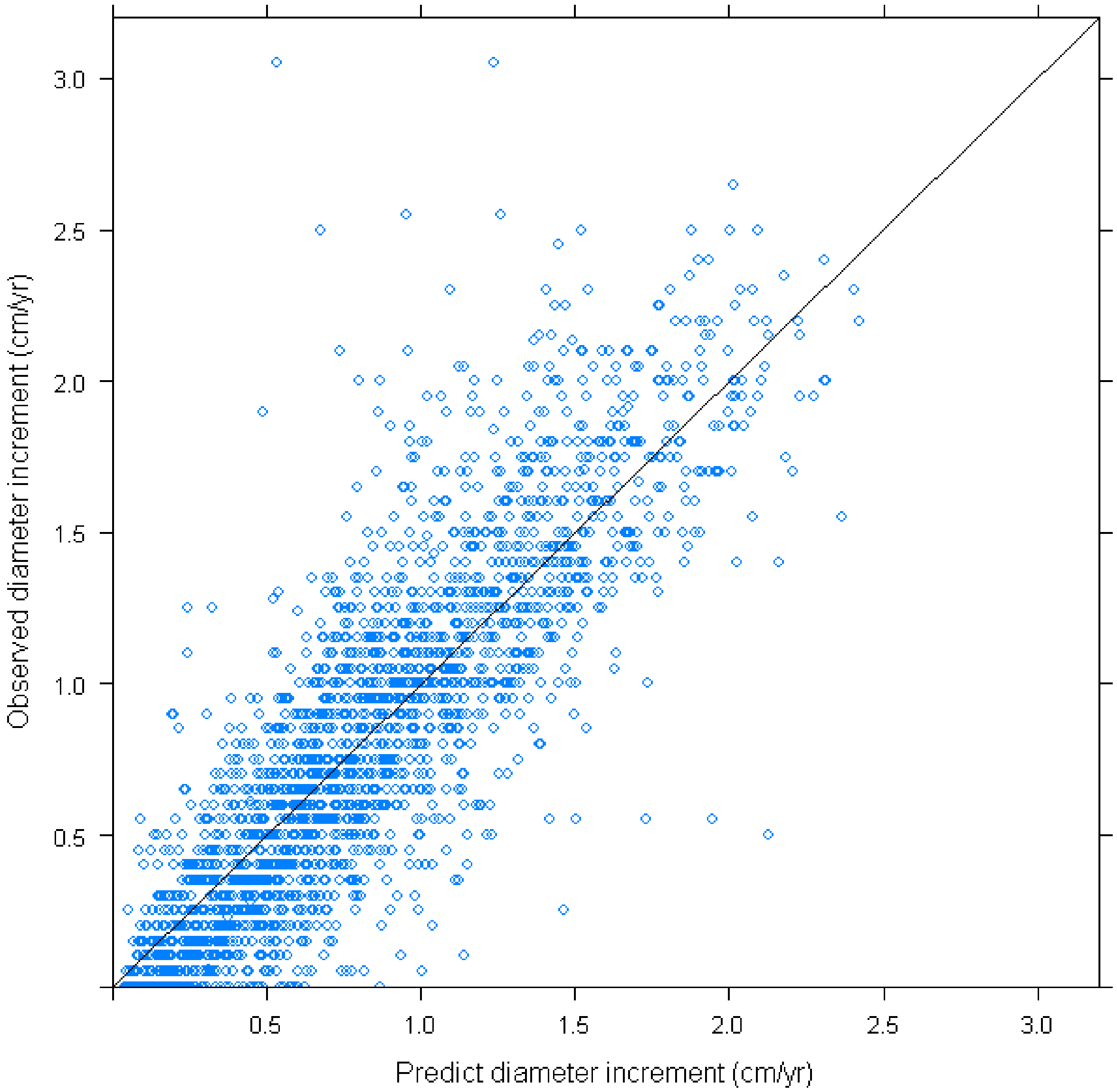


Figure 4. Diameter increment of western hemlock at different levels of foliage retention with different annual foliage retention change.

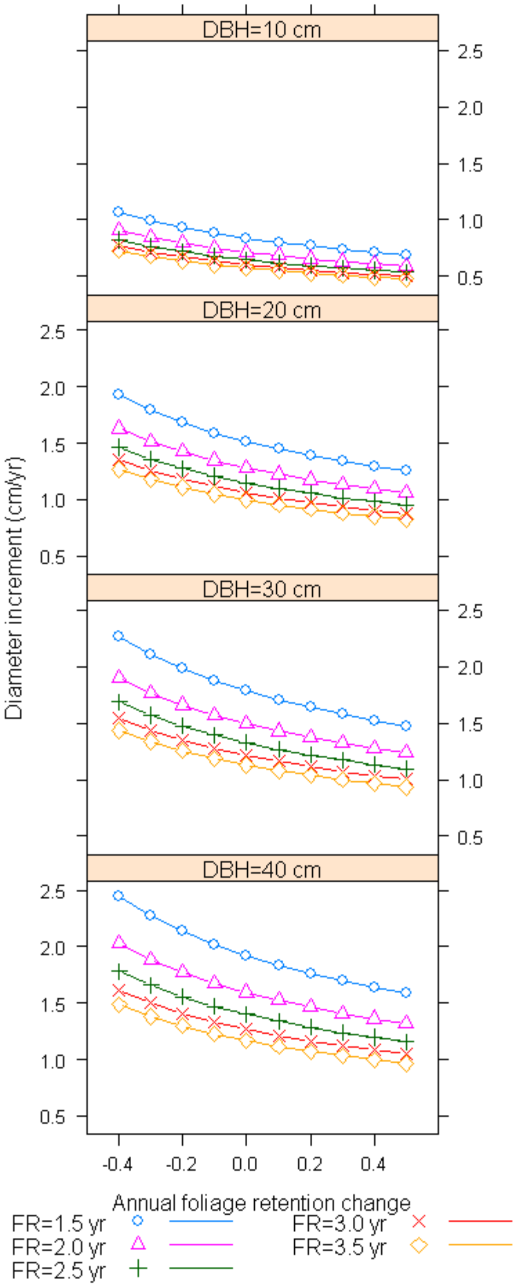


Figure 5 Proportional diameter increment of western hemlock by diameter relative to that implied in healthy Douglas-fir stands. Assumes no annual change in Douglas-fir foliage retention.

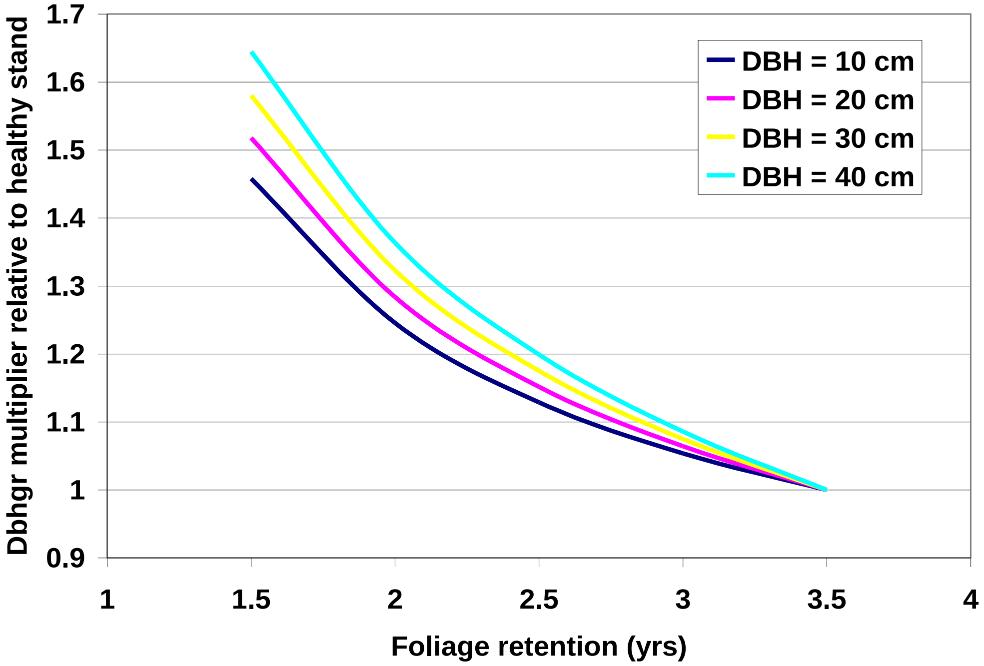
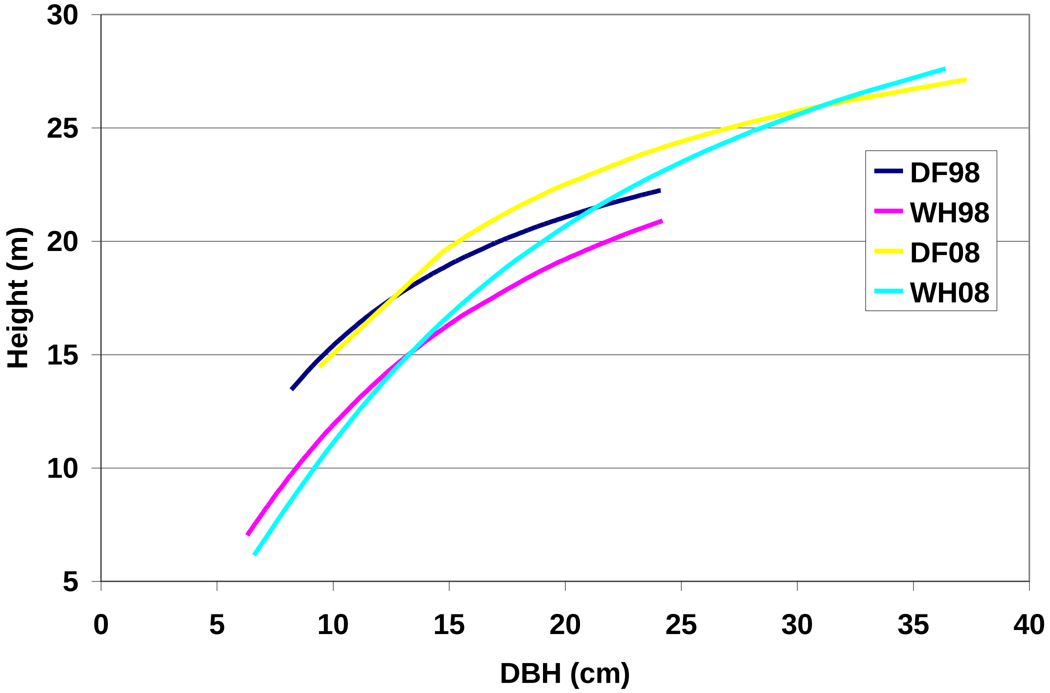


Figure 6 Douglas-fir and western hemlock height-diameter curves from plot 132 (1998 foliage retention of 1.68 years) in 1998 and 2008.



Fertilization impacts on Swiss needle cast disease severity in Douglas-fir

Robin L. Mulvey, David C. Shaw, Douglas A. Maguire
Department of Forest Engineering, Resources and Management, College of Forestry, Oregon State University

Abstract

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 as lime (calcium carbonate), calcium as 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. Fertilization treatment effects on infection index (mean fruiting body density) were tested by mixed-effects models that accounted for site as a blocking factor. Treatment effects on infection index at each of the study locations were also tested by ten separate ANOVAs. 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 ameliorates or exacerbates Swiss needle cast severity in western Oregon.

Keywords: Swiss needle cast, Douglas-fir, *Phaeocryptopus gaeumannii*, fertilization

Abbreviations: Swiss needle cast (SNC)

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, 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 and endemic within the range of Douglas-fir in western North America and was long considered innocuous in this region, a foliage epidemic affecting hundreds of thousands of acres has emerged in the Coast Range of Oregon and Washington since the 1990s (Shaw et al., 2011). Many questions have arisen about the potential of various silvicultural treatments to ameliorate the disease (Filip et al., 2000).

Several climate factors are correlated with moderate and severe disease. These include abundant leaf wetness from fog and precipitation during the sporulation period (especially 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; Zhao et al., 2011). 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 speculation about possible predisposing effects of N levels and nutrient imbalance on disease development and severity (El-Hajj et al., 2004). As a result, managers are interested in the potential of fertilization regimes that may ameliorate or offset growth losses from SNC, and currently avoid regimes that may exacerbate the 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 (Engelhard, 1989; Datnoff et al., 2007). 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).

Few 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 nutrient concentrations and disease severity do not allow causal inferences to be drawn, because nutrient concentrations are confounded with other environmental factors and tree physiological conditions. 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. *P. gaeumannii* infects through needle stomata, and then colonizes the intercellular region of host needles. 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. *P. 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 conditions, host nutritional status, or both (Manter et al., 2005).

Some have speculated that high levels of N relative to other macro and micronutrients may increase nutrient availability in the apoplast where it can be accessed by *P. gaeumannii* (El-Hajj et al., 2004; Perakis et al., 2005). In the region of the epidemic in the Pacific Northwest, foliar N levels often exceed the established 1.4% threshold for N-limitation in coastal Oregon Douglas-fir (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, which ranged from 0.85 to 1.74%, were positively correlated with soil N levels and negatively correlated with foliage retention. It was 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 in observational studies, as these factors covary with distance-from-coast along with many climatic variables that are known to strongly influence abundance of the causal fungus (Manter et al., 2005; Stone et al., 2008a).

N fertilization (as urea) has been a common management practice used to increase tree growth and yield, and timber growers in coastal Oregon and Washington are concerned that, in areas of moderate to severe SNC, N fertilization may worsen disease 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 (Personal communication M. Gourley, Starker Forests, Inc., Corvallis, OR, USA, Jan 2011). Influenced by theories regarding nutrient imbalance and SNC, some managers are fertilizing with lime to ameliorate growth loss from disease by lowering the ratio of N to other essential nutrients. 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 thoroughly 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 objective was pursued by implementing a controlled fertilization experiment at 16 study locations chosen to represent a range of disease severity (Unpublished: 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 responses to these fertilization treatments across a range of SNC severity has been reported separately (Unpublished: Mainwaring et al., 2009; Mainwaring and Maguire, 2010).

Material and Methods

Study Site Descriptions

Sites were distributed across a range in elevation, aspect and SNC severity from the Oregon and southwest Washington Coast Ranges 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 for at least seven years. Sites were broadly distributed through the region of interest and were chosen to avoid prior fertilization. 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 (Unpublished: Mainwaring et al., 2009; Mainwaring and Maguire, 2010).

Table 1
Name and site information for 10 Douglas-fir fertilization study sites in western Oregon assessed for Swiss needle cast disease severity.

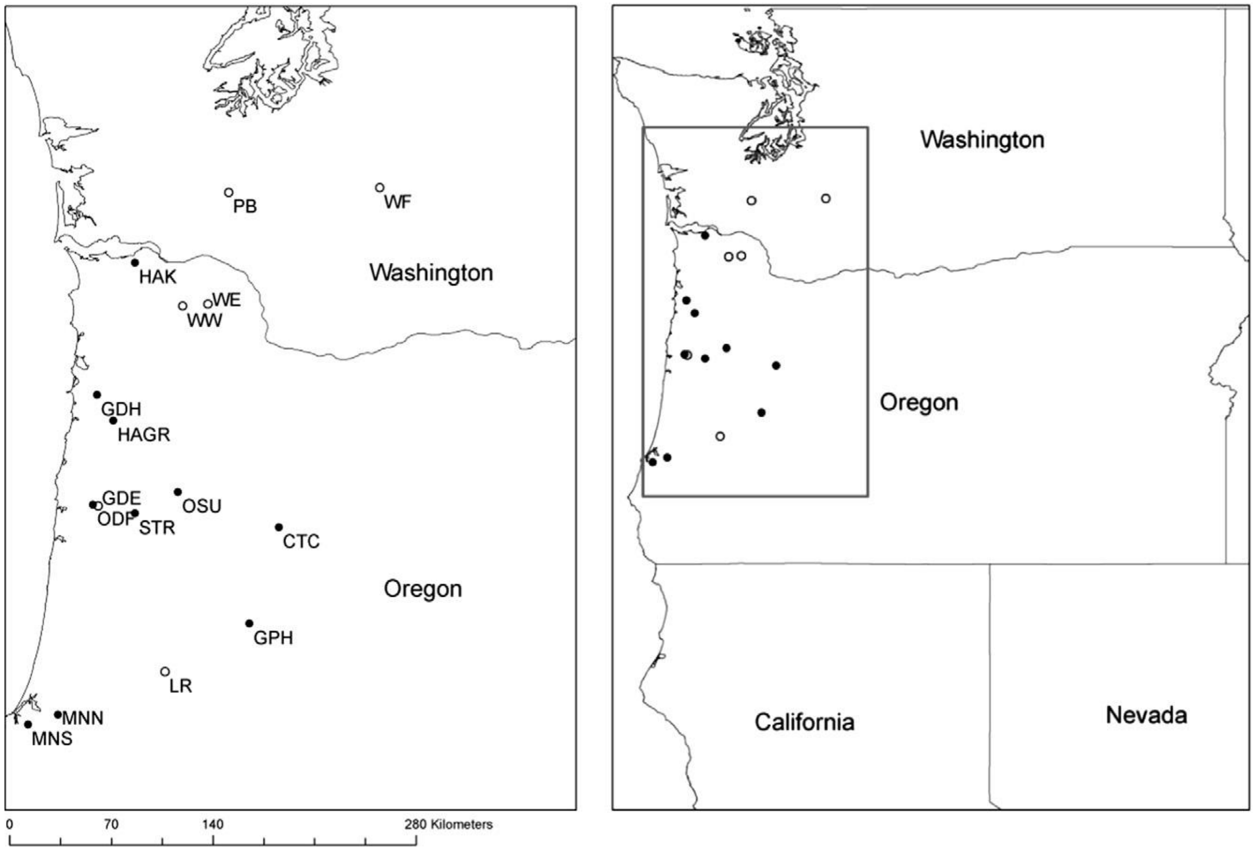
Site	Location	Landowner[a]	Location	Elevation (m)	Distance (km)[b]	Slope (%)	Aspect	Fol. Ret.[c]
GDH	Hemlock	Stimson (Green Diamond[a])	T3S, R9W, S8	122	11.6	10	S	1.62 (0.45)
MNS	Menasha-south	Cambell (Menasha[a])	T26S, R13W, S10	61	11.6	30	E	2.66 (0.71)
ODF	Elk City	Oregon Dept. Forestry	T11S, R10W, 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[a])	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)

[a] Landowner at start of study.

[b] Distance is km from the Pacific Ocean.

[c] Mean foliage retention (Fol. Ret.) provided for 2006 (pre-treatment); std. dev. in parentheses.

Fig. 1. Douglas-fir fertilization study locations in the Oregon and Washington Coast Ranges and the foothills of the Cascade Range, Pacific Northwest, USA. Black circles represent stands that were sampled for disease severity assessment; white 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) vegetation zone, which spans much of western Oregon and Washington (Franklin and Dyrness, 1973). 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 redcedar, Douglas-fir and red alder dominate this highly productive region (Franklin and Dyrness, 1973).

The more extensive *Tsuga hetrophylla* zone tends to experience relatively greater temperature and moisture extremes that 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 Ranges, organic matter is high. Dominant tree species include Douglas-fir and climax western hemlock and western redcedar (Franklin and Dyrness, 1973).

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 except the site-specific Kinsey blend (Table 2). One site (OSU) also received an N+P treatment (448 kg ha^{-1} N and 112 kg ha^{-1} P) in the form of 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); and 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 study sites in western Oregon. Kinsey treatment applications rates displayed in Table 3.

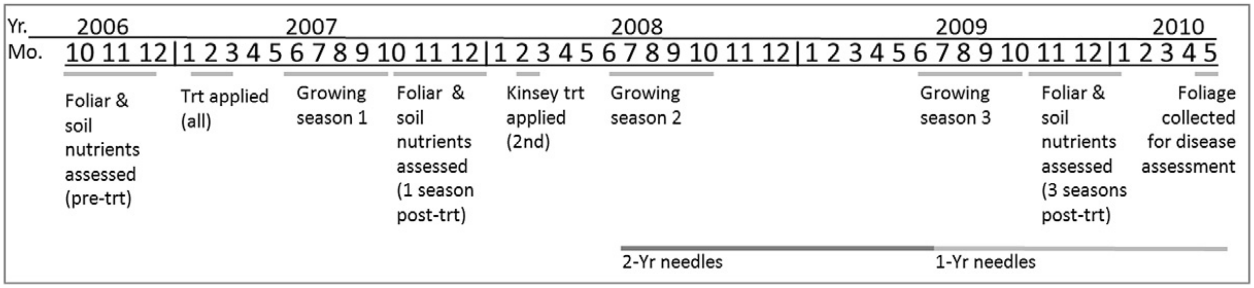
Treatment	**Material**	**Chemical**	**Material appl.**	**Elemental appl.**	**Expected outcome**
Control	-	-	-	-	-
N	urea	$(NH_2)_2CO$	493	225	increased N
Ca	lime (calcium carbonate)	$CaCO_3$	2915	1020	increased Ca & soil pH
Ca	calcium chloride	$CaCl_2$	291	105	increased Ca w/o pH change
P	monosodium phosphate	NaH_2PO_4	2240	580	increased P & soil pH

Table 3
Kinsey fertilization 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[a]								
	GDH	MNS	ODF	HAGR	MNN	HAK	STR	OSU	CTC
Fertilizer application rates (kg ha^{-1})									
NH_4H_2POH	255	255	255	255	255	255	—	255	255
K_2SO_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
$K_2Mg_2(SO_4)_3$	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^{-1})									
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

[a] Sites ordered by increasing distance from coast.

Fig. 2. Timeline of activities required for Douglas-fir the fertilization study, including foliar and soil nutrient analyses, treatment (trt) applications, and disease assessment relative to the three growing seasons.



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 subject or 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 subject 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 at the start of the experiment with the other fertilization treatments, and lime was applied during the following winter of 2007–08. Mineral soil samples were collected one and three growing seasons after treatment for assessment of fertilization impacts on soil chemistry.

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, treatments were designed to elevate the initial availability of a specific elemental nutrient, with the exception of the Kinsey regime that involved a blend of nutrients. Two Ca treatments were applied to distinguish between the impacts of Ca accompanied by increased soil pH (lime) and the impacts of Ca alone (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.

Foliage Collection for Disease Assessment & Foliar Chemistry

One- and two-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 higher order branches growing off of this lateral. One- and two-yr-old needles from each tree were stored separately in labeled polyethylene bags for disease severity assessment. The minimum number of needles for sampling a given age class on a given tree was set at 30, but 25 trees either had no new growth or retained insufficient 1- or 2-yr-old needles on the collected branch. At least seven of the ten trees per treatment had sufficient needles at each site; in total, 1120 samples from 565 trees were assessed for disease severity.

Branches were also collected before treatment (Oct-Dec 2006), one growing season after treatment (Oct-Dec 2007) and three growing seasons after treatment (Oct-Dec 2009) for foliar chemistry assessment (Fig. 2). One-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. One-yr-old needles collected in Oct-Dec 2009 for nutrient analysis were from the same cohort as the one-yr-old needles collected in May 2010 for disease severity assessment; i.e., both of these collections were made prior to the 2010 growing season. Foliar nutrients were assessed as percent or $\mu g\ g^{-1}$ dry weight.

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 midrib). 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.

Statistical Analyses

One-way ANOVA was used to evaluate treatment effects on soil and foliar chemistry across sites (Insightful Corp., S-PLUS, 2007). Needle age classes were analyzed separately for all comparisons related to disease severity. Mixed effects analysis was used to assess fertilization treatment effect on infection index (average pseudothecia density) after accounting for site as a random block effect, and also allowed for comparisons between infection indices of individual treatments and the control (Insightful Corp., S-PLUS, 2007). Beta-coefficients from mixed effects analysis were used to rank treatments across sites. One-way ANOVA was used to assess with-in site treatment differences in infection index, and beta-coefficients from these tests were used to rank treatments within sites (Insightful Corp., S-PLUS, 2007). Simple linear regression models evaluated the relationship between foliar nutrients and infection index of 2-yr-old needles at the site-level (Insightful Corp., S-PLUS, 2007). Site-level values were obtained by pooling and averaging infection indices for all sample trees at each site, and pooling and averaging nutrient levels across all treatments at each site.

Standard methods were used to verify that data met the assumptions of statistical tests. Graphical representations were used to assess distribution shape and variance. Boxplot midlines represented the median of the distribution, top and bottom box limits represented the 75th and 25th quartiles, 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 positive 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, the scope of inference was limited to Douglas-fir stands within the geographic region that met the age, stand density and previous treatment criteria.

Results

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).

Table 4
Mean initial soil nutrient and pH levels (before treatment) in the Douglas-fir fertilization experiment by site. Standard deviation in parentheses.

Site[a]	pH	C (%)	Ca (μg g^{-1})	K (μg g$^{-}{}_{1}$)	Mg (μg g^{-1})	N (%)	Na (μg g^{-1})	P (μg g^{-1})
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)

[a] Sites ordered by increasing distance from coast.

Most fertilization treatments caused expected changes in soil pH, P, and Ca (Table 5). The N treatment did not significantly increase soil N, and increases in soil N for the control treatments at several sites complicated interpretation. The N treatment lowered soil pH at all but one site (HAK) and reduced Ca at most sites (data not shown), but these changes were not statistically significant. Lime and Kinsey treatments significantly increased soil Ca (Table 5), with relatively larger increases on sites closer to the coast with lower initial levels of soil Ca (data not shown). The mean decrease in Ca associated with $CaCl_2$ treatment was strongly influenced by one site, and $CaCl_2$ actually increased soil Ca at seven of ten sites by an average of 40%. The magnitude and durability of soil Ca increases were greater for the lime treatment compared to the $CaCl_2$ treatment (data not shown). Dramatic and significant increases in soil P were observed for the P treatment, which also caused relatively larger increases on sites closer to the coast with lower initial levels of soil P (data not shown).

Table 5
Average 3-yr change (final – initial) and average proportional 3-yr change (final – initial) / initial) in soil chemistry by treatment (trt) in the Douglas-fir fertilization experiment. Standard deviation in parentheses. Bold indicates nutrient changes that were targeted by trts.

	pH	Ca (µg g^{-1})		N (%)		P (µg g^{-1})	
Trt	Change	Change	Proportional change	Change	Proportional change	Change	Proportional change
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[a]	-0.08	-10	0	**0**	**0**	**20**	**0.93**

[a] Treatment only applied at site OSU.

* Significant change in nutrient level relative to the control treatment ($p \leq 0.05$).

** Significant change in nutrient level relative to the control treatment ($p \leq 0.01$).

Foliar Chemistry

Initial 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 initial foliar nutrient levels (before treatment) in the Douglas-fir fertilization experiment. Standard deviation in parentheses.

Site[a]	N : Ca	Ca (%)	K (%)	Mg (%)	N (%)	P (%)	B (µg g^{-1})	Mn (µg g^{-1})	Zn (µg g^{-1})
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)

[a] Sites ordered by distance from coast.

N and P were the only treatments to significantly change foliar nutrient levels over the three-year study, either as absolute change in concentration or as relative change from initial concentration (Table 7). Treatment effects on foliar Ca were not statistically significant ($\alpha = 0.05$) and were difficult to interpret due to changes in foliar Ca in the control treatment at many sites, and inconsistent treatment effects on foliar.

One year after fertilization, the N treatment significantly increased foliar N, but this effect was not significant after three years. Increases in foliar N for the N treatment were highest on the most inland sites (data not shown), which had relatively lower initial levels of foliar N. The N:P treatment increased N substantially, but the significance of this change could not be tested because it was only applied at one site.

After three years, the P treatment resulted in the largest and only significant increases in foliar P relative to initial levels (average proportional increase 20%). The N treatment resulted in a statically significant decrease in P concentration.

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 significant pulse in B one and three years after treatment ($p < 0.001$).

Table 7. Average 1-yr and 3-yr change (final-initial) and proportional change ([final-initial]/initial) in foliar nutrient levels by treatment (trt). Standard deviation in parentheses. Bold indicates nutrient changes that were targeted by trts.

Yr 1 vs. Initial						
	Ca (%)		N (%)		P (%)	
Trt	Change	Proportional change	Change	Proportional change	Change	Proportional change
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)
CaCl^2	__-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[a]	-0.05	-0.07	0.98	0.71	-0.01	-0.07

Yr 3 vs. Initial						
	Ca (%)		N (%)		P (%)	
Trt	Change	Proportional change	Change	Proportional change	Change	Proportional change
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)
CaCl^2	__-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 (0.01)**__	__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[a]	0.15	0.24	0.28	0.2	-0.04	-0.21

[a] Treatment only applied at site OSU.

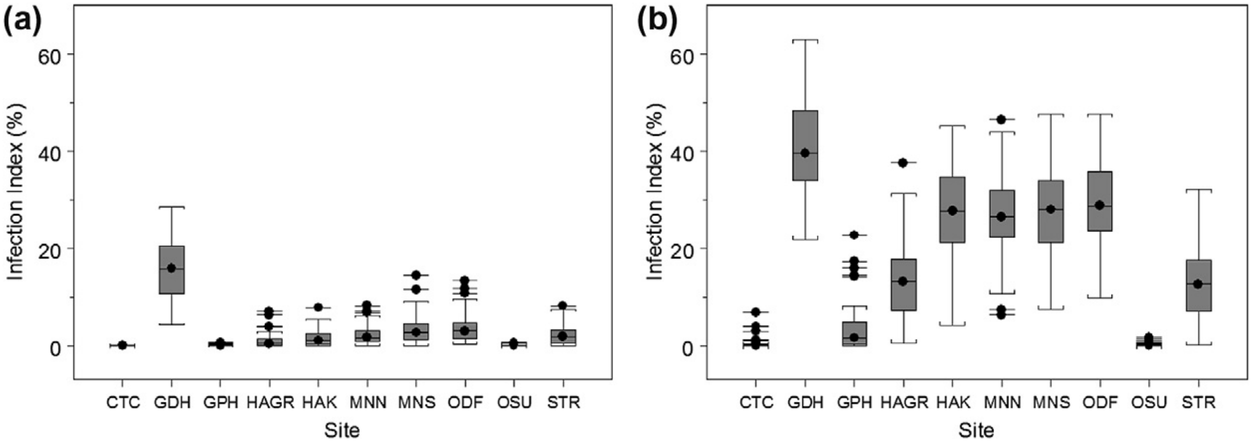
* Significant change in nutrient level relative to the control treatment ($p \leq 0.05$).

** Significant change in nutrient level relative to the control treatment ($p \leq 0.01$).

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 low levels of infection (median infection index < 5%) for 1-yr-old needles.

Fig. 3. Swiss needle cast infection index by site for (a) 1-yr-old needles and (b) 2-yr-old needles collected in May 2010, three growing seasons after fertilization treatments were applied.



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

Treatments did not significantly affect infection index of 1- or 2-yr-old needles across sites (p-values 0.47 and 0.14, respectively; Table 8). The unfertilized control exhibited the highest infection index for both needle age classes; slight but statistically significant differences (α= 0.05) in infection index were detected in mixed-effects comparisons between individual treatments and the control (indicated by [*]; right column Table 8). Across all sites, differences in estimated mean infection index between the highest- and lowest-ranked treatments (Max-Min) was only 0.6% for 1-yr-old needles and 3.2% for 2-yr-old needles, representing negligible differences in infection between treatments (Table 8).

Table 8
Swiss needle cast infection index across sites by needle age class from the Douglas-fir fertilization trials.

Needle Age	Mean[a]	Median[a]	sd[a]	n	Min[b]	Max[b]	p-value[c]	Treatment Ranks[c] (highest to lowest infection index)
1	3	0.9	5.2	565	2.7	3.3	0.47	control, P, $CaCl_2$, N, Kinsey, lime
2	18	17.5	15.2	555	16.7	19.9	0.14	control, N, Kinsey, $CaCl_2$*,lime*, P*

[a] Mean, median and standard deviation (sd) summarize tree-level infection indices (n samples).
[b] Min and max summarize treatment-level infection indices.
[c] P-values for treatment effect and treatment ranks are based on linear mixed effects analyses with site as a random block effect (*significant difference in infection index between individual treatments and the control at α = 0.05).

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

No significant treatment effect on infection index was detected within individual study sites (all p-values > 0.05; Table 9). 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 9). Treatment-ranks also differed between needle age classes at many sites.

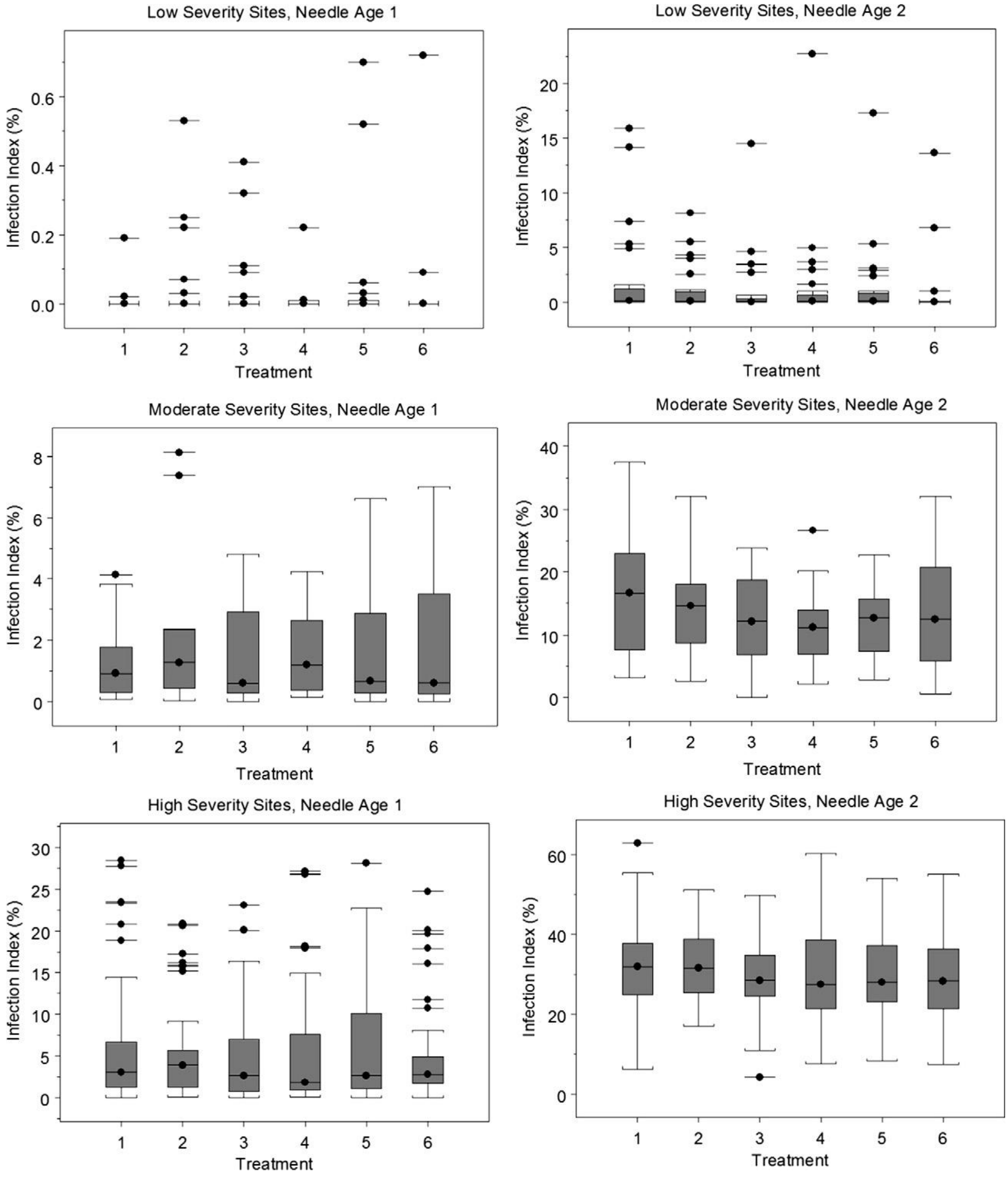
Table 9
Swiss needle cast infection index by site and needle age class from the Douglas-fir fertilization trials.

Site[a]	Needle Age	Mean[b]	Median[b]	sd[b]	n	ntrt[c]	Min[d]	Max[d]	p-value[e]	Treatment Ranks[f] (highest to lowest infection index)
GDH	1	15.7	15.8	6.7	58	6	11.8	19.1	0.11	1,4,5,2,6,3
	2	40.6	39.3	9.3	51		35.6	49.0	0.09	4,1,2,6,5,3
ODF	1	3.8	3.0	3.0	56	6	2.5	5.7	0.24	5,4,2,3,1,6
	2	29.4	28.7	8.4	56		25.7	31.3	0.78	4,1,2,3,5,6
HAK	1	1.6	1.1	1.6	55	6	0.9	2.6	0.13	6,3,4,1,2,5
	2	27.5	27.6	9.6	55		24.6	35	0.13	6,1,4,5,3,2
MNS	1	3.4	2.7	2.9	56	6	2.0	5.4	0.11	1,5,4,2,6,3
	2	27.3	28.0	9.2	54		20.1	30.7	0.49	1,2,6,4,3,5
MNN	1	2.4	1.7	2.0	57	6	1.6	3.5	0.37	2,1,3,6,5,4
	2	27.1	26.4	9.0	56		22.1	32.2	0.27	2,1,4,3,5,6
HAGR	1	1.1	0.4	1.4	59	6	0.5	1.8	0.36	6,1,4,5,2,3
	2	13.6	13.2	7.8	60		10.9	17.7	0.49	1,6,3,2,5,4
STR	1	2.1	1.8	1.9	54	6	1.2	2.9	0.48	2,3,5,6,4,1
	2	13.0	12.7	7.5	55		10.8	15.7	0.67	2,1,6,4,3,5
GPH	1	0.1	0	0.2	46	5	<0.1	0.1	0.37	5,3,2,4,1
	2	3.7	1.6	5.2	46		2.8	5.1	0.91	1,4,5,3,2
CTC	1	<0.1	0	0.1	57	6	0	0.1	0.19	6,2,4,5,3,1
	2	0.6	<0.1	2.1	56		<0.1	2.4	0.14	6,2,5,1,4,3
OSU	1	<0.1	0	0.1	67	7	0	0.1	0.55	5,2,3,7,1,4,6
	2	0.1	0	0.3	66		<0.1	0.2	0.21	7,5,4,1,2,3,6

[a] Sites ordered from highest to lowest mean infection index on 2-yr-old foliage.
[b] Mean, median and standard deviation (sd) summarize tree-level infection indices (n samples).
[c] Ntrt is the number of treatments (trts) compared at each site.
[d] Min and max summarize treatment-level infection indices.
[e] ANOVA p-values test the null hypothesis of no treatment effect at each site.
[f] Treatment ranks are based on ANOVA beta coefficients. Trts: (1) control, (2) N, (3) lime, (4) $CaCl_2$, (5) P, (6) Kinsey, and (7) N: P.

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 9). The most severely impacted site (GDH) displayed the greatest difference in mean infection index between the best- and worst-ranked treatments, 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).

Fig. 4. Swiss needle cast infection index by treatment (trt) and each needle age class for sites grouped by disease severity level (low, moderate, high). Low = OSU, CTC, GPH; moderate = STR, HAGR, and high = GDH, HAK, MNN, MNS, ODF. Each graph depicts infection indices for 7-10 trees/trt/site for 1- and 2-yr-old needles. Trts: (1) control, (2) N, (3) lime, (4) $CaCl_2$, (5) P, and (6) Kinsey.



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

Linear regression models of infection index of 2-yr-old needles and foliar nutrient levels measured before and 3 years after treatment provided strong evidence that Ca, K, P, B, and Mn were negatively correlated with infection index (Table 10). Scatter plots revealed correlation between these factors and distance-from-coast (not shown). There was no evidence of a strong linear relationship between disease severity and foliar N or the ratio of N:Ca, as indicated by linear regression p-values >0.05 and lack of evidence for a non-zero regression slope, respectively.

Table 10

Linear relationships between infection index of 2-yr-old needles (collected May 2010) and foliar nutrient levels pre- and post-treatment in the Douglas-fir fertilization experiment. Nutrients that had a significant linear relationship with infection index (at $\alpha = 0.05$) are shaded.

Nutrient		Pre-treatment (2006)	Post-treatment (2009)
N:Ca	p-value	0.00	0.00
	non-0 slope	0.16	0.12
	R^2	0.81	0.87
%Ca	p-value	0.00	0.00
	non-0 slope	0.00	0.00
	R^2	0.86	0.89
%N	p-value	0.22	0.15
	non-0 slope	0.31	0.25
	R^2	0.18	0.24
%K	p-value	0.01	0.00
	non-0 slope	0.00	0.00
	R^2	0.58	0.65
%Mg	p-value	0.05	0.01
	non-0 slope	0.01	0.00
	R^2	0.39	0.58
%P	p-value	0.02	0.01
	non-0 slope	0.00	0.00
	R^2	0.53	0.56
B (μg g^{-1})	p-value	0.00	0.02
	non-0 slope	0.00	0.00
	R^2	0.73	0.51
Mn (μg g^{-1})	p-value	0.01	0.00
	non-0 slope	0.00	0.00
	R^2	0.63	0.83

Discussion

The potential effects of fertilization on SNC severity in western Oregon is of great interest to Douglas-fir timber growers, with respect to possible deleterious effects of conventional nitrogen fertilization and possible ameliorating effects of other nutrients. This study found no evidence that fertilization treatments applied at the levels tested 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, even though they covered a wide range of initial disease severity levels, soil nutrient content, 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.

Ground-applied mineral nutrients must infiltrate the soil, remain in available form, be absorbed by the roots, and be transported to the foliage before potential affects on a foliar pathosystem are likely to be realized or detected. Foliar chemistry assessments showed that most foliar nutrient levels were not significantly altered by fertilization treatment. Fertilization effects on foliar chemistry differed by site, and were significant only for the P (increased P), N (increased N and decreased P) and Kinsey (increased B) treatments. Fertilization effects on soil chemistry were evident for the P (increased pH and P), Kinsey (increased pH and Ca) and lime (increased pH and Ca) treatments. It was important to report that some treatments measurably and significantly changed foliar and/or soil chemistry, particularly in the absence of treatment effects on disease severity.

There was no significant difference in infection index between treatments within sites. When data from all sites were pooled, the null hypothesis of no treatment effects could not be rejected. Although some differences in infection index were detected when individual treatments were directly compared to the control treatment, which had the highest infection index when all sites were pooled, 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 index between sites. At the site with the highest SNC severity, approximately 40% of the stomata on 2-yr-old needles were occluded by pseudothecia, compared to 0.1% at the lowest severity site.

Site-level comparisons supported previously observed correlations between disease severity and levels of several foliar nutrients (e.g., Ca) (Perakis et al., 2005), but did not support a strong relationship between infection levels and foliar N or the ratio of 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 control trees. 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. The progeny test site was located at approximately 700 m elevation and needle retention averaged 2.7 yrs (El-Hajj et al., 2004). It is unclear why this study obtained markedly different results than our experiment, particularly because increases in foliar N were not dramatic and apparently did not exceed the threshold for N-limitation in coastal Douglas-fir (Perakis et al., 2005). 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 tree age; the interior host subspecies (*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 the levels of fertilizer applied did not affect disease severity in our study, some did directly stimulate tree growth on these same sites (Unpublished: 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. For example, significant growth responses to N treatment occurred on sites with relatively lower site indices and higher soil pH. Site indices of 110 ft (33.5 m; high site III) or 120 ft (36.6 m; low site II) at age 50 are considered moderate for Douglas-fir in the Coast Range (King 1966). Ideally, managers should assess soil and/or foliar chemistry in their stands in order to select the most appropriate fertilization regimes, but the diagnostics for identifying stands that are likely to respond are poorly understood. More work on this topic would help timber growers 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 have also found no direct interaction between silvicultural regime and disease severity (Hood and Sandberg, 1979; Mainwaring et al., 2005; Shaw et al., 2011). In other words, various silvicultural regimes did not alter the host-pathogen interaction, but instead 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. If present, these defense responses might provide a basis 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; Sugimoto et al., 2010; Wallis et al., 2011). Thinning and other silvicultural activities also have the potential to influence 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.

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 would 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 specific fertilizer applications, not foliar or soil nutrient levels per se, impact disease severity and tree growth, and the study design accomplished this objective. A longer-term experiment with repeated fertilizer applications could also help to evaluate pathogen-nutrient dynamics over time. Fertilization treatments at the rates applied in this experiment did not affect the density of fungal fruiting bodies on the foliage of Douglas-fir trees.

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trees, collecting foliage for nutrient and disease severity assessment. Disease severity assessments were primarily conducted by Alexis Danley, Andrew Luoma and Alex Martin.

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List of Refereed Publications

Disease Distribution, Severity and Epidemiology

Hansen, E. M., Stone, J. K., Capitano, B. R., Rosso, P., Sutton, W., Winton, L., Kanaskie, A. and M. G. McWilliams. 2000. Incidence and impact of Swiss needle cast in forest plantations of Douglas-fir in coastal Oregon. Plant Disease. 84: 773-779.

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Stone, J. K., Hood, I. A., Watt, M. S. and J. L. Kerrigan. 2007. Distribution of Swiss needle cast in New Zealand in relation to winter temperature. Australasian Plant Pathology. 36: 445-454.

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