



Oregon State
UNIVERSITY

OSU

College of Forestry

Swiss Needle Cast Cooperative
Annual Report
2013

SNCC Income Sources and Expenditures: 2013

Income

Membership dues	60,000
Oregon State Legislature	95,000
Carry-over	<u>256,640</u>
 Total 2013 Budget	 \$411,640

Expenditures

Salaries and wages	139,396
Travel	20,654
Operating expenses	11,639
Contract Work	18,512
Materials and Supplies	11,820
Indirect Costs	<u>26,263</u>
 Total 2013 Expenditures	 \$228,284



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Winter 2014

To: SNCC Membership

From: David Shaw, Director SNCC

Re: Annual Report

2014 finds us in the throes of installing our new SNCC – Douglas-fir Research and Monitoring Plot Network. This network will extend from the California border to SW Washington State, and go from the coast to 35 miles inland. We have divided the area into panels, and five plots go into each panel, and there are four panels east to west, with five panels north to south in Oregon and one panel in SW Washington, for a possible total of 120 plots (see report from Gabriela Ritokova in this Annual Report).

This research and monitoring plot network will replace the original 76 plot GIS network installed by the cooperative and Doug Maguire group in the mid-1990's that was restricted to the NW Coast Range. The new network will allow for a greater area of inference, while also monitoring the margins of the epidemic, allowing on-the-ground plot monitoring of whether disease symptoms are moving east.

The Research and Monitoring Plot Network will provide growth data linked to site environment, soils, tree attributes (needle retention) and disease severity. The network will also provide a framework for other epidemiology studies and associated Douglas-fir projects, as well as providing mensurational data to CIPS.

The SNCC budget allocations are predominantly focused on this plot network in the near-term. However, we continue to engage in other projects and collaborations, as well as outreach concerning Swiss needle cast and Douglas-fir management. For example, we continue the annual aerial survey in Oregon, and are funding research on soils and disease (Jeff Hatten), potential for remote sensing applications (Thomas Hilker), and database archiving of past research projects.

We anticipate collaborations with others working on Swiss needle cast, and this spring 2014 we will have a visiting forest pathology graduate student from Spain who will spend several months working on our new plot network. We also anticipate collaborating with members of OSU's Botany and Plant Pathology Department and others to develop a plan for a more definitive understanding of the molecular ecology of *Phaeocryptopus gaeumannii*.

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

Swiss needle cast aerial survey in Oregon (Kanaskie and McWilliams).....	5
Swiss Needle Cast Survey in California (Heath, Moore, Noyes).....	9
SNCC Research and Monitoring Plot Network (Ritokova, Shaw, Maguire, Mainwaring, Browning, Littke, Gourley, Filip, Kanaskie).....	11
A new and novel technique for mapping the extent of Swiss Needle Cast (SNC) across coastal Washington, Oregon and Northern California (Hilker).....	15
Growth response of young Douglas-fir to nitrogen, calcium, phosphorus, and blended fertilizers in Oregon and Washington: Growth period two, 4-6 years (Mainwaring, Maguire, Perakis).....	18
Assessing the role of soils in affecting Swiss needle cast severity: A need for additional study (Hatten).....	27
Tree-ring stable isotopes record the impact of a foliar fungal pathogen on CO ₂ assimilation and growth in Douglas-fir (Saffell, Meinzer, Woodruff, Shaw, Voelker, Lachenbruch).....	30
Tree-ring analysis of the fungal disease Swiss needle cast in western Oregon coastal forests (Lee, Beedlow, Waschmann, Burdick, Shaw).....	42
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 (Zhao, Maguire, Mainwaring, Wehage, Kanaskie).....	56

Appendix

List of Refereed Publications.....	65
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2013 Swiss Needle Cast Aerial Survey

Alan Kanaskie and Mike McWilliams, Oregon Department of Forestry

The enclosed maps show the approximate size and location of areas of Douglas-fir forest with symptoms of Swiss needle cast (SNC) detected during an aerial survey conducted in May, 2013.

Survey procedures:

The Oregon Coast Range survey was flown on May 1, 2, 3, and 9 and covered approximately 2.6 million acres of forest. Weather conditions and symptom development both were excellent during the survey period. 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 Curry County, and from the coastline eastward until obvious symptoms were no longer visible. We did not survey the Cascade Range in 2013, but Swiss needle cast does occur at damaging levels in some areas.

Results of the survey:

The 2013 survey results show an increase in the area of forest with symptoms of Swiss needle cast compared to the previous 3 years and reached an all-time high for the fourth year in a row. We mapped 524,518 acres of Douglas-fir forest with obvious symptoms of Swiss needle cast (Figure 1). As has been the case for the past several years, the easternmost area with obvious SNC symptoms was approximately 28 miles inland from the coast in the Highway 20 corridor, but most of the area with symptoms occurred within 18 miles of the coast. Figures 2 and 3 show the trend in damage from 1996 through 2013. This year's increase in SNC likely is due in part to prolonged wet weather in spring of 2012 which was very conducive to infection.

The Swiss needle cast aerial survey provides a conservative estimate of damage because observers can map only those areas where disease symptoms have developed enough to be visible from the air. We know (from permanent plot data and ground checks) that Swiss needle cast occurs throughout the survey area, but that discoloration often is not severe enough to enable aerial detection. The total area of forest affected by Swiss needle cast is far greater than indicated by the aerial survey. The aerial survey does, however, provide a reasonable depiction of the extent of moderate and severe damage, and coarsely documents trends in damage over time.

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

Additional Notes:

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

The GIS data and a .pdf file can be accessed via the ODF web page at:
<http://www.oregon.gov/ODF/privateforests/fhMaps.shtml>

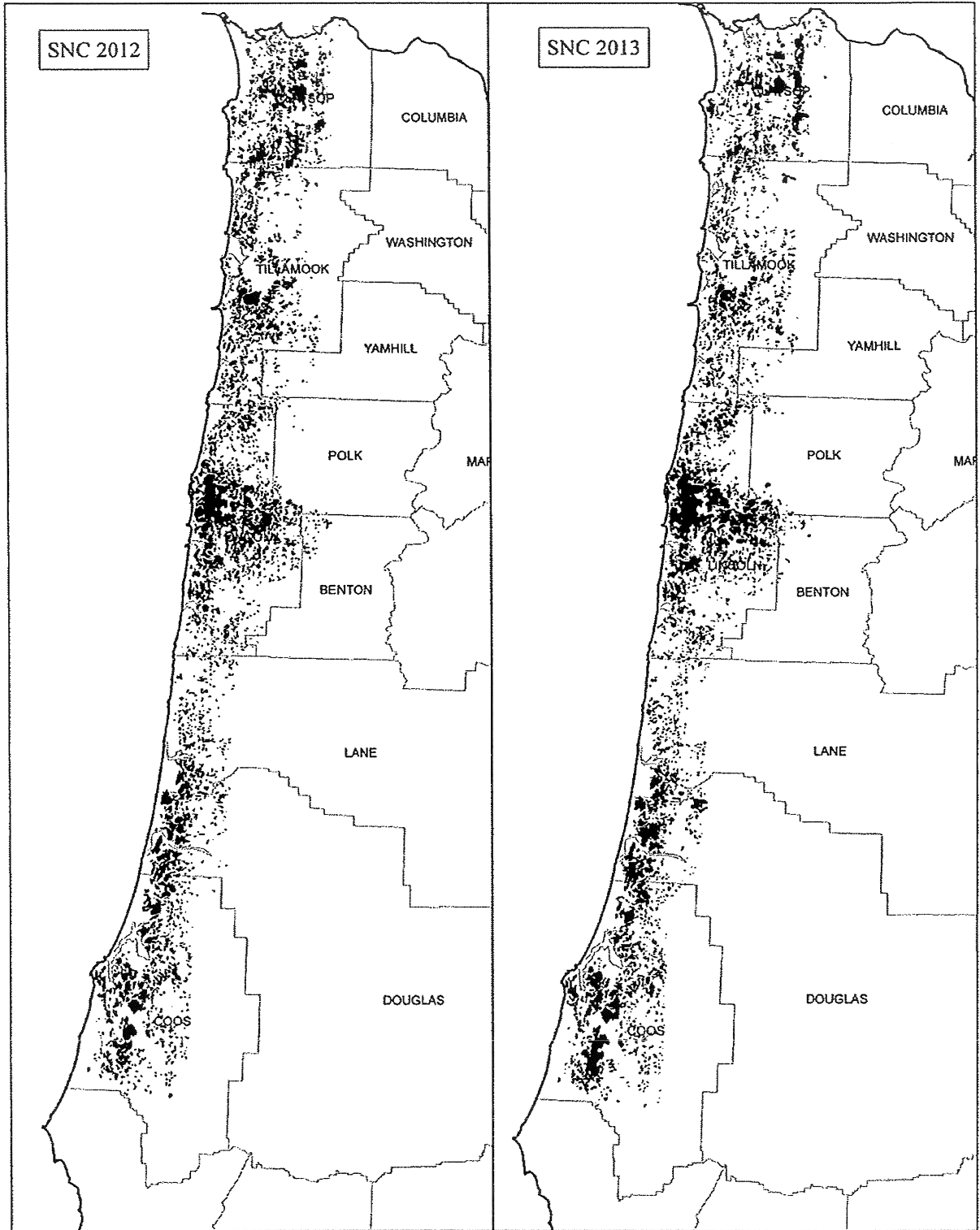


Figure 1. Areas of Douglas-fir forest with symptoms of Swiss Needle Cast detected in the 2012 and 2013 aerial surveys.

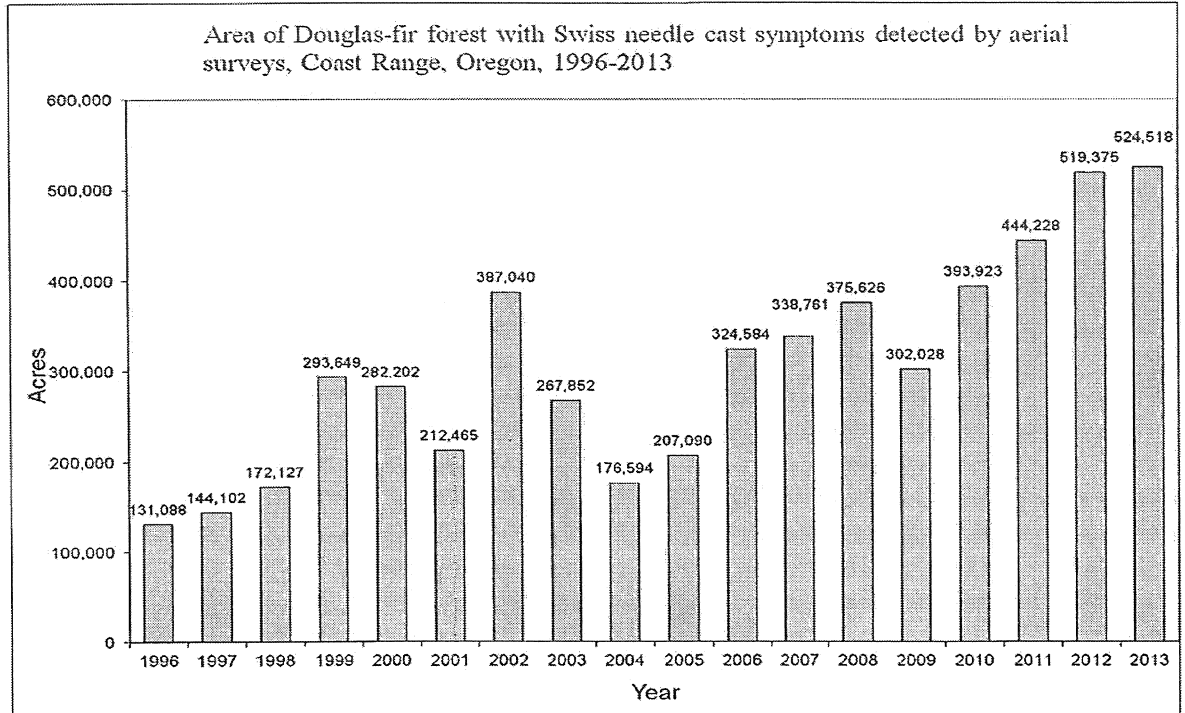


Figure 2. Area of Douglas-fir forest in western Oregon with symptoms of Swiss needle cast detected during aerial surveys conducted in April-June, 1996-2013 (2008 area estimated from partial survey consisting of 3 sample blocks).

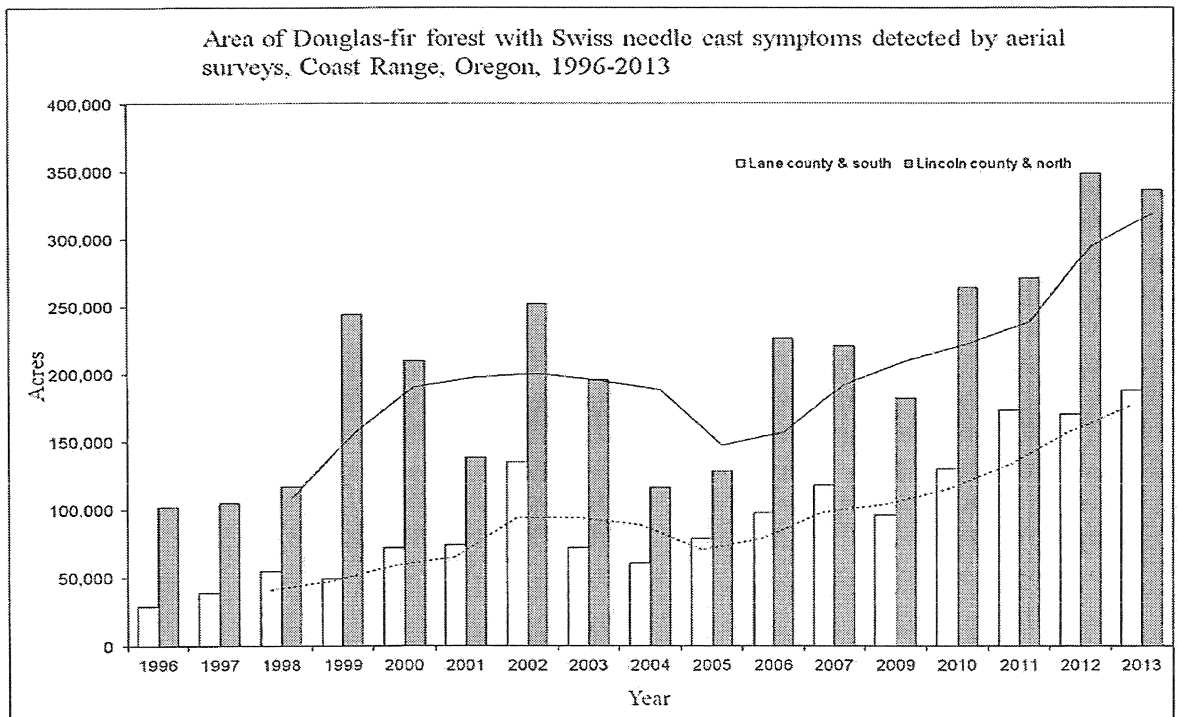
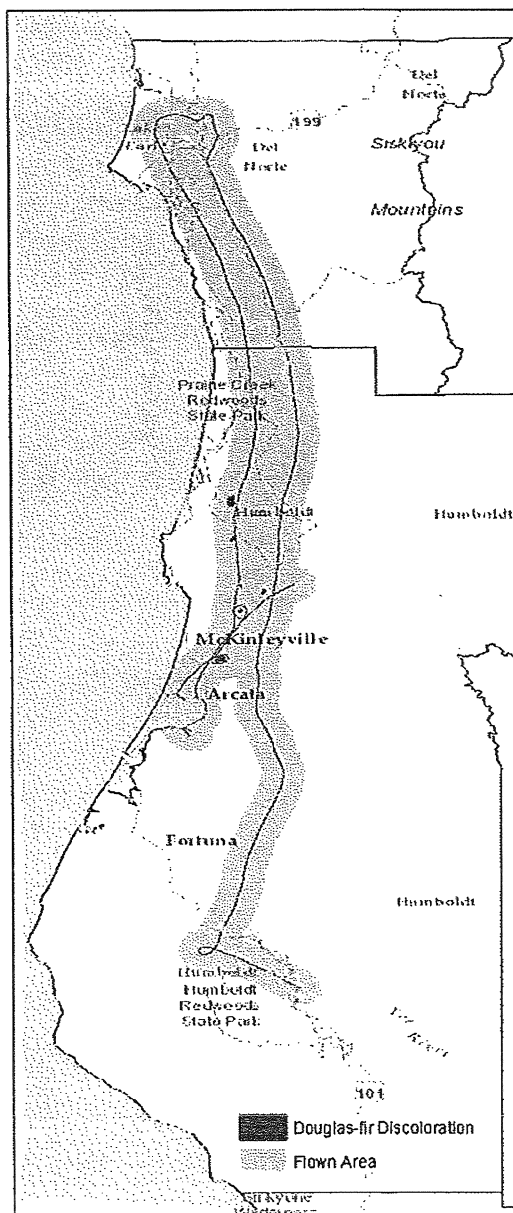


Figure 3. Area of Douglas-fir forest in western Oregon with symptoms of Swiss needle cast detected during aerial surveys conducted in April-June, 1996-2013; north and south halves of survey area (2008 area estimated from partial survey consisting of 3 sample blocks).

Swiss Needle Cast Special Survey



Background: Annual aerial detection surveys for Swiss needle cast (SNC) have been conducted in Oregon since the 1990's and have been conducted in Washington as well. This is the first attempt to survey for SNC from the air in California. The disease has been reported in private timberlands around Arcata in the last few years. Funding for this survey came from the Swiss Needle Cast Cooperative at OSU.

Objective: Detect and map areas with visible SNC on the Humboldt/Del Norte Coast of California. Mapped areas will be passed on to cooperators for verification of the disease.

Surveyors: Z. Heath, J. Moore, B. Noyes.

Dates: May 14th, 2013.

Methodology: Areas of discolored Douglas-fir were mapped visually by surveyors using digital aerial sketch-mapping systems flying in a light fixed-wing aircraft approximately 1,000 feet above ground level. Photos of symptomatic trees were taken as well.

Details:

232 miles were flown, covering about 600,000 acres in Humboldt and Del Norte Counties. See Figure 1. Very few areas of Douglas-fir discoloration was mapped. About nine discrete areas totaling 363 acres were mapped between Eureka and Crescent City. These areas appeared a pale yellow color and may be the signature of poor site conditions rather than SNC. See Figures 2 & 3.

Figure 1. Flown area and mapped tree discoloration



Figure 2. Site 1.



Figure 3. Site 2.

Direct questions pertaining to this report to Zachary Heath (email: zheath@fs.fed.us phone: 530-759- 1751). Report Date May 15th, 2013.

SNCC Research and Monitoring Plot Network

Gabriela Ritokova, Dave Shaw, Doug Maguire, Doug Mainwaring, John Browning, Willis Littke, Mark Gourley, Greg Filip, Alan Kanaskie

Introduction

Among the long term objectives of the SNCC is a constant monitoring of disease conditions. While this can be accomplished qualitatively with the results of the annual aerial survey, quantitative assessment of the tree growth loss resulting from Swiss needle cast requires periodic measurements. This has been accomplished up until now with the Growth Impact Study (GIS) plot network.

During the final remeasurement of the the GIS plots (2008), it was decided that their utility had become limited. The original sample of 10-30 year old GIS stands is now 25-45, which is considered outside the age range of those stands for which information is especially valuable. Furthermore, ground observation of foliage retention, the original methodology for determining disease severity, has become difficult to impossible as a result of crown recession and canopy closure. In addition, these plots were distributed only between Newport and Astoria, thereby providing inference only to the northern Oregon Coast Range.

In order to address these limitations, the decision was made to install a new monitoring plot network, which is foreseen to provide disease condition and growth loss information for at least 10 years. These plots will be put in 10-20 year stands, thereby addressing the shortcomings of the aged GIS network. In addition, these plots will be distributed as far south as the California border, and as far north as southern Washington.

These plots will not only provide periodic information about disease severity, growth loss and its geographic distribution, but will also offer sites to be used for other SNC research, be it epidemiological, climatological, or other forms.

Methods

Criteria for selection:

Stands should not be treated for ten years. We will install 1/5 acre plots, where all trees will be tagged and measured. Trees may be cored, and may have some branches removed.

General stand parameters:

- 10-30 year old Douglas-fir
- Sample stand is 80% BA Douglas-fir
- Avoid dense understory vegetation, especially salal
- 300-400 trees per acre density
- Installing square 1/5 acre plot +(0.5 chain buffer)=0.58 ac
- No thinning PCT or fertilization in past 5 years

At each plot.

A 1/5 acre plot will be laid out, and all trees tagged. Field methods will follow Kanaskie and Maguire, March 30, 2002 Field Specifications and Manual for Rating Swiss Needle Cast in Douglas-fir. The following is adapted from that document but specific to the 1/5 acre plot, and needle retention will be estimated in years.

Sampling matrix

We identified four zones based on distance from coast (in miles): 0-5, 5-15, 15-25, and 25-35. Each of these zones was equally divided (north-south), following township lines as closely as possible. Each block spans approximately 58 miles north-south. This resulted in 20 sampling blocks. Attached map shows these blocks.

In addition to the 20 cell matrix in coastal Oregon, 4 sampling blocks were established in SW Washington

Sites

During the summer of 2013, 24 sites were established in Oregon on land owned by Starker, Stimson, ODF, and The Campbell Group. In Washington, eight sites were established on land owned by the DNR.

Plots within the stands were chosen subjectively.

Measurements

Following the establishment and marking of plot boundaries, all trees were given a unique numbered tag. Following the conclusion of the 2013 growing season, all trees were measured for dbh and species was recorded. A forty tree height sample was collected, such that it included the 10 largest trees by dbh, the four smallest by dbh, and the final 26 were ranged across the diameter distribution. In the spring, the 10 largest trees will be assessed for foliage retention, and needles will be sampled for pseudothecial occlusion, and foliar nutrition. In addition, soil samples will be collected for Jeff Hatten's soil study.

Summary statistics

Table 1: data from the 16 plots for which data has been entered

Plot	Douglas-fir				Other species	
	Trees per plot	Av. Dbh (cm)	Av. Ht (m)	Av. CR	Trees per plot	Av. Dbh (cm)
F 25-3	100	10.5	8.12	0.92		
F 25-4	163	13	11.37	0.74	1	3.5
DNRL-51	92	14.4	13.38	0.63	178	7
DNRL-251	90	19.4	17.43	0.63	15	6.4
T 151	51	22.6	17.75	0.6	19	16.8
T 15-2	78	19.3	15.73	0.79	13	8.4
T 25-5	51	17.6	12.67	0.94	2	10.1
T 51	52	23.9	16.04	0.77	4	23
T 53	88	16.5	15.53	0.64	14	8.3
T52	12	19.7	13.98	0.69	2	13.6
T02	63	22	16.94	0.66	2	17.2
T01	52	24.3	15.71	0.7	13	10.1
DNRL-151	118	9.1	7.81	0.79		
DNRL252	87	20.6	15.42	0.62	26	6.3
DNRS151	48	18.9	13.62	0.65	25	9.4
DNRS251	50	18	11.67	0.85	59	6.3

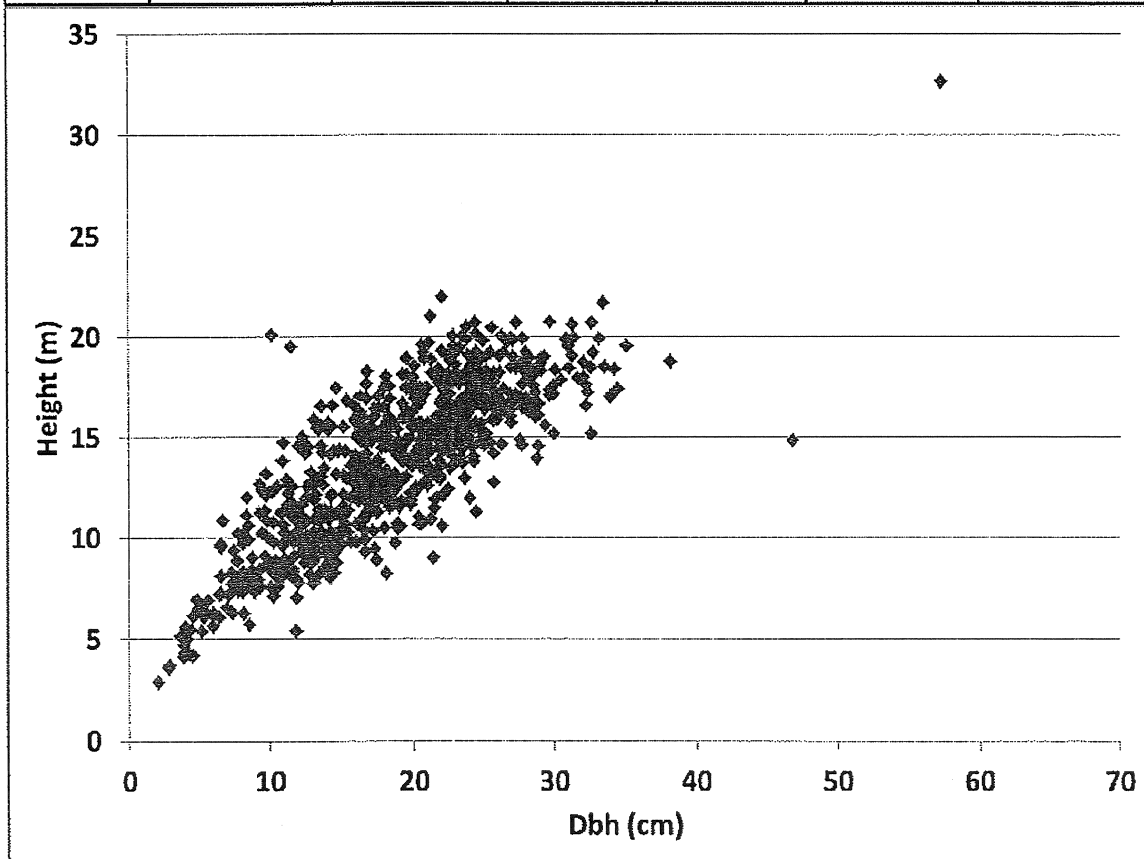
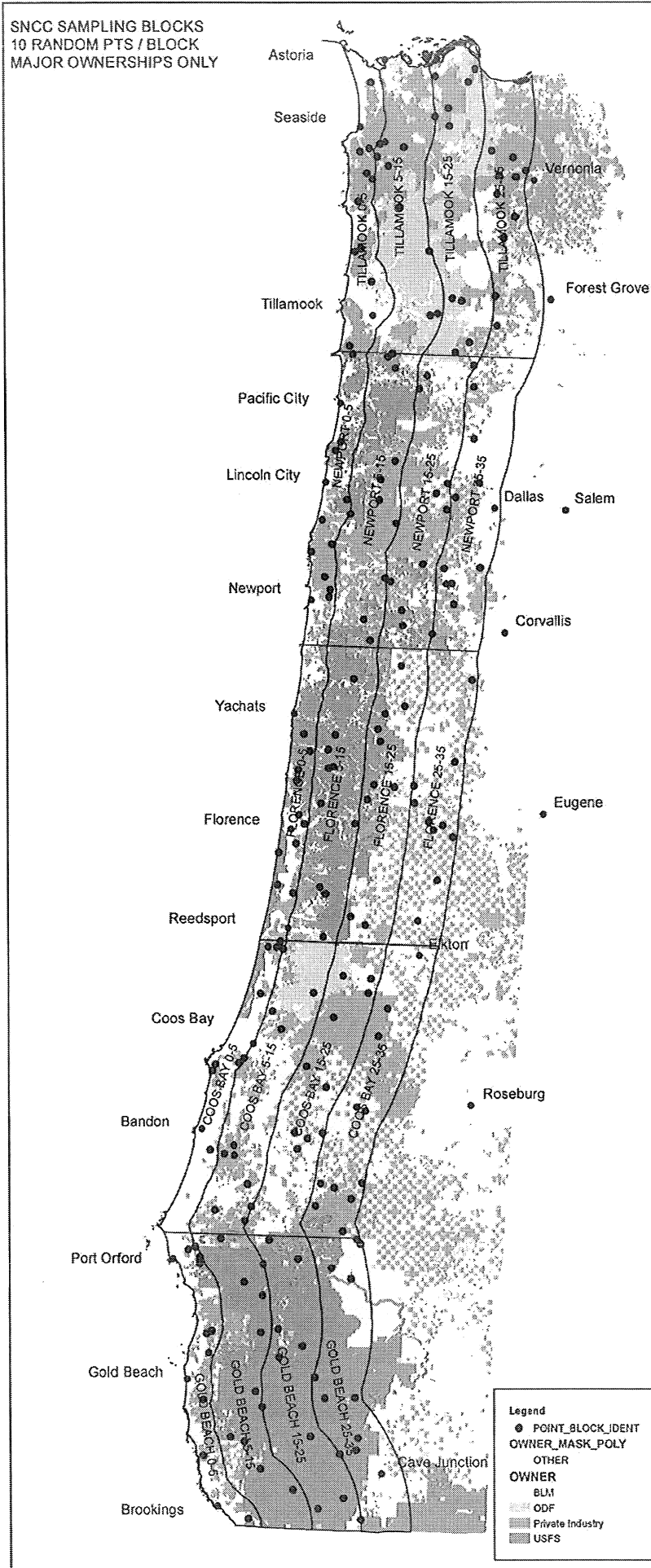


Figure 1: Height-diameter relationships for the 16 plots for which data has been entered

SNCC SAMPLING BLOCKS
10 RANDOM PTS / BLOCK
MAJOR OWNERSHIPS ONLY



A new and novel technique for mapping the extent of Swiss Needle Cast (SNC) across coastal Washington, Oregon and Northern California

Thomas Hilker (PI), College of Forestry, Oregon State University, Corvallis OR 97330

Introduction

Forest decline is a major concern in association with global climate change (Kurz et al., 2008; Laurance et al., 2012). Recent changes in regional climate appear to promote outbreaks of many native diseases and insects (Bentz et al., 2010; Woods et al., 2005), causing widespread decrease in forest health and loss in biodiversity. In the Pacific Northwest (PNW), Swiss needle cast (SNC), a native fungal disease is spreading along the coast of Washington, Oregon and Northern California affecting 525,000 acres of Douglas-fir forest (Kaanaskie, McWilliams. 2013), and causing significant economic loss (Kimberley et.al. 2011).

Current state of the art mapping includes visual interpretation from helicopter or aircraft, which is costly and not sufficiently accurate, because a) weather conditions may not permit enough flight hours to cover the entire coast range, and b) smaller areas may be overlooked, or their extent may not fully be assessed. In addition to mapping the current extent, assessment of the historical range of the disease would also be useful to better understand its causes and develop mitigation strategies. However, reliable data do currently not exist across the coast range.

Objective

The objective of this work is to implement a remote sensing technique that will allow us to map the extent of forest decline and disturbance across coastal PNW at a spatial resolution of 30m since 1982. Our work is based on previous research during which we have shown that time series of satellite data may be used to assess changes in vegetation density over time (Hilker et al., 2013a, Hilker et al 2013b). Time series analysis overcomes the need to differentiate between spatial variability of vegetation density and disease related effects such as decreased leaf area

caused by tree pathogens or phytophagous insects. We will focus our effort on the coast range of the PNW. Once established, our technique will, however, be equally applicable also to other areas and diseases that affect foliage density and growth rates or cause stand replacing disturbances.

Benefit to the SNC

The objective of this work is to accurately map the severity of SNC and determine forest health and forest decline due at a fine spatial resolution across the landscape. This will not only provide a more accurate and cost effective mapping of SNC and in the future but can also used to investigate severity and impacts in the past. The availability of Landsat data since the early 1980s (Landsat 4), will provide entirely new possibilities to establish relationships between forest diseases and environmental changes that have taken place in recent decades.

2.1 Methods

The analysis is based on multi-spectral satellite imagery from the TM and ETM+ sensors on board Landsat 5 and 7 (Cohen and Goward, 2004). Landsat's spatial resolution of 30 m, and extent of 185 x 185 km per scene has proven utility for monitoring vegetation change at regional scales (Hansen et al., 2008; Wulder et al., 2008) and numerous forest

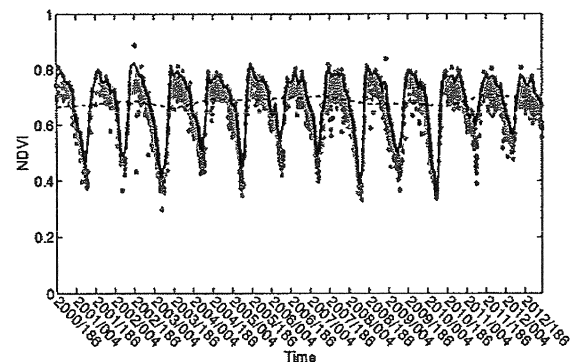


Fig 1 Time series for NDVI fitted using TIMESAT (black line). The red line represents the annual mean. For areas affected by disease such as SNC, we expect to see a decline in NDVI over time, as the foliage density is expected to decrease.

change algorithms have been developed, validated, and applied (Zhu and Woodcock, 2012) e.g. (Collins and Woodcock, 1996; Healey et al., 2005; Masek et al., 2008). Time series of Landsat based observations could potentially also be used to obtain changes in forest cover over time (Cohen et al., 2001), which could then be compared to model predicted changes in leaf area (such as growth and yield tables).

2.2 Data

A total of 3879 Landsat 4 (MSS) and 5 (TM) images between 1984 and 2012 were downloaded from USGS and atmospherically corrected using Landsat Ecosystem Disturbance Adaptive Processing System (LEDAPS) (Masek et al., 2006). Cloud screening was performed using Boston University's fmask algorithm for object based cloud detection (Zhu & Woodcock, 2012) and Landsat data were composited to obtain monthly averages of the normalized difference vegetation index (NDVI). Figure 2 shows an example of a composited Landsat NDVI from 7/1991. Changes in vegetation greenness were obtained by first removing the monthly mean NDVI for each month between 1984 and 2012 from the respective composite to eliminate seasonal variations in the dataset. In a second step, a Savitzky Golay filtering method was applied to reduce noise levels in the data (Jonsson and Eklundh 2002). Gaps between missing observations were filled using a moving window of 2nd degree polynoms, similar to the TIMESAT algorithm described by Jonsson and Eklundh (2002).

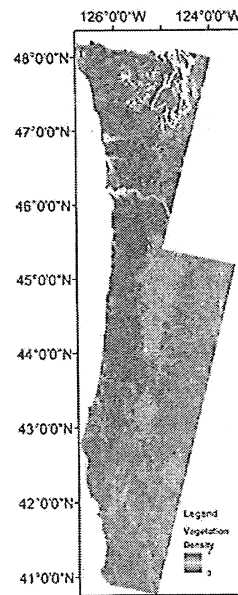


Fig 2: Landsat derived vegetation density; the example shows 7/1991

2.1 Mapping disturbance and recovery

Monthly estimates of stand replacing disturbances were obtained from time series of NDVI observations using sudden drops in vegetation greenness to identify disturbances. A “broken stick” regression technique was used to define trajectories in vegetation greenness over time. The technique fits multiple linear regression models a dataset and identifies breakpoints in the regression based on least squares optimization. Figure 3 shows a conceptual figure of a disturbance trajectory based on the broken stick technique.

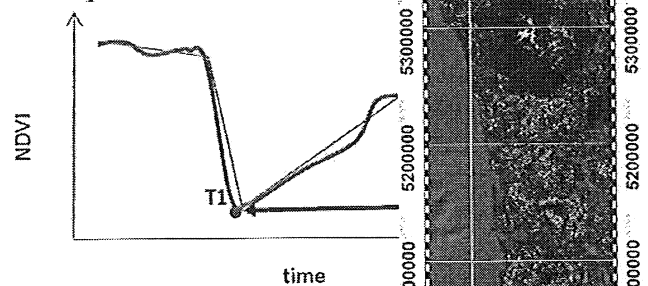


Figure 3: Conceptual figure of the “broken stick” technique to identify changes in NDVI (blue line) over time.

Time of disturbance (T1) and recovery time (T2-T1) can be estimated from the NDVI time series. SNC infested stands that have been subject to harvesting will be expected to show a slower than average recovery rate along the latitudinal respective gradient because the disease would prevent growth of the re-established stands. For those areas that have not been subject to harvesting, we would expect to see a stagnation or even decline in vegetation density, as poor foliage retention leads to reduced canopy cover.

3. Results

Figure 4 shows a Landsat

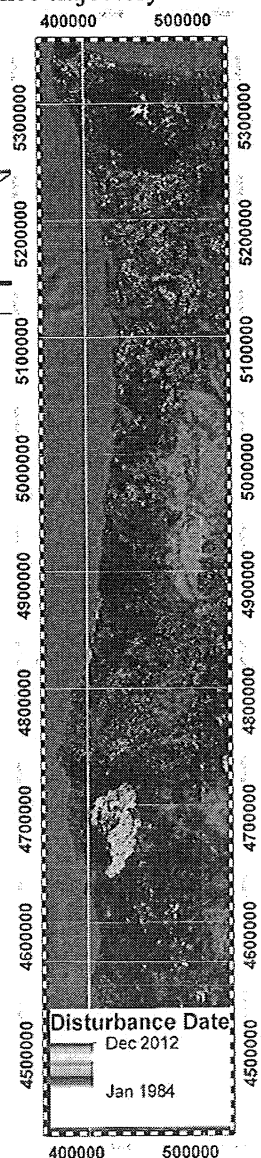


Fig. 4: Landsat mapped disturbances along the West Coast since 1984

based estimate of disturbances in coastal Washington and Oregon since 1984. The color of the disturbed areas corresponds to the month of disturbance, running as continuous number from Jan 1984 through Dec. 2012. The map contains both man made disturbances through cut-blocks as well as natural disturbances such as through the biscuit wildfire (large turquoise area in the south). Annual disturbance rates were on average about 900km² but peaked in 2002 as a result of the biscuit wildfire which burned about 2000km². Figure 5 shows a histogram of annual disturbance rates. Please note that the accuracy in disturbance rates during the in the 1980s is somewhat limited as a result of lack of available images, and consequently some of the disturbances that occurred in the early 1980's may have been mapped only in the late 1980s. The biscuit wildfire is clearly visible in the histogram, and so is the economic crisis leading to a sharp reduction in harvesting rates in 2008 and 2009.

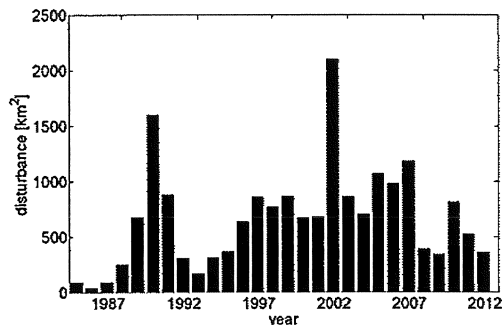


Figure 5: Annual histogram of stand replacing disturbances estimated from time series of Landsat images.

Figure 6 shows an estimate of NDVI trends for all areas at a 30 km stretch along the coast that have not been subject to harvesting. Green areas shown in this map represent areas for which there has been no significant increase in vegetation greenness since 1984, the red areas represent forest stands that saw a decline in vegetation greenness over the last 30 years (harvested areas have been excluded).

5. Future work/Next steps

Next steps of this work include validation

of the estimated NDVI trends with field data using SNC plots to verify whether SNC is a driver of the decline in NDVI. For all disturbed areas (which have been identified so far, but not evaluated, we will use a physiologically based model, 3PG, to compare predicted re-growth versus actual regrowth to identify areas for which the regrowth remained below the expected rate.

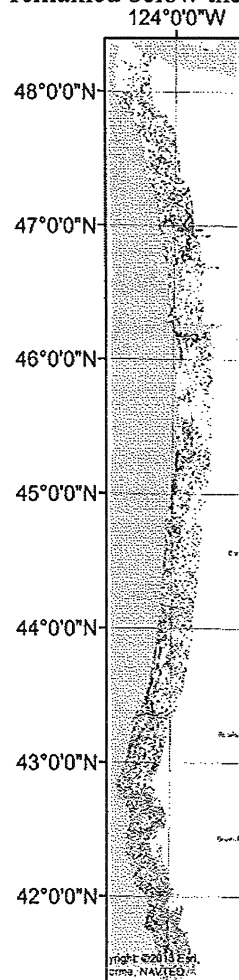


Figure 6: NDVI trends in non-disturbed forest stands. Green areas show stands where NDVI remained neutral over the last 30 years, red areas represent forest stands in which NDVI has decreased significantly since 1984 (by up to 0.3% per year)

Growth response of young Douglas-fir to nitrogen, calcium, phosphorus, and blended fertilizers in Oregon and Washington: Growth period two, 4-6 years

Doug Mainwaring, Doug Maguire, and Steve Perakis

Abstract

We tested six fertilizer treatments for their ability to increase stem volume growth response of dominant and co-dominant trees in young Douglas-fir plantations of western Oregon and Washington. The marginal regional responses to N, lime, and P apparent during the first three-year growth period were no longer apparent, and site-level predictors of response were no longer significant. Positive responses to specific nutrients at specific sites were in some cases sustained. A very general relationship between six-year growth response and change in crown-base sapwood area does point to an increase of leaf area as an important means of response, regardless of fertilizer type.

Introduction

Nitrogen (N) is widely considered to be the most common growth limiting nutrient in terrestrial ecosystems worldwide, particularly in temperate forests (LeBauer and Treseder 2008). In the Pacific Northwest, USA, field experiments in both natural and planted second growth forests demonstrate widespread N limitation of growth in Douglas-fir (Miller and Pienaar 1973). Consequently, N fertilization is widespread in commercial forests of the region, for example, with nearly 40,000 ha of timberland fertilized annually in Oregon through the 1990s (http://www.oregon.gov/ODF/STATE_FORESTS/FRP/annual_reports.shtml). The magnitude of Douglas-fir growth response to N fertilization can depend on a number of factors, such as intrinsic site productivity, nitrogen availability, degree of crown closure, and the combination of crown size and foliar density.

Douglas-fir response to N fertilization varies regionally across the Pacific Northwest, and in some cases, such as the coastal forest province, up to one-third of stands can show negligible and even negative growth responses to N fertilization (Peterson and Hazard 1990). High N soils may also be depleted in available base cations such as calcium (Ca) and magnesium (Mg) due to elevated nitrification, soil acidification, and coupled nitrate and base cation leaching loss (Perakis et al. 2006).

High N concentrations are a particular concern in Douglas-fir stands within the coastal zone where Swiss needle cast (SNC) is currently at epidemic levels. In such stands, where N fertilization has been ineffective at improving tree growth (Mainwaring et al. 2005), and where increased N has been implicated in exacerbating disease expression (El-Hajj et al. 2004), exploring the effectiveness of other non-nitrogen nutrient amendments on tree growth is an obvious alternative.

In order to understand nutritional limits to Douglas-fir growth on high-N forest soils of the Pacific Northwest, in the fall of 2006 a field experiment was initiated to test individual tree response to numerous nutrients. Three-year results indicated that across the region, dominant trees exhibited a marginal positive response to nitrogen, lime, and phosphorus. In addition, site factors were identified which could help identify which stands would respond to specific nutrients, namely nitrogen, calcium, and phosphorus. Response to nitrogen was positive related to the soil calcium:nitrogen ratio, response to calcium (lime or CaCl_2) was negatively related to

foliar calcium concentration and soil pH, and response to phosphorus was negatively related to foliar phosphorus and soil pH. This report addresses the growth response of the same trees during the growth period 4-6 years following treatment.

Methods

Study sites

Sixteen study sites were distributed across a range in elevation, aspect, and Swiss needle cast 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). Target stands were mid-rotation Douglas-fir plantations of operational density that had received no previous thinning or fertilization (Table 1).

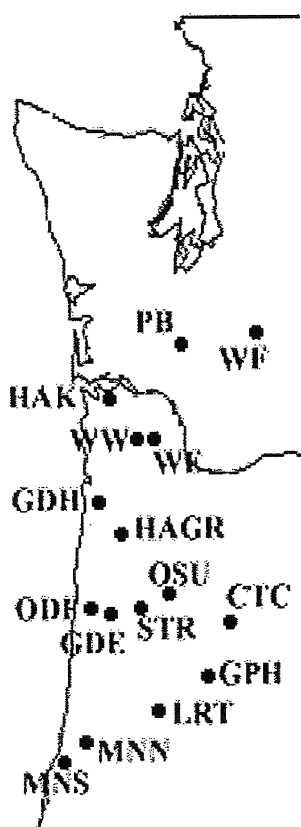


Figure 1 Location of the 16 "Beyond N" fertilizer trials in Oregon and Washington.

Sites received either seven treatments (twelve sites) or only five of the seven treatments (four additional sites) (Table 1). The five treatments common to all 16 sites included the following amendments and rates: 1) untreated control (no fertilization); 2) nitrogen (225 kg N ha⁻¹ as urea); 3) calcium (1020 kg Ca ha⁻¹ as lime (prilled, 34% Ca²⁺), intended to provide Ca and increase soil pH); 4) calcium (105 kg Ca ha⁻¹ as CaCl₂, intended to provide Ca but with minimal influence on soil pH), and 5) phosphorus (580 kg P ha⁻¹ as monosodium phosphate). Twelve of the 16 sites also received two site-specific blends (for applied quantities, see Beyond Nitrogen write-up in SNCC 2007 annual report). The Kinsey blend was based on an analysis of soil chemistry and targeted a specific base cation saturation ratio (65% Ca, 15% Mg, and 3.5% K; Albrecht 1975). Attaining this ratio typically necessitated a multi-year application regime. The Fenn prescription entailed a single application of a blended fertilizer to bring foliar nutrient concentrations above deficiency levels defined by Walker and Gessel (1991) with modifications based on operational trials implemented by the late George Fenn (forest landowner from Elkton, Oregon).

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. 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 was applied during February-April 2007. The Kinsey treatment was designed as a two-year regime, with non-lime materials applied during February-April 2007 and lime

applied during the winter of 2007-2008.

Measurements

The following dimensions were recorded prior to the growing season of 2007 for all measurement trees located at the center of each treatment plot: dbh, height, height to lowest live branch, and breast-height sapwood width. All other trees within the fixed-area treatment plot

were also measured for initial dbh (nearest 0.1 cm) and plot basal area was computed as a measure of local stand density. To standardize foliage sampling, the southernmost branch in the fifth whorl from the tip of the tree was identified. The largest 4-yr-old lateral was removed from this branch on each tree for chemical analysis of foliage and estimation of foliage retention. The samples for foliar chemistry were a composite sample of current year foliage from trees receiving the same treatment at a given site.

Two soil cores of surface mineral soil (0-10 cm) were collected from opposite sides of each subject tree perpendicular to the slope, composited by treatment within sites, and subsampled for chemical analysis.

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

Plot	Tree attributes						Plot attributes							
	Quadratic mean dbh (cm)	Ht. (m)	Crown ratio	Foliage retention (yrs)	BH age (years)	Site Index (m @ 50 yrs)	Fol. N (%)	Fol. P (%)	Fol. Ca (%)	DF density (trees/ha)	DF basal area (m ² /ha)	pH	soil N (%)	soil Ca (%)
CTC	27.9	23.1	0.57	3.38	23.0	41.8	1.30	0.145	0.540	977	35.4	5.34	0.32	0.316
GDE	39.1	28.1	0.51	2.77	27.1	46.0	1.46	0.115	0.205	512	43.4	4.86	0.58	0.034
GDH	29.2	21.1	0.64	1.62	19.8	41.3	1.43	0.115	0.185	724	32.6	4.74	0.59	0.012
GPH	23.4	17.2	0.64	3.64	15.0	47.5	1.26	0.150	0.530	921	24.9	5.97	0.19	0.196
HAGR	27.2	16.6	0.75	2.22	15.9	46.5	1.51	0.140	0.310	683	27.9	5.00	0.45	0.049
HAK	32.0	23.9	0.60	2.36	21.8	46.9	1.31	0.135	0.295	630	37.3	5.05	0.55	0.023
LRT	36.8	22.6	0.65	3.35	21.1	43.1	1.24	0.175	0.540	435	36.3	5.84	0.16	0.106
MNN	27.4	17.8	0.70	2.22	13.3	54.1	1.42	0.110	0.205	782	31.4	4.93	0.83	0.017
MNS	29.5	20.9	0.61	2.66	20.0	46.6	1.43	0.110	0.300	768	33.9	5.23	0.51	0.060
ODF	25.9	16.9	0.69	2.34	14.7	48.9	1.56	0.135	0.290	877	30.2	4.79	0.55	0.030
OSU	25.9	18.0	0.67	3.31	14.8	46.9	1.27	0.179	0.608	819	32.6	6.46	0.21	0.307
PB	26.4	21.5	0.47	3.41	20.4	45.1	1.30	0.175	0.455	1186	36.5	5.80	0.21	0.070
STR	29.2	20.2	0.65	2.71	17.7	48.7	1.27	0.175	0.490	754	35.8	5.30	0.28	0.116
WE	19.6	12.9	0.71	2.13	13.0	44.1	1.44	0.190	0.520	1544	31.4	6.00	0.17	0.147
WF	35.1	20.2	0.79	3.65	20.0	42.7	1.23	0.170	0.415	476	39.7	4.95	0.25	0.042
WW	29.5	23.0	0.59	2.28	28.4	36.2	1.19	0.210	0.350	708	35.4	5.58	0.18	0.149

All measurements were repeated in the fall of 2009, after the end of the third growing season since treatment. Changes in foliar and soil chemistry resulting from these treatments will be reported in a later paper.

Chemical analysis was performed by the Central Analytical Laboratory at OSU.

Analysis

Fertilizer treatment effects were tested on two different response variables to provide insight into the distribution of growth responses: 1) three-year stem volume growth (Bruce and Demars 1974) and 2) crown base sapwood cross sectional area.

Treatment effects were tested by analysis of covariance under a generalized randomized complete block design. The final covariates chosen for use for all volume growth tests were $Dbh^2 \times Ht$ and plot-level basal area. Sapwood area at breast height was computed by assuming a circular stem cross-section and by estimating diameter inside bark at breast height from dbh (Larsen and Hann 1985). Sapwood area at crown base was then estimated from an existing regional sapwood taper function (Maguire and Batista 1996).

Replication within sites allowed testing of site \times treatment interactions and identification of site-specific treatment effects.

To test the hypothesis that volume growth response can be predicted from initial soil and/or foliar chemistry, a separate analysis was performed by replacing site or block effects with attributes that characterized each site, e.g., site index, soil variables, and foliar nutrient

concentrations.

Results

Regional volume growth

The regional volume growth analysis with covariates yielded an insignificant treatment effect ($p=0.30$), and an insignificant block \times treatment interaction ($p=0.16$), indicating that after adjusting for tree size and stand density, responses to treatment were site-specific rather than general across the region. Multiple comparisons indicated that stem volume growth did not differ among treatments.

Site-specific analysis of covariance indicated that volume growth increases were significant following N treatment at one site (ODF), lime treatment at one site (WW), Kinsey treatment at one site (ODF), and the Fenn treatment at one site (ODF). In addition, one site demonstrated a marginally significant increase in volume growth following nitrogen treatment (WW), one following lime treatment (MNN), and one following phosphorus treatment (WW). *Change in crown-base cross sectional area (6-yr)*

The regional analysis with covariates yielded a significant treatment effect ($p=0.032$), and an insignificant block \times treatment interaction ($p=0.117$), indicating that after adjusting for tree size and stand density, responses to treatment were general across the region. Over the six year period, only the lime treatment exhibited a significant change in sapwood area at crown base, increasing 16.8%. When the analysis was confined to the first or second growth periods, the increase in sapwood was marginally significant for the lime treatment in period 1 ($p=0.067$) though not in period 2 ($p=0.104$).

Site-specific analysis of covariance, indicated that sapwood area increases were significant following N treatment at one site (WW), lime treatment at one site (CTC), and CaCl_2 treatment at one site (WW). In addition, two sites demonstrated a marginally significant increase in crown sapwood area following nitrogen treatment (CTC, GPH), one following lime treatment (WW), one following phosphorus treatment (CTC), and one following Fenn treatment (CTC). One site also showed a marginal decrease in sapwood area following nitrogen treatment (OSU).

Volume growth as characterized by site

Variables for predicting volume growth response of measurement trees in the first three following treatment included tree attributes, site factors (e.g., site index), and variables representing various soil and foliar nutrient concentrations; however, the variables selected for predicting volume growth response varied by treatment. When remeasurement data from period 2 was used within the period 1 model forms, neither the fertilizer treatments nor treatment interactions were significant factors in explaining volume growth. When simplified model forms without interactive treatment terms were used, treatment remained an insignificant factor in explaining growth.

Discussion

Previous studies have concluded that nitrogen-fertilized Douglas-fir can demonstrate a long-term direct response of up to 15 years since treatment (Hann et al. 2003), with a peak response varying from 2 to 5 years (Curtis 1981, Miller et al. 1988) after fertilization. In contrast, a recent analysis of intensively managed plantations has concluded that the direct response to N-fertilization is complete within four years (Hann et al. 2013). In the case of the two sites showing positive responses to N fertilization during the first three year period (CTC, WW), the more productive site (CTC) did not continue to show a significant response in the second three-year period while the less productive site (WW) did. This suggests that the length

of the direct positive effect of fertilization can vary by site, and agrees with previous assertions that this is related to site productivity (Miller et al. 1986).

In contrast to expectations, the only site that exhibited a significant positive response to nitrogen during the second three-year period had the greatest initial foliar N at the time of treatment (ODF, 1.56%). This site exhibited a relatively low foliage retention as a consequence of Swiss needle cast (SNC), and did not respond during the first three-year period. At the start of the first growth period, foliage retention among N-treated trees at ODF averaged 1.91 years (vs 2.66 years at the start of the second growth period). While this change was not significantly different from that on the control plots (from 2.41 years to 2.55 years) as a result of a large amount of variation among individual trees, previously established relationships between foliage retention and growth (Maguire et al. 2011) suggest that the N-treated trees would exhibit greater growth in period 2 as a result of the large average increase in foliage retention. A glance at crown base sapwood cross sectional area and crown length together as an index of crown sparseness (CL:SA, Maguire and Kanaskie 2002), indicates that over the six years of the study crowns densified marginally on both the N and Fenn treated trees at the ODF site ($p=0.105$ and 0.056 , respectively), a further indication that the period 2 responses at ODF were related to increases in leaf area. While SNC-infected trees are not believed to provide a sufficient response from N fertilization to make the effort financially sound (Mainwaring et al. 2005), moderately infected sites such as the ODF site can benefit from significant changes in foliage retention as a result of annual variation in climate and subsequent changes in disease abundance (Zhao et al. 2011). If coincident with fertilization treatment, trees may be able to increase total foliar content of many nutrients, and show gains in foliar quantity and stemwood increment. Trees at ODF showed large though insignificant increases in sapwood area, and this may explain the general responsiveness to fertilization during growth period two across most treatments at ODF. Foliar N concentration within the N and Fenn-treated trees at the ODF site was lower at year three than

year zero, which also suggests an increase in total leaf area, and a subsequent dilution of foliar nitrogen as a result.

Period two volume growth was relatively good on both the ODF and WW sites, with 50 and 75% of the fertilizer treatments on the respective sites exhibiting marginal or significant responses, and an implied double-digit percentage improvement on non-responding treatments on the same sites. Site-specific explanations for these responses were not apparent, though the sites differ markedly in their foliar N concentration, stand-level leaf area, and apparent soil depth and drainage class. Another important difference was the response of volume growth to fertilization: the WW site

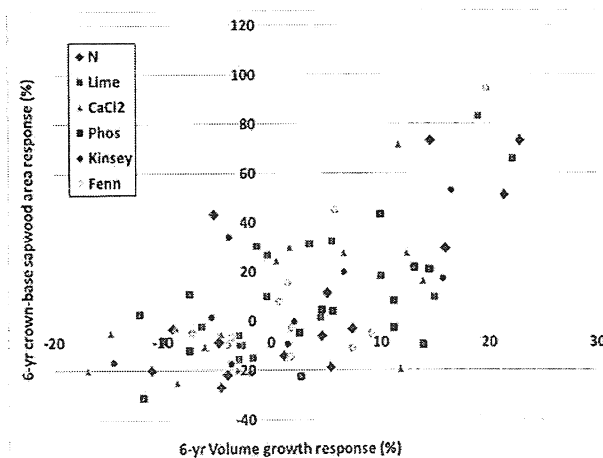


Figure 2 Mean volume growth response of fertilized trees (proportion of control mean) versus crown base sapwood cross sectional area.

responded immediately and sustained through period 2. Though the delayed responses at ODF may be the result of changing SNC conditions, this probably doesn't explain the delayed responses to lime at MNN and WW, and to phosphorus at WW. The slower rate at which lime is

incorporated into the soil may help explain the delayed response to lime on responsive sites, though the same would not be true of P.

Direct response to nitrogen fertilization has been attributed to an immediate increase in foliar N concentration and photosynthesis (Mitchell and Hinckley 1993), improved efficiency of photosynthesis and water use (Brix and Mitchell 1986), and the expansion and densification of the crown (Brix and Ebell 1969). Increase in tree-level photosynthetic surface area is a logical means by which trees increase volume growth, and trees within this study did demonstrate a direct relationship between volume growth response and an increase in crown base sapwood cross-sectional area (figure 2).

The manner with which this direct response, though of high variability, and apparently independent of fertilizer type, is distributed among trees within a stand, does highlight the inferential problem of relating tree-level results to stand-level response. The expansion of tree

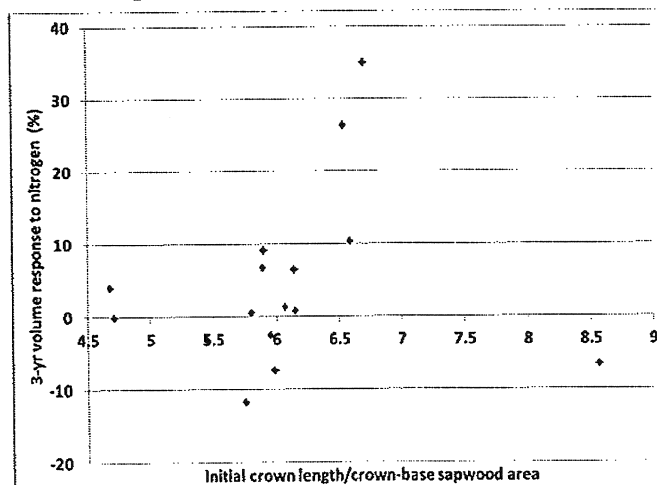


Figure 3 Mean volume growth response of nitrogen treated trees (relative to control) versus pre-treatment crown sparseness [(Crown length)/(crown base sapwood cross sectional area)] (cm/cm^2).

crowns and the enhancement of growth that results necessarily affects stand differentiation, to the advantage of trees in an initially dominant position. Therefore, the positive response of the winners is tempered by the increased suppression and mortality of the losers, which has been witnessed elsewhere (Brix 1993). As a result, the response of dominant trees isn't necessarily indicative of entire stands.

Nevertheless, dominant trees may provide a good index of response likelihood. Due to the positive relationship between crown density and light attenuation, response to fertilization would be promoted by low initial foliar density. Consistent with this idea (with one notable exception), sites in this study showing a positive

response to nitrogen within the first three year period had sparser crowns (a greater initial CL:SA) (figure 3). Douglas-fir crown density is directly related to relative stand height (Maguire and Kanaskie 2002), indicating that dominant trees would generally have the greatest crown density within a stand. Dominant trees may thus serve as indicators of response, given both their ability to outcompete neighbors and aggrandize space, and to reflect the current site capacity for foliar density. Additional work would be needed to develop this idea quantitatively. Figure 3 indicates that the relationship between response and CL:SA is present over a small range of CL:SA, this metric shows wide variability within dominant trees within a stand: the average standard deviation of CL:SA within the stands of this dataset is approximately $0.98 \text{ cm}/\text{cm}^2$. Furthermore, previous work has shown that the range in CL:SA can vary with age, Swiss needle cast incidence, and other stand factors (Maguire and Kanaskie 2002, Mainwaring and Maguire, unpublished).

Conclusions

1) Site-level positive volume responses during the first three-year period were sustained in the

second three-year period on some but not all sites, suggesting that the length of time of the direct effect of fertilization is site-dependent.

2) Some sites that were unresponsive in the first three-year period had a positive response to fertilization in the second three year period, likely due to the coincidental variation in foliage retention due to SNC.

3) A generally positive relationship was apparent between crown base sapwood cross-sectional area and stem volume response, regardless of treatment, suggesting the importance of initial crown condition and canopy position as an indicator of fertilizer response.

Acknowledgements

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Disclaimer: Any use of trade names is for descriptive purposes only and does not imply endorsement by the US Government.

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Assessing the role of soils in affecting Swiss needle cast severity: A need for additional study.

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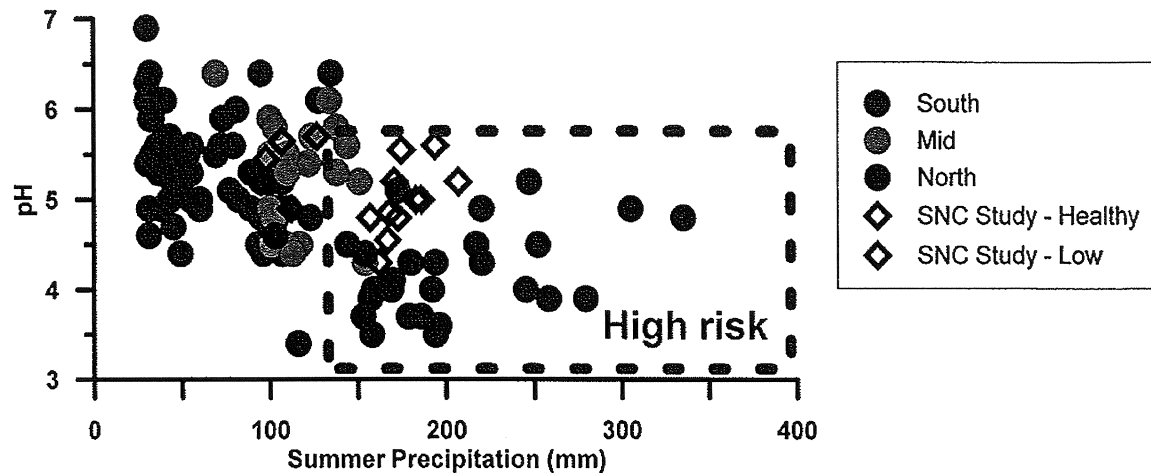
Swiss needle cast severity has been shown to correlate significantly with climate (Zhao *et al.*, 2011; Zhao *et al.*, 2012). Generally the disease is more severe with proximity to the coast. There has been recent work showing that high foliar and soil nitrogen, low soil calcium, and low soil pHs are significantly correlated with SNC severity (e.g. Waring *et al.*, 2000). This suggests soils have some control over the disease. However, other studies have shown that soil N (and other nutrients) has been shown to have similar relationships with the same climatic gradient that SNC does, but these studies have not examined the full latitudinal gradient of SNC (e.g. Perakis *et al.*, 2006; Perakis *et al.*, 2013). Therefore, it has been very difficult to separate the influence of soil from that of climate over the range of SNC in the coast ranges of Oregon and Washington. We hypothesize that there is an interaction of climate and soil along a latitudinal gradient that affects SNC occurrence and severity.

We examined data (n=16-25 depending on variable) from a 1999 survey of “healthy” and SNC affected trees (Waring *et al.*, 2000). These data included many common soil variables (A horizons), foliar retention, and foliar chemistry. We combined this data with climatic data from PRISM using Climate WNA (means calculated from 1961-1990) to get a first approximation of the importance of soil in affecting SNC severity. An all subsets regression of the uncorrelated soil and climatic variables resulted in many strong models. A four parameter model explained 99% of the variability and included 3 soil variables (soil N%, extractable P, and % <2mm) and one climate variable (average minimum autumn temperature). This dataset was also examined using stepwise linear regression. We found that foliar retention was best explained by soil N, summer precipitation, and average minimum autumn temperature. The standardized coefficients ranged from -0.45 to -0.85 suggesting a similar level of importance for each of these parameters. The bottom line is that soils appeared to be an important factor in predicting SNC severity.

Since there appears to be evidence supporting the hypothesis that soils and climate interact to affect SNC severity, we examined the relationships of soil and climate characteristics across the range of potential SNC sites in the United States (N. CA to W. WA). We plotted the soil and climate variables from soils examined in the Waring *et al.* (2000) publication. Those soils from stands with low needle retention (<3 yrs) were colored red and “healthy” (needle retention >3yrs) were colored black. We are showing the relationship between soil pH and summer precipitation in the following figure (see next page). Low and high foliar retention stands tend to form separate groups. We suggest that these groups may be showing threshold behavior. Below a pH of 5.5 and above a summer precipitation of 150mm may result in stands with a high risk of having low foliar retention (dashed box in following figure).

We then examined the range of surface soil characteristics along the coast from Northern California to Western Washington. This soil data was extracted from the NRCS pedon data set (NCSS data set) and the climate data was extracted from the PRISM data set using Climate

WNA . We split the data into South (all points south of Coos county Oregon), Mid (Oregon Coast), and North (Western Washington). From this preliminary analysis it appears that the southern sites may have the lowest risk of low foliar retention due to either high soil pH or low summer precipitation. On the other hand it appears that sites in the North and Mid coast may have the highest susceptibility to low foliar retention. This analysis is preliminary and only used here to show that the connections of soil to SNC severity is worthy of additional study.



The proposal

We propose to leverage the permanent plot study currently being established by the Swiss Needle Cast Cooperative (SNCC). The SNCC permanent plot network will consist of 100 permanent plots across a 5 latitude zones and 4 distance-from-coast zones that spans a range from Northwest CA to Southwest WA states. Each zone (20) has 5 replicate plots. The sites are being phased in over 3 years. The SNCC is collecting data on tree growth, disease severity, and stand characteristics. Additionally, the SNCC is collecting foliar samples that can be utilized for this study.

We propose to collect soils from 5 locations within each plot that will be composited by depth. Soils will be collected from O-horizons, 0-10, 10-20, and 20-30cm. Soils will be analyzed for 1) pH 2) total C, N, and S, 3) KCl extractable N, 4) NH_4 -acetate extractable Ca, Al, K, Mg, Mn, Fe, Cu, B, and Zn, and 5) extractable P. Foliar samples being collected by the SNCC and analyzed for SNC impacts will be analyzed for total concentrations of C, N, S, Ca, Al, K, Mg, Mn, Fe, Cu, B, and Zn. Climate and weather variables will be extracted from the PRISM database for every plot. These variables will include monthly, seasonal, and annual precipitation, temperature, and dew point among others.

Using multivariate procedures such as ordination (canonical correspondence analysis (CCA), principle coordinates analysis (PCA)) we will examine the importance of soils and climate in predicting the response of Douglas-fir to SNC. We can then model the response within important classes as they emerge from the multivariate analysis using regression techniques. These data can be used with growth and SNC data collected from the permanent

plots in the coming 10 years of the SNCC study. The ultimate goal is to develop and refine models of SNC severity and occurrence and its effects on Douglas-fir growth.

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Original Article

Tree-ring stable isotopes record the impact of a foliar fungal pathogen on CO₂ assimilation and growth in Douglas-fir

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ABSTRACT

Swiss needle cast (SNC) is a fungal disease of Douglas-fir (*Pseudotsuga menziesii*) that has recently become prevalent in coastal areas of the Pacific Northwest. We used growth measurements and stable isotopes of carbon and oxygen in tree-rings of Douglas-fir and a non-susceptible reference species (western hemlock, *Tsuga heterophylla*) to evaluate their use as proxies for variation in past SNC infection, particularly in relation to potential explanatory climate factors. We sampled trees from an Oregon site where a fungicide trial took place from 1996 to 2000, which enabled the comparison of stable isotope values between trees with and without disease. Carbon stable isotope discrimination ($\Delta^{13}\text{C}$) of treated Douglas-fir tree-rings was greater than that of untreated Douglas-fir tree-rings during the fungicide treatment period. Both annual growth and tree-ring $\Delta^{13}\text{C}$ increased with treatment such that treated Douglas-fir had values similar to co-occurring western hemlock during the treatment period. There was no difference in the tree-ring oxygen stable isotope ratio between treated and untreated Douglas-fir. Tree-ring $\Delta^{13}\text{C}$ of diseased Douglas-fir was negatively correlated with relative humidity during the two previous summers, consistent with increased leaf colonization by SNC under high humidity conditions that leads to greater disease severity in following years.

Key-words: *Phaeocryptopus gaeumannii*; *Pseudotsuga menziesii*; stable isotopes; Swiss needle cast; tree-rings.

INTRODUCTION

Swiss needle cast (SNC) disease of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] is caused by stomatal blockages by the fruiting bodies (pseudothecia) of the fungus *Phaeocryptopus gaeumannii* (T. Rohde) Petr., which results in premature needle abscission (Manter *et al.* 2000). SNC was present in the Pacific Northwest before it was considered an

economically important disease. The first record of the fungus and SNC appeared in the mid-1920s after a severe SNC epidemic of U.S.-imported Douglas-fir in Switzerland (Boyce 1940). It was not until the late 1980s that the fungus began causing serious needle loss and growth reductions to Douglas-fir in the United States. Attempts to understand the potential influence of climate on the recent rise in disease severity have suggested that warm winter and spring temperatures and spring/summer leaf wetness may facilitate fungal growth and reproduction (Rosso & Hansen 2003; Manter *et al.* 2005; Coop & Stone 2007; Latta *et al.* 2009; Black *et al.* 2010; Zhao *et al.* 2011).

Previous research using Douglas-fir tree-ring widths attempted to identify historic SNC epidemics and the cause of the sudden prevalence of the disease (Black *et al.* 2010). Although Black *et al.* (2010) provided one potential avenue for understanding the history and onset of SNC, tree-ring widths can be sensitive to numerous environmental variables that could confound a SNC signal or yield false positives for infection when there was no disease (e.g. climate signals, or disturbances associated with defoliating insect outbreaks, fires, windstorms, etc.; McCarroll & Loader 2004; Barnard *et al.* 2012). To more accurately quantify past SNC symptoms in tree-rings, a method is needed that can distinguish physiological responses to SNC from environmental noise. With this information, it would not only be possible to improve our knowledge of the epidemiology of SNC, but also to define clearer relationships between SNC symptoms and the climate factors that exacerbate them. As explained later, stable tree-ring isotope signatures should provide such information.

SNC restricts gas exchange of Douglas-fir needles. In spring, spores land and germinate on current-year foliage, and hyphae begin colonizing the needle surface and interior (Hansen *et al.* 2000). In the most severe cases, the fungus produces pseudothecia that occlude stomata and reduce stomatal conductance (g_s) by about 83% and carbon dioxide assimilation rate (A) by about 72% by the following late spring or early summer (Manter *et al.* 2000). The ratio of intercellular [CO₂] (c_i) to that in the surrounding atmosphere (c_a) is modified by g_s and A , such that a decrease in g_s will

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cause c_i to decrease, and a decrease in A will cause c_i to increase, but not enough to compensate for the impact of the decline in g_s (Farquhar *et al.* 1989). Biochemical discrimination against the heavier stable carbon isotope ^{13}C ($\Delta^{13}\text{C}$) during CO_2 assimilation is directly related to c_i/c_a , and thus, $\Delta^{13}\text{C}$ is also influenced by g_s and A (Farquhar *et al.* 1982; Evans *et al.* 1986). The physical blockage of stomata in trees with SNC causes a reduction in g_s and a weaker decline in A , such that c_i/c_a should decrease, causing the $\Delta^{13}\text{C}$ of fixed carbohydrates to decrease. In addition, reduced g_s in trees with SNC could potentially cause changes in tree-ring oxygen isotope fractionation ($\Delta^{18}\text{O}$) (Barbour 2007). According to the original model of Farquhar & Lloyd (1993), a reduction in g_s and therefore, transpiration (E) would result in decreased advection of unenriched xylem water to the sites of carboxylation. The resulting increase in the relative impact of back diffusion of ^{18}O -enriched water from the sites of evaporation to the sites of carboxylation would cause a potential increase in ^{18}O fixed into carbohydrates. Alternatively, sufficiently low levels of E , comparable with those reported for Douglas-fir (e.g. Cernak *et al.* 2007), have been reported to cause the effective path length (L) for water movement through the leaf to increase exponentially with decreasing g_s and E (Song *et al.* 2013). Taken together, because changes in g_s and A likely affect the $\Delta^{13}\text{C}$ and $\Delta^{18}\text{O}$ of carbohydrates fixed by diseased trees, tree-rings could record the signal imparted by the effects of SNC on g_s and A in a given year. If SNC indeed has an effect on tree-ring $\Delta^{13}\text{C}$ and/or $\Delta^{18}\text{O}$, then we need to understand how $\Delta^{13}\text{C}$ and $\Delta^{18}\text{O}$ change in response to disease symptom severity to be able to reconstruct past disease severity using these stable isotopes in tree-rings, and to better understand the response of the disease to meteorological variables.

The objectives of the present study were to determine: (1) whether analysis of tree-ring $\Delta^{13}\text{C}$ and $\Delta^{18}\text{O}$ can serve as a diagnostic tool for the detection of past SNC infection in Douglas-fir and (2) which climate factors may modify the strength of the signal. We sampled trees at the site of a fungicide trial where there are known years of severe SNC and years of low SNC. We hypothesized that $\Delta^{13}\text{C}$ would be higher in tree-rings during years of low SNC than during years of severe SNC. In contrast, we hypothesized that tree-ring $\Delta^{18}\text{O}$ during years of low SNC would be lower than that of years of severe SNC, based on the model of Farquhar & Lloyd (1993). For both carbon and oxygen analyses, we used co-occurring western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] as a non-host reference species. Previous research suggests that severity of SNC infection increases under warmer winters and wetter springs and summers [e.g. greater fog, precipitation, relative humidity (RH)], thus we expected to find lower $\Delta^{13}\text{C}$ and higher $\Delta^{18}\text{O}$ following winters with above average temperatures or wet conditions during spring and summer of the previous year.

MATERIALS AND METHODS

Carbon stable isotope conceptual approach

We investigated $\Delta^{13}\text{C}$ patterns of plant cellulose ($\Delta^{13}\text{C}_{\text{cell}}$) as influenced by SNC because this signal should integrate, at the

canopy level, the physical and biochemical processes known to be affected by SNC at the leaf level. Because the carbon isotope ratio of the atmospheric CO_2 ($\delta^{13}\text{C}_{\text{atm}}$) changes over time and influences the carbon isotope ratio of plant cellulose ($\delta^{13}\text{C}_{\text{cell}}$), this effect can then be accounted for by calculating $\Delta^{13}\text{C}_{\text{cell}}$ (‰), following Farquhar *et al.* (1982):

$$\Delta^{13}\text{C}_{\text{cell}} = \frac{\delta^{13}\text{C}_{\text{atm}} - \delta^{13}\text{C}_{\text{cell}}}{1 + \delta^{13}\text{C}_{\text{cell}}}, \quad (1)$$

where annual values of past $\delta^{13}\text{C}_{\text{atm}}$ have been estimated by McCarroll & Loader (2004; data from 1989 to 2003) and for more recent years from monitoring at Mauna Loa, Hawaii (<http://cdiac.ornl.gov/>; data from 2004 to 2011). C_3 photosynthesis causes $\Delta^{13}\text{C}_{\text{cell}}$ to be related directly to c_i/c_a , as described by Farquhar *et al.* (1989):

$$\Delta^{13}\text{C}_{\text{cell}} = a + (b - a) \left(\frac{c_i}{c_a} \right), \quad (2)$$

where a is fractionation resulting from diffusion of CO_2 from the ambient air through the stomata to the intercellular spaces (4.4‰), and b is fractionation associated with carboxylation by rubisco (−27‰). Equation 2 is an approximation that does not account for other variables that influence $\Delta^{13}\text{C}$ such as differences between c_i and $[\text{CO}_2]$ at the sites of carboxylation (c_c) related to variation in mesophyll conductance. Nevertheless, Eqn 2 has proven to be adequate for relating variation in plant tissue $\Delta^{13}\text{C}$ to variation in c_i/c_a driven by changes in A/g_s in a broad range of species (Cernusak *et al.* 2013).

SNC infection starts in newly expanded leaves, but in the most severe cases, the fungus does not affect gas exchange until the pseudothecia emerge during spring in the year following infection (Manter *et al.* 2000; Stone *et al.* 2008). The physical blockage of stomata causes a decline in A , but a stronger relative reduction in g_s , such that c_i/c_a should decrease, causing the $\Delta^{13}\text{C}$ of fixed carbohydrates to decrease (Manter *et al.* 2000). However, there are potential limitations on the utility of tree-ring $\Delta^{13}\text{C}_{\text{cell}}$ values as integrators of temporal variation in the severity of SNC symptoms. SNC-induced biochemical limitations on assimilation rates (Manter *et al.* 2000) may eventually cause c_i/c_a to increase resulting in higher $\Delta^{13}\text{C}_{\text{cell}}$ values. Additionally, hyphae in the leaf may continue to increase in mass through the summer following initial infection, causing further decreases in photosynthesis (Manter 2000), which could cause the needles experiencing the most severe symptoms to contribute less to tree-ring $\Delta^{13}\text{C}_{\text{cell}}$. Another consideration is that in the most extreme cases of infection, nearly all needles on the tree eventually develop a negative carbon balance (i.e. consuming more carbon than they fix) and abscise during the second year of infection (Manter *et al.* 2003), thus reducing the impact of photosynthate from these needles on $\Delta^{13}\text{C}_{\text{cell}}$. Despite these potential caveats, the effect of the fungus on $\Delta^{13}\text{C}_{\text{cell}}$ 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 focused on the central portion of the tree-ring, hereafter referred to

as *middlewood* (*sensu* Roden *et al.* 2011), which contains cellulose synthesized from sugars produced in spring and early summer before abscission of the most severely infected needles.

A final consideration is the effect of the relationship between leaf mesophyll conductance (g_m) and $\Delta^{13}C_{\text{cell}}$. Flexas *et al.* (2008) restrict the definition of g_m to the diffusion of CO_2 through leaf mesophyll, including intercellular air spaces, the cell wall, and the intracellular liquid pathway. Several studies have addressed how changes in g_m due to a variety of influences, such as water and nutrient stress, can lower c_c without a concurrent change in g_s (Flexas *et al.* 2008, 2012; Seibt *et al.* 2008). Reduced c_c results in less discrimination against ^{13}C and a lower $\Delta^{13}C_{\text{cell}}$, assuming there are no concurrent changes in the biochemical capacity of photosynthesis to offset the changes due to a reduction in g_m . Capitano (1999) demonstrated that there is significant hyphal growth inside the needles of Douglas-fir with SNC, which could potentially cause g_m to decrease, and thus $\Delta^{13}C_{\text{cell}}$ to decrease. The potential impact of the fungus on g_m should amplify the $\Delta^{13}C_{\text{cell}}$ signal in tree-rings by reducing c_c , although previous research with Douglas-fir has suggested that $\Delta^{13}C_{\text{cell}}$ may remain rather constant under changing g_m (Warren *et al.* 2003). In either case, changes in g_m should not negatively affect the ability to use the analysis of $\Delta^{13}C_{\text{cell}}$ as a diagnostic tool for the detection of past SNC infection in Douglas-fir tree-rings, but it does limit the extent to which changes in $\Delta^{13}C_{\text{cell}}$ could be directly attributed to changes in g_s .

Oxygen stable isotope conceptual approach

We used stable isotope values of ^{18}O from the tree-ring cellulose of Douglas-fir as another potential indicator of variation in SNC symptom severity. The carbohydrates that become tree-ring cellulose carry a signal imparted by the oxygen stable isotope ratio ($\delta^{18}\text{O}$) of leaf water, which is primarily influenced by the isotopic composition of source water entering the leaf from the xylem and ^{18}O -enrichment at the sites of evaporation within the leaf (Craig & Gordon 1965; Dongmann *et al.* 1974). According to the Craig–Gordon model (Craig & Gordon 1965), the steady-state isotopic enrichment of oxygen over plant source water at the sites of evaporation in the leaf ($\Delta^{18}\text{O}_{\text{es}}$) is:

$$\Delta^{18}\text{O}_{\text{es}} = \varepsilon^* + \varepsilon_k + (\Delta^{18}\text{O}_v - \varepsilon_k) \left(\frac{e_a}{e_i} \right), \quad (3)$$

where ε^* is the equilibrium fractionation factor between liquid water and gaseous water (i.e. vapour); ε_k is the kinetic fractionation factor as vapour diffuses from leaf intercellular spaces to the atmosphere; $\Delta^{18}\text{O}_v$ is the isotopic difference between vapour and plant source water; and e_a/e_i is the ratio of atmospheric to intercellular vapour pressure.

Evaporative enrichment is complicated by several factors, such as the mass flow of unenriched water from the xylem that opposes the diffusion of enriched water from the sites of evaporation back towards the xylem (i.e. the Péclet effect; Farquhar & Lloyd 1993), which results in spatial

heterogeneity in the isotopic composition of leaf water from the xylem to the site of evaporation (Wang & Yakir 1995). Evaporative enrichment is also affected by non-steady-state conditions (Farquhar & Cernusak 2005). Based on previous research that has shown little difference between steady- and non-steady-state models of leaf water enrichment in conifers (Lai *et al.* 2006; Seibt *et al.* 2006; Barnard *et al.* 2007; Snyder *et al.* 2010), we used the steady-state model for isotopic enrichment of mean lamina mesophyll water ($\Delta^{18}\text{O}_L$) proposed by Farquhar & Lloyd (1993) for this study. $\Delta^{18}\text{O}_L$ is estimated using the equation (Farquhar & Lloyd 1993):

$$\Delta^{18}\text{O}_L = \frac{\Delta^{18}\text{O}_{\text{es}}(1 - e^{-\rho})}{\rho}, \quad (4)$$

where ρ is the Péclet number, a dimensionless ratio of the advection of unenriched source water to the evaporative sites to the back diffusion of enriched water from evaporative sites, which is calculated as follows:

$$\rho = \frac{EL}{CD}, \quad (5)$$

where E is the leaf transpiration rate ($\text{mol m}^{-2}\text{s}^{-1}$), L is the effective path length (m) for water movement from the veins to the site of evaporation, C is the density of water (mol m^{-3}), and D is the diffusivity (m^2s^{-1}) of H_2^{18}O in water. The parameter L is a product of the distance of the pathway from the xylem to the evaporative surface and a scaling factor that adjusts for the tortuosity of the path (Farquhar & Lloyd 1993).

The integration of $\Delta^{18}\text{O}_L$ into plant cellulose ($\Delta^{18}\text{O}_{\text{cell}}$) is described by the following equation (Barbour & Farquhar 2000):

$$\Delta^{18}\text{O}_{\text{cell}} = \Delta^{18}\text{O}_L(1 - p_{\text{ex}}p_x) + \varepsilon_o, \quad (6)$$

where p_{ex} is the proportion of oxygen atoms that exchange with xylem water during cellulose construction at the meristem, p_x is the proportion of unenriched xylem water at the site of cellulose construction (value of 1 when the cellulose was collected from mature, suberized stems), and ε_o is a fractionation factor of +27‰ to adjust for water/carbonyl exchange (Sternberg 1989; Yakir & Deniro 1990).

In the case of SNC, reduced g_s and E in diseased Douglas-fir trees could cause increases in $\Delta^{18}\text{O}_{\text{cell}}$ due to a reduction in the Péclet number provided the relative impact of the fungus on stomatal blockage and suppression of E is greater than its potential to increase L through internal proliferation of hyphae (Farquhar & Lloyd 1993). For this study, we utilize $\delta^{18}\text{O}_{\text{cell}}$, without calculating the difference from source water ($\Delta^{18}\text{O}_{\text{cell}} = \delta^{18}\text{O}_{\text{cell}} - \delta^{18}\text{O}_{\text{sw}}$) because we do not have information on the year-to-year variation in source water isotopes. However, because all sampled trees were the same age and located on the same site with the same primary source water, we assumed that differences in $\delta^{18}\text{O}_{\text{cell}}$ between trees and treatments in any year reflected differences in $\Delta^{18}\text{O}_L$ rather than $\delta^{18}\text{O}_{\text{sw}}$.

Treatment group	Age (years)	DBH (cm)	Height (m)	Crown width (m)
Treated Douglas-fir	29 (2)	31.7 (1.2)	22.2 (1.0)	6.7 (0.7)
Untreated Douglas-fir	28 (1)	28.0 (4.2)	19.7 (1.4)	5.0 (1.0)
Western hemlock	23 (4)	37.0 (9.3)	21.4 (2.5)	5.3 (1.5)

Table 1. Characteristics of each treatment group ($n = 6$ trees per treatment group), including age at breast height, diameter at breast height (DBH), height, and crown width (diameter) with one standard deviation from the mean in parentheses

Field site and sampling

We sampled trees in two Douglas-fir stands and one western hemlock stand at a coastal site near Beaver, Oregon (45.3°N, 123.8°W) where Douglas-fir trees exhibit chronic, severe SNC symptoms (Stone *et al.* 2007). From 1996 to 2000, the Oregon Department of Forestry applied Bravo® fungicide (chlorothalonil, Syngenta Crop Protection, Greensboro, NC, USA) twice annually to the trees in one stand (treated Douglas-fir), which dramatically reduced SNC disease severity, while the trees in the other stand remained unsprayed (untreated Douglas-fir; Johnson *et al.* 2003; Stone *et al.* 2007). This experimental site thus provided a unique opportunity to quantify the impact of variation in SNC disease severity on tree-ring $\delta^{13}\text{C}_{\text{cell}}$ and $\delta^{18}\text{O}_{\text{cell}}$ through comparative analyses of stable isotope chronologies in treated and untreated Douglas-fir prior to, during, and after fungicide application. We determined the site severity index (site average of approximately 1.5 to 2 years of needle retention) using the standard SNC sampling method (e.g. Maguire *et al.* 2002). In January 2012, we collected four increment cores (12 mm diameter) from each of six trees of similar age, diameter at breast height, height and crown width in both the fungicide-treated stand and the untreated stand (Table 1). We also collected four cores from each of six trees in a nearby western hemlock stand to use as a baseline of climate impacts on stable isotope chronologies in a co-occurring species that does not become infected by SNC.

Additionally, we collected twigs and foliage from the terminal branches of six Douglas-fir trees at another coastal site with severe SNC near Tillamook, Oregon, called Prairie Hill (45.5°N, 123.8°W) to characterize the $\delta^{13}\text{C}$ signal closer to the source of carbohydrate synthesis in the crown. Sunlit upper canopy branches were not readily accessible at the site where fungicide had been applied. The branches were separated into segments representing growth increments from the years 2012, 2011, 2010 and 2009 (cohort years), and then separated into twigs and foliage. Bark and phloem were removed from the twigs to isolate the twig wood for isotopic analysis.

Annual growth analysis

We measured the ring widths of increment cores with a stereo microscope interfaced with a Velmex measuring table and Measure J2X® measuring software (<http://www.voortech.com/projectj2x/>). The cross-dating program COFECHA (Holmes 1983; Grissino-Mayer 2001) was used to detect either missing or false rings. The ring widths for the four cores from each tree were averaged for each year and basal area increment (BAI, the transverse area of a given growth ring, cm^2) was calculated assuming ring circularity to characterize annual tree growth from 1989 to 2011.

Stable isotope analyses

The middlewood was sliced from each tree-ring from 1989 to 2011 with a scalpel and ground into a fine powder using a ball-mill. Middlewood was defined as the portion of the ring that included the latter 75% of earlywood and the initial 25% of attached latewood from the same year. The ring material from all four cores was pooled for each tree to minimize the effect of differences in isotope signatures around the circumference of the tree. The α -cellulose of each tree-ring was isolated following Leavitt & Danzer (1993). The tree-ring $\delta^{13}\text{C}_{\text{cell}}$ and $\delta^{18}\text{O}_{\text{cell}}$ were measured by stable isotope ratio mass spectrometry (IRMS). All $\delta^{13}\text{C}_{\text{cell}}$ measurements were carried out at the Oregon State University (OSU) in the College of Earth, Ocean and Atmospheric Sciences (CEOAS) Stable Isotope Laboratory using an elemental analyser (NA 1500, Carlo Erba, Milan, Italy) connected to an IRMS (DeltaPlus, Thermo Finnigan, Bremen, Germany). All $\delta^{18}\text{O}_{\text{cell}}$ measurements were carried out at the University of California, Davis, Stable Isotope Facility in the Department of Plant Sciences using a pyrolysis system (PyroCube, Elementar Analysensysteme GmbH, Hanau, Germany) interfaced to an IRMS (PDZ Europa 20-20, Sercon Ltd., Cheshire, UK). Measurement precision (1 SD) was better than 0.06‰ for $\delta^{13}\text{C}_{\text{cell}}$ and 0.24‰ for $\delta^{18}\text{O}_{\text{cell}}$ of tree-rings as determined from sample replicates.

Twig and foliage tissues were oven-dried and ground to a fine powder, packaged as whole tissue into tin capsules, and analysed for $\delta^{13}\text{C}$ using an IRMS at the OSU CEOAS Stable Isotopes Laboratory. Measurement precision was better than 0.10‰ for $\delta^{13}\text{C}$ for twig and foliage tissues as determined from sample replicates. Current-year needles were not expected to show significant fungus-induced alteration in their gas exchange, and thus, current-year wood attached to current-year foliage should not show a strong isotopic signal from the fungus unless a substantial fraction of current-year wood was derived from carbohydrates produced by older foliage. Because the effect of the fungus on needle physiology increases over time, we sought to detect the $\delta^{13}\text{C}$ signal in the newer wood on older shoot extension increments that was built with carbohydrate produced by older needles, and therefore was expected to contain a stronger carbon isotope signal associated with fungal disruption of gas exchange. Since older tissues of twig wood are composed of different layers of wood made in different years, twig wood $\delta^{13}\text{C}$ values were adjusted with a calculation that estimated the $\delta^{13}\text{C}$ of wood produced in the most recent year for each growth increment cohort year. This calculation assumes that the amount of wood from each year was the same for growth increments older than year 0, such that the calculated value of $\delta^{13}\text{C}$ for growth increment x ($\delta^{13}\text{C}_{\text{calc},x}$) based on the

observed value for growth increment x ($\delta^{13}\text{C}_{\text{obs}x}$) where x equals the number of years beyond the sampling year (i.e. 0, 1, 2, 3 years) was:

$$\delta^{13}\text{C}_{\text{calc}1} = (\delta^{13}\text{C}_{\text{obs}1} \times 2) - \delta^{13}\text{C}_{\text{obs}0}, \quad (7)$$

$$\delta^{13}\text{C}_{\text{calc}2} = (\delta^{13}\text{C}_{\text{obs}2} \times 3) - \delta^{13}\text{C}_{\text{obs}0} - \delta^{13}\text{C}_{\text{calc}1}, \quad (8)$$

$$\delta^{13}\text{C}_{\text{calc}3} = (\delta^{13}\text{C}_{\text{obs}3} \times 4) - \delta^{13}\text{C}_{\text{obs}0} - \delta^{13}\text{C}_{\text{calc}1} - \delta^{13}\text{C}_{\text{calc}2}. \quad (9)$$

The preceding equations do not take into account the potential contribution of non-structural carbohydrates formed in prior years to the current-year twig wood increment. Incorporation of photosynthate produced by younger, less heavily infected needles would tend to dampen the expected twig age-related trend in the $\delta^{13}\text{C}$ signal. Values of $\delta^{13}\text{C}_{\text{calc}}$ were transformed to $\Delta^{13}\text{C}$ using the procedure described above for tree-ring $\delta^{13}\text{C}_{\text{cell}}$.

Climate data

Estimates of climate data, including monthly and annual average precipitation, temperature, and dew point, were obtained from the PRISM Climate Group at the OSU (<http://prism.oregonstate.edu>). Average monthly and annual RH values were calculated from temperature and dew point temperature values. Fog occurrence data were acquired from J. Johnstone, using the methods employed by Johnstone & Dawson (2010). The average fog frequencies of the Southwest Oregon Regional Airport in North Bend, Oregon, and of the Astoria Regional Airport in Warrenton, Oregon, were calculated and averaged to estimate the monthly and annual average fog frequency for the Oregon coast. Growing season averages included data from May through July, and summer averages included data from June through September.

Statistical analyses

Three separate repeated measures analysis of variance tests with an AR1 covariance structure were used to determine the difference in mean BAI, as well as mean tree-ring $\Delta^{13}\text{C}_{\text{cell}}$ and $\delta^{18}\text{O}_{\text{cell}}$, between treated and untreated Douglas-fir, and western hemlock, at the Beaver site for each year from 1989 to 2011. A linear model using generalized least squares with an AR1 covariance structure was used to compare the relationship between mean tree-ring $\Delta^{13}\text{C}$ and mean BAI for the treated Douglas-fir trees. Another linear model using generalized least squares with an AR1 covariance structure was used to describe and compare mean $\Delta^{13}\text{C}$ of twig wood, and foliage, from the Prairie Hill site with increasing tissue age.

To detect the impact of climate on disease severity, we analysed climate influences (mean monthly temperature, precipitation, RH and fog occurrence) on the two tree-ring stable isotope series of each species (mean tree-ring $\Delta^{13}\text{C}_{\text{cell}}$ and $\delta^{18}\text{O}_{\text{cell}}$ of untreated Douglas-fir and western hemlock) using Pearson's correlation coefficients (r). Correlations with

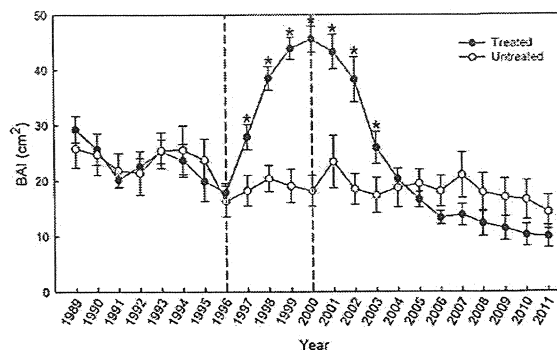


Figure 1. Mean basal area increment (BAI) of fungicide-treated and untreated Douglas-firs at the Beaver, Oregon site during the years of observation (1989–2011; $n = 6$ trees per treatment group). The treatment period is indicated by vertical dashed lines (1996–2000, inclusive). Bars represent one standard error. Asterisks indicate years of significant difference between treated and untreated Douglas-fir (results of repeated measures analysis of variance with an AR1 covariance structure).

a magnitude of at least 0.42 corresponds approximately with the 95% confidence level for a Gaussian white noise process ($n = 23$ years; 1989–2011), so we considered any correlation exceeding ± 0.42 as significant and an indicator of an important relationship to inform our interpretation of the data.

RESULTS

Annual growth

Because of the significant interaction between the effect of treatment and year on mean annual BAI ($F_{22,230} = 4.79$, $P = 0.0001$), the rest of the analyses discussed later will describe a difference in mean annual BAI between treatments for each year of observation separately. The annual growth trajectories of the treated and untreated Douglas-fir were essentially indistinguishable before imposing the fungicide treatment in 1996 (Fig. 1). There was a 1 year lag before BAI differed between treatments after treatment began. Mean annual BAI of the fungicide-treated Douglas-fir was significantly greater than that of untreated Douglas-fir beginning in the second year of treatment (1997) and increased each year until a peak average difference of about 27.4 cm² between treatment groups [95% confidence interval (CI): (19.4, 35.5)] in the final year of treatment (2000). Thereafter, growth of the treated trees declined over three years until 2004 when there was no longer a statistically significant difference between treated and untreated trees.

Branch carbon stable isotopes

At the Prairie Hill site where we collected branches from Douglas-fir trees with severe SNC, there was a significant interaction between tissue type (twig wood or foliage) and growth increment age on mean $\Delta^{13}\text{C}$ ($F_{1,41} = 12.84$, $P = 0.001$), indicating that the rates of change in $\Delta^{13}\text{C}$ per increase in

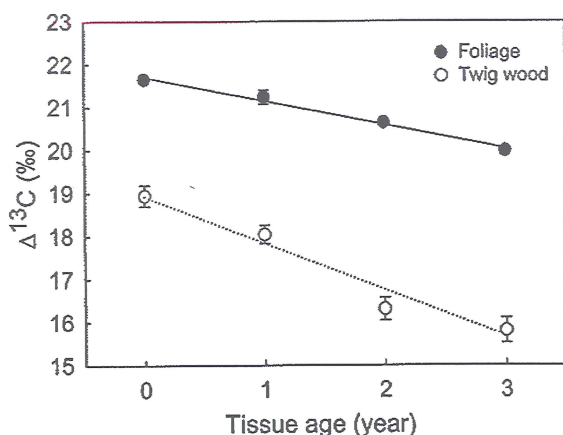


Figure 2. $\Delta^{13}\text{C}$ of foliage and twig wood samples from branch cohorts aged 0–3 years old from heavily infected Douglas-fir at the Prairie Hill site ($n = 6$ trees). Lines represent the regression results of a general least squares model with an AR1 covariance structure fit to foliage (solid) and twig wood (dotted; $P = 0.001$). Twig wood values were adjusted as described in *Materials and Methods*. Bars represent 1 SE.

growth increment age for twig wood and foliage were significantly different. The mean $\Delta^{13}\text{C}$ of twig wood decreased with tissue age by about 1.08‰ per cohort year [95% CI: (−1.27, −0.89)], and the mean $\Delta^{13}\text{C}$ of foliage decreased by about 0.56‰ per cohort year [95% CI: (−0.77, −0.34)] (Fig. 2).

Tree-ring carbon stable isotopes

Because the treatments were applied during 5 years of our 23 year time series, treatment effects (treated Douglas-fir, untreated Douglas-fir, western hemlock) on mean tree-ring $\Delta^{13}\text{C}_{\text{cell}}$ varied over time causing a significant interaction between time and treatment (1989–2011; $F_{44,325} = 1.54$, $P = 0.02$). The mean tree-ring $\Delta^{13}\text{C}_{\text{cell}}$ of treated Douglas-fir became steadily greater after treatment began in 1996, and was significantly greater than untreated Douglas-fir from 1999 to 2002 (Fig. 3). The mean difference in tree-ring $\Delta^{13}\text{C}_{\text{cell}}$ between treated and untreated Douglas-fir reached a maximum in 2001 [about 1.59‰; 95% CI: (0.66, 2.52)], and thereafter declined until there was no statistically significant difference between treated and untreated Douglas-fir in 2003.

Before the fungicide treatment was applied (1989 to 1995), mean tree-ring $\Delta^{13}\text{C}_{\text{cell}}$ differed significantly between treated Douglas-fir and western hemlock by about 1.81‰, but from the year that treatment began through 3 years following the end of treatment (1996–2003), there was no statistically significant difference between these two groups (Fig. 3). Following 2003 and to the end of the observation period in 2011, there was a significant difference in mean tree-ring $\Delta^{13}\text{C}_{\text{cell}}$ between treated Douglas-fir and western hemlock. Mean tree-ring $\Delta^{13}\text{C}_{\text{cell}}$ values between untreated Douglas-fir and western hemlock were significantly different in every year of the observation period except for two years (1989 and 2000). The

mean difference in $\Delta^{13}\text{C}_{\text{cell}}$ between untreated Douglas-fir and western hemlock was about 1.39‰. The mean difference in $\Delta^{13}\text{C}_{\text{cell}}$ between treated Douglas-fir and western hemlock was 0.06‰ for the years 1999–2002.

The relationship between mean BAI and mean tree-ring $\Delta^{13}\text{C}$ of treated Douglas-fir over the observation period (1989–2011) was such that BAI increased by 9.57 cm² for every 1‰ increase in $\Delta^{13}\text{C}_{\text{cell}}$ [95% CI: (5.36, 13.78), $P = 0.0002$; Fig. 4].

Tree-ring oxygen stable isotopes

There was not a significant interaction between treatment (treated Douglas-fir, untreated Douglas-fir, western hemlock) and year of observation on mean tree-ring $\delta^{18}\text{O}_{\text{cell}}$ between 1989 and 2011 ($F_{22,367} = 1.40$, $P = 0.06$; Fig. 5). After accounting for year of treatment in the model, there was no

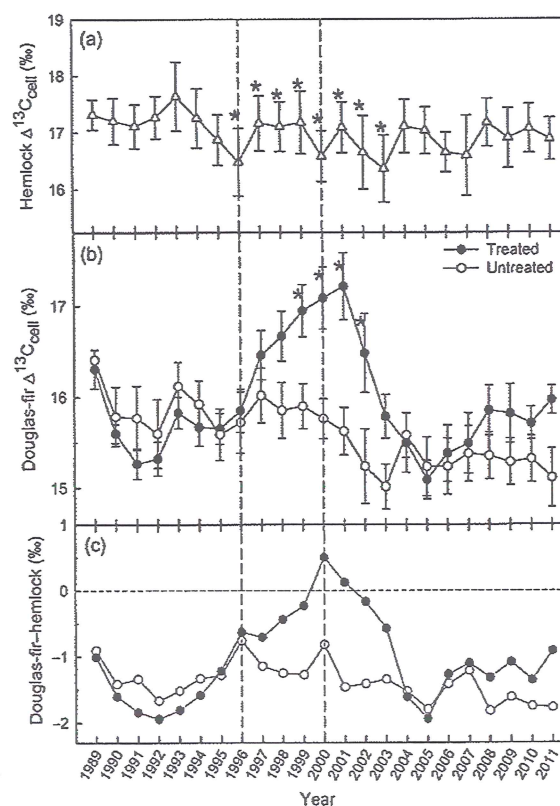


Figure 3. Mean $\Delta^{13}\text{C}_{\text{cell}}$ of western hemlock (a), fungicide-treated and untreated Douglas-fir (b) and the difference in $\Delta^{13}\text{C}_{\text{cell}}$ between treated and untreated Douglas-fir and hemlock (c) at the Beaver, Oregon site during the years of observation (1989–2011; $n = 6$ trees per treatment group). The treatment period is indicated by vertical dashed lines (1996–2000, inclusive). Bars represent 1 SE. Asterisks in (a) indicate years of no difference between western hemlock and treated Douglas-fir, and in (b) indicate years of significant difference between treated and untreated Douglas-fir (results of repeated measures analysis of variance with an AR1 covariance structure).

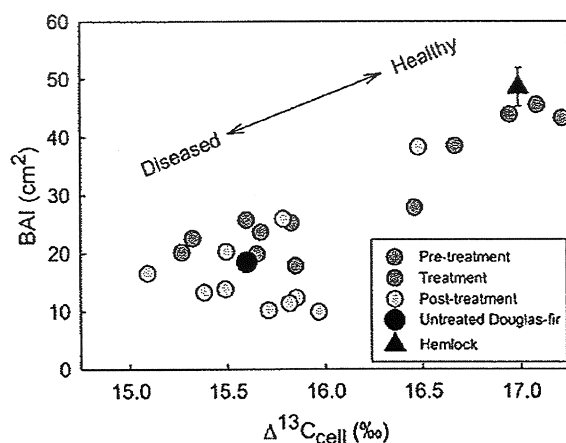


Figure 4. Scatterplot of mean tree-ring $\Delta^{13}\text{C}_{\text{cell}}$ and mean basal area increment (BAI) of fungicide-treated Douglas-fir post-, during and pre-treatment. Values for untreated Douglas-fir and western hemlock were averaged across all trees over the entire observation period (1989–2011) within each group. Bars represent 1 SE.

significant difference in mean tree-ring $\delta^{18}\text{O}_{\text{cell}}$ between treated and untreated Douglas-fir (Fig. 5). The mean tree-ring $\delta^{18}\text{O}_{\text{cell}}$ of western hemlock was about 0.61‰ greater than that of treated Douglas-fir [95% CI: (0.38, 0.84)], and about 0.60‰ greater than that of untreated Douglas-fir [95% CI: (0.37, 0.82); Fig. 5].

Climate Analyses

Because of the lack of difference in mean tree-ring $\delta^{18}\text{O}_{\text{cell}}$ between treatments during the treatment period, and thus the absence of evidence in support of using tree-ring $\delta^{18}\text{O}_{\text{cell}}$ as an indicator of variability in SNC disease severity, we only discuss tree-ring $\Delta^{13}\text{C}_{\text{cell}}$ in our climate analyses. The average previous December temperature was negatively correlated with $\Delta^{13}\text{C}_{\text{cell}}$ of western hemlock ($r = -0.47$; Fig. 6). Previous July precipitation displayed a positive correlation with $\Delta^{13}\text{C}_{\text{cell}}$ of untreated Douglas-fir ($r = 0.43$). There were also significant positive relationships between previous December fog occurrence and $\Delta^{13}\text{C}_{\text{cell}}$ of untreated Douglas-fir ($r = 0.51$). The strongest significant correlations were between RH in the previous June, July, August and September, growing season, summer and summer two years previous, and $\Delta^{13}\text{C}_{\text{cell}}$ of untreated Douglas-fir ($r = -0.51, -0.49, -0.54, -0.57, -0.51, -0.62, -0.60$, respectively), indicating that $\Delta^{13}\text{C}_{\text{cell}}$ decreased with increasing humidity of the previous years. There were no significant correlations between RH and $\Delta^{13}\text{C}_{\text{cell}}$ of western hemlock.

DISCUSSION

Annual BAI of treated Douglas-fir increased soon after the fungicide treatment began and was more than twice that of untreated trees by the fifth year of treatment (Fig. 1). Tree-ring $\Delta^{13}\text{C}_{\text{cell}}$ of treated Douglas-fir (low SNC) was greater

than that of untreated Douglas-fir (severe SNC) from the fourth year of treatment through two years after the treatment ended, reaching a peak difference of about 1.5‰ in 2001 (Fig. 3). The increase in $\Delta^{13}\text{C}_{\text{cell}}$ during the fungicide treatment and the increase in radial growth of treated trees were consistent with decreased diffusional limitation on needle gas exchange. We also found evidence of a cumulative effect of *P. gaeumannii* on $\Delta^{13}\text{C}$ of tissues in the canopy, where older twig wood and foliage had lower $\Delta^{13}\text{C}$ than newer tissues (Fig. 2). The relationship between BAI and tree-ring $\Delta^{13}\text{C}_{\text{cell}}$ (Fig. 4) demonstrated that treated Douglas-fir had values similar to western hemlock during the treatment period (Fig. 3), which suggests that the use of $\Delta^{13}\text{C}_{\text{cell}}$ in Douglas-fir tree-rings may be a practical technique for tracking SNC disease history, provided a suitable, co-occurring, non-infected reference species like western hemlock is also used to develop a reference $\Delta^{13}\text{C}_{\text{cell}}$ chronology. When we used the climate response difference between Hemlock and untreated Douglas-fir $\Delta^{13}\text{C}_{\text{cell}}$ as a proxy for disease symptom severity in Douglas-fir, disease severity was most strongly correlated with high RH in previous summer and growing season months (Fig. 6). In contrast to our tree-ring $\Delta^{13}\text{C}_{\text{cell}}$ results, there were no distinguishable differences in tree-ring $\delta^{18}\text{O}_{\text{cell}}$ between treated and untreated Douglas-fir during the years of the fungicide treatment and both are offset by $\sim 0.6\%$ from western hemlock (Fig. 5).

Annual growth and carbon stable isotopes

In agreement with previous research at the Beaver site, annual growth of treated Douglas-fir increased in response to the fungicide treatment (Johnson *et al.* 2003). We identified a 1 year lag in the annual growth response after the first

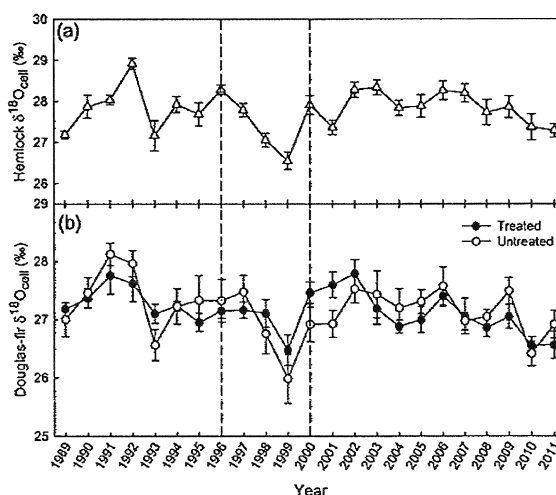


Figure 5. Mean tree-ring $\delta^{18}\text{O}_{\text{cell}}$ of western hemlock (a), and fungicide-treated and untreated Douglas-firs (b) at the Beaver, Oregon site during the years of observation (1989–2011; $n = 6$ trees per treatment group). The treatment period is indicated by vertical dashed lines (1996–2000, inclusive). Bars represent 1 SE.

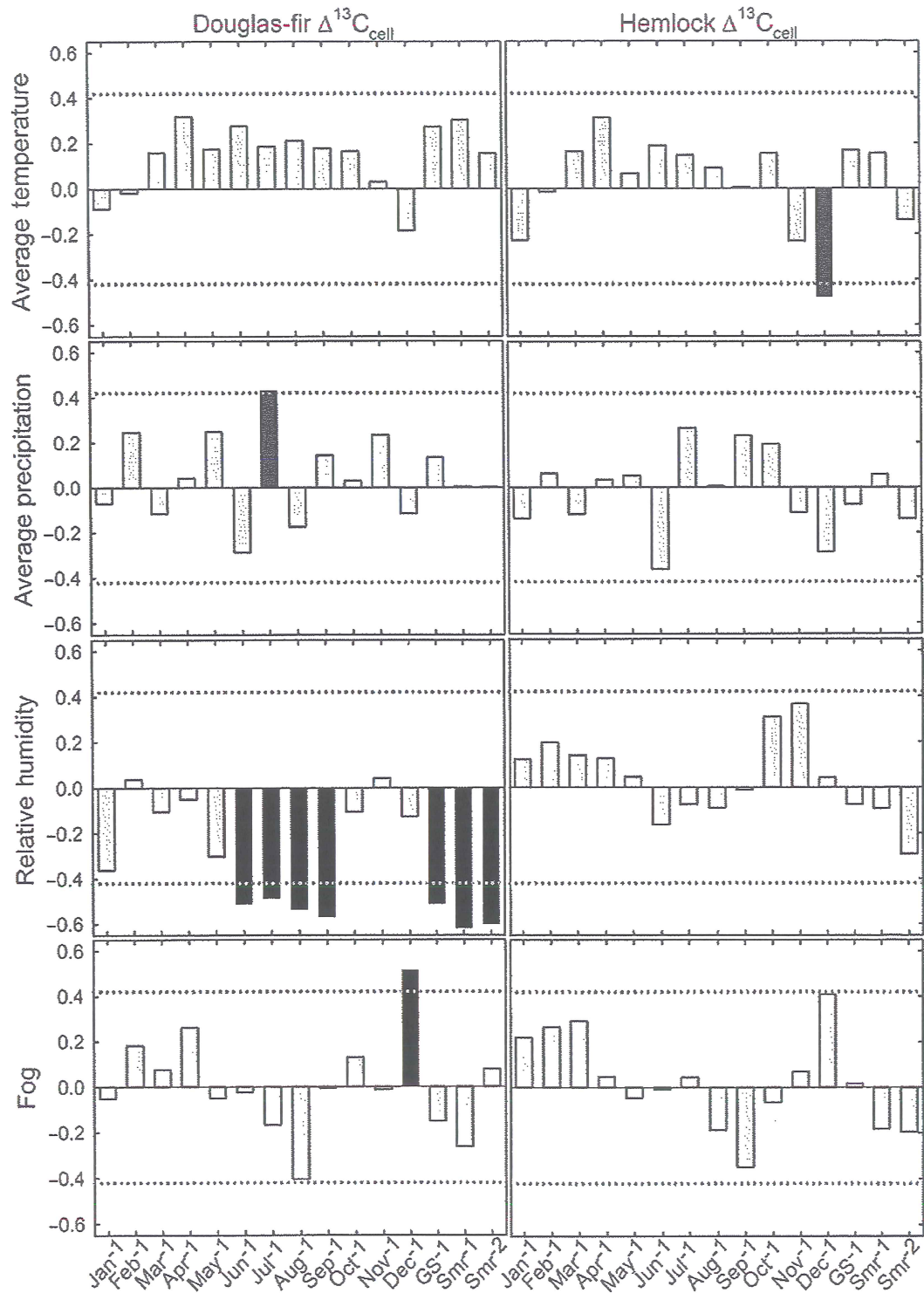


Figure 6. Pearson correlation coefficients (r) of Douglas-fir and western hemlock tree-ring $\Delta^{13}\text{C}_{\text{cell}}$ and various climate variables at different times of year: monthly values of the previous year (e.g. Jan-1), previous growing season average (May–July; GS-1), previous summer average (June–September; Smr-1), and summer two years previous average (Smr-2). Red, dotted lines represents significance at 95% confidence level (0.42/–0.42).

year of treatment, as well as a 3 year lag in the return to pre-treatment growth levels after the last year of treatment. These lags are likely due to the nature of the life cycle of *P. gaeumannii* and the progression of disease in Douglas-fir foliage (Stone *et al.* 2008). After initial infection of current-year foliage, it takes at least a year for *P. gaeumannii* to produce the pseudothecia that result in disease symptoms that include reduced carbon dioxide assimilation and foliage loss. Thus, it would take a year after the first application of fungicide for there to be a notable difference in foliage retention and annual growth between treated and untreated trees. Furthermore, because the fungus only infects new foliage, each subsequent year of treatment meant that the treated trees had one more cohort of healthy, productive foliage, which explains why annual growth steadily increased over the treatment period and why there was a 1 year lag before annual growth began to decline back to pre-treatment levels after the last year of treatment. Needle retention on the Oregon coast is anywhere between three and four needle cohorts for healthy Douglas-fir (Shaw *et al.* 2011), so the 3 year lag before annual growth of treated trees returned to pre-treatment levels after the final year of treatment represents the steady annual progression of additional diseased needle cohorts in the absence of the fungicide treatment.

The response of tree-ring $\Delta^{13}C_{\text{cell}}$ to fungicide treatment over time was similar to the pattern that we observed in annual growth. There was a difference in the number of years that BAI and tree-ring $\Delta^{13}C_{\text{cell}}$ between treated and untreated trees were significantly different, such that there was a 3 year lag after treatment began and a 2 year lag after treatment ended for tree-ring $\Delta^{13}C_{\text{cell}}$. It is possible that more healthy needle cohorts were required to produce a significant change in tree-ring $\Delta^{13}C_{\text{cell}}$ than were required to produce changes in annual growth, which could explain why the difference in $\Delta^{13}C_{\text{cell}}$ between Douglas-fir treatment groups required more time to manifest after treatment began and less time to diminish after treatment ended. Incorporation of non-structural carbohydrates produced in prior years into current-year wood may also have contributed to the lag in the appearance of the $\Delta^{13}C$ signal in treated trees. Nevertheless, the overall trajectory of the tree-ring $\Delta^{13}C_{\text{cell}}$ response to treatment was essentially consistent with that of annual growth.

We verified the $\Delta^{13}C_{\text{cell}}$ signal that was identified in tree-rings was also present in the crown at the source of carbohydrate synthesis. The $\Delta^{13}C$ of both foliage and twig wood decreased with increasing tissue age (Fig. 2), a trend opposite to that reported for branches on healthy Douglas-fir trees in which the $\Delta^{13}C$ of foliage typically decreases with decreasing age from the branch base to tip because of increasing hydraulic constraints on stomatal conductance (Panek & Waring 1995; Panek 1996; Warren & Adams 2000). Thus, the cumulative impact of intensification of SNC symptoms over time on leaf gas exchange dominated over normal axial trends in hydraulic limitation of stomatal conductance. Foliage and twig wood $\Delta^{13}C$ values were clearly different, consistent with previous research showing that non-photosynthetic tissues, such as those found in branch and stem wood, are typically

enriched in ^{13}C (lower $\Delta^{13}C$) by between 1 and 3‰ compared with leaves on the same branch or tree (Cernusak *et al.* 2009). Because the secondary growth of twigs is largely derived from carbohydrate exported from needles attached to them, the $\Delta^{13}C$ of both tissues should decrease over time at roughly the same rate. However, twig wood $\Delta^{13}C$ declined at about twice the rate of foliage across the same 4 year sequence. The bulk mass of foliage is cellulose that is laid down in the first year when SNC is still in the early stages of inoculation. Foliar cellulose does not turn over, so changes in foliar $\Delta^{13}C$ with increasing age must be associated with leaf constituents that are produced under increasing SNC-related constraints on stomatal conductance after the needle is developed (e.g. non-structural carbohydrate and other substances that undergo metabolic turnover). Furthermore, the exported carbohydrate from foliage and the secondary growth of the attached twig that it ultimately builds would show progressively lower $\Delta^{13}C$ with each cohort year. Thus, twig wood of diseased trees would be expected to have a greater rate of decrease in $\Delta^{13}C$ with age compared with foliage as the carbohydrate exported from older needles would have a lower $\Delta^{13}C$ signal than the bulk mass of the needle itself.

Mean tree-ring $\Delta^{13}C_{\text{cell}}$ of treated Douglas-fir and western hemlock were not significantly different from the year treatment began through three years following treatment, which roughly follows the trend in significant differences between the mean tree-ring $\Delta^{13}C_{\text{cell}}$ of treated and untreated Douglas-fir during and after the treatment period. When we examined the positive relationship between mean tree-ring $\Delta^{13}C_{\text{cell}}$ and BAI of treated Douglas-fir, $\Delta^{13}C_{\text{cell}}$ and BAI during the treatment period were similar to those of western hemlock (Fig. 4). These results suggest that there is clear potential in using tree-ring $\Delta^{13}C_{\text{cell}}$ and BAI chronologies as a means to track SNC disease history provided a suitable co-occurring reference species like western hemlock is available. Applying this method, years when disease was low or absent within a Douglas-fir tree-ring $\Delta^{13}C_{\text{cell}}$ chronology would not be significantly different from the same years in a tree-ring $\Delta^{13}C_{\text{cell}}$ chronology of nearby western hemlock, and the degree of divergence in tree-ring $\Delta^{13}C_{\text{cell}}$ of the two species in a given year should be related to SNC disease severity for that year (Fig. 3). It would be beneficial to use BAI in conjunction with tree-ring $\Delta^{13}C_{\text{cell}}$ since both variables appear to track disease severity and could potentially identify non-SNC influences on tree growth and physiology when one variable changes while the other remains constant.

Oxygen-stable isotopes

Contrary to our hypothesis, tree-ring $\delta^{18}O_{\text{cell}}$ did not differ between treated and untreated Douglas-fir in response to treatment. Previous research has demonstrated that high RH (~60–70%) can mask the effects of reduced stomatal conductance on $\delta^{18}O_L$, and thus the signal imparted to tree-ring cellulose, because there is so little evaporative enrichment of leaf water and the isotopic exchange with atmospheric vapour is much higher under high RH (Roden & Ehleringer 1999; Barbour & Farquhar 2000; Brooks & Mitchell 2011). To

explore the effects of variation in g_s and L (effective path length) on $\Delta^{18}O_{\text{cell}}$ under the mean growing season RH at our site (78%, May–July), we used Eqns 3–6. A reference value for g_s of $0.14 \text{ mol m}^{-2} \text{ s}^{-1}$, typical for healthy, non-water-limited Douglas-fir was applied (Bond & Kavanagh 1999). Stomatal conductance was then varied between 0 and $0.14 \text{ mol m}^{-2} \text{ s}^{-1}$ with L set between 33 and 2400 mm, representative of the range of L reported for several conifer species (Wang *et al.* 1998; Song *et al.* 2013). Source water $\delta^{18}O$ was set to the 5 year average for precipitation in Newport, Oregon (-7.05‰ ; J.R. Brooks, unpublished data). Leaf and air temperature were set for average summer time conditions determined from the PRISM climate data as 15°C . Boundary layer conductance was set to $2 \text{ mol m}^{-2} \text{ s}^{-1}$. We assumed that $\Delta^{18}O_v$ was in equilibrium with source water, and therefore was equal to $-\epsilon^*$ (Barbour 2007). Finally, in Eqn 6 we set p_{ex} to 0.4, and p_x to 1 (Brooks & Mitchell 2011).

The results of this modelling exercise suggested that even under near complete loss of stomatal conductance in diseased trees, the difference in $\Delta^{18}O_{\text{cell}}$ between diseased and healthy trees with a typical L (33 mm) would only be about 0.46‰. Moreover, Manter *et al.* (2000) found that Douglas-fir seedlings with SNC that were sampled in May and June had g_s values of around $0.02\text{--}0.05 \text{ mol m}^{-2} \text{ s}^{-1}$, while control seedlings had values around $0.08\text{--}0.12 \text{ mol m}^{-2} \text{ s}^{-1}$. Although we sampled mature Douglas-fir and not seedlings, it is possible that the magnitude of difference in g_s between treated and untreated trees was not as great as in this modelling exercise, thus yielding an even smaller difference in $\delta^{18}O_{\text{cell}}$ between treatments. Furthermore, the model demonstrates that as L increases the difference in $\Delta^{18}O_{\text{cell}}$ from the control value should increase. Although L may be slightly modified by the presence of fungal hyphae in the needle, the lack of difference in our observed tree-ring $\delta^{18}O_{\text{cell}}$ between treated and untreated Douglas-fir suggests that any difference in L between treatments was minimal.

In summary, the blockage of stomata by pseudothecia and/or hyphae within the leaf mesophyll may indeed affect $\delta^{18}O_{\text{cell}}$ when RH is low, but because RH was rather high at our site, we did not observe any influence of the fungus on $\delta^{18}O_{\text{cell}}$. Because SNC is more prevalent in coastal regions where RH is normally high, our results imply that stable isotopes of oxygen in tree-rings would not serve as a reliable indicator of variability in SNC disease severity.

Disease severity and climate

The most prevalent relationships we observed were a negative correlation between previous summer and growing season averages of RH (previous June, July, August, September, growing season, and summer; and two summers previous) and Douglas-fir tree-ring $\Delta^{13}C_{\text{cell}}$. The strongest of these correlations were with RH of the previous summer ($r = -0.62$) and two summers previous ($r = -0.60$). A typical physiological response of healthy trees to low RH (and thus, high vapour pressure deficit) is to close stomata, causing $\Delta^{13}C_{\text{cell}}$ to decrease during the same year. In the case of Douglas-fir with SNC, we observed the opposite; low RH was

related to increased $\Delta^{13}C_{\text{cell}}$. Previous research has shown that spring and summer leaf wetness in the year of initial infection is positively correlated with disease severity (Hansen *et al.* 2000; Rosso & Hansen 2003), which is likely due to increased spore germination on leaf surfaces. The negative relationship between previous summer RH and Douglas-fir tree-ring $\Delta^{13}C_{\text{cell}}$ likely reflects higher leaf wetness through increased nightly dew frequency and amounts and lower evaporation rates of this dew when the spores are germinating. In turn, greater leaf wetness, particularly from dew that would presumably wash off fewer spores than rainfall, would promote greater spore adhesion to needles and more successful germination on foliage. Subsequent increases in pseudothecia-blocked stomata would result in lower $\Delta^{13}C_{\text{cell}}$ in the following year or two when that foliage would be contributing substantial photosynthate. Accordingly, this response would not be observed in a species that is not susceptible to SNC, like western hemlock, which did not demonstrate any relationship between RH and tree-ring $\Delta^{13}C_{\text{cell}}$.

Variation in SNC disease severity has been correlated primarily with warm winter temperatures and wet spring and summer conditions, with some studies also reporting a negative relationship between high summer temperatures and disease severity (Rosso & Hansen 2003; Zhao *et al.* 2011). Although our results agreed with the positive relationship between July RH and disease severity reported by Latta *et al.* (2009), we did not find any evidence for a relationship between any of the measures of temperature, precipitation, or fog occurrence and disease severity as measured with tree-ring $\Delta^{13}C_{\text{cell}}$. The relationship between climate and SNC severity in past studies has been explored using different measures of disease, such as needle retention (Rosso & Hansen 2003; Coop & Stone 2007; Latta *et al.* 2009; Zhao *et al.* 2011), pseudothecia abundance (Manter *et al.* 2005), and growth (i.e. tree-ring width; Black *et al.* 2010). Although these measures are reasonable assessments of disease signs and symptoms, some have potential confounding factors that could complicate efforts to determine their respective relationships to climate. For example, needle retention can be influenced by stand density, tree age, temperature, water availability, nutritional status, herbivory and functional net photosynthesis (reviewed by Ewers & Schmid 1981; Chabot & Hicks 1982; Pouttu & Dobberty 2000; Xiao 2003), and tree-ring widths are sensitive to a variety of environmental signals (McCarroll & Loader 2004) independent of disease severity. Although there are certainly factors other than SNC that could potentially affect tree-ring $\Delta^{13}C_{\text{cell}}$, differences in carbon stable isotope signatures of diseased Douglas-fir and a healthy reference species may eliminate noise contributed by other factors that affect needle retention and tree-ring width and provide another perspective of the relationship between climate and SNC disease severity.

The results of the present study demonstrated that SNC causes reduced $\Delta^{13}C_{\text{cell}}$ values. However, without information regarding disease status, these results could be interpreted very differently with traditional stable isotope theory, particularly when attempting climate reconstruction with tree-ring stable isotopes. Thus, future related studies should

consider the potential impacts of disease when interpreting stable isotope signals in tree-rings.

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Tree-ring analysis of the fungal disease Swiss needle cast in western Oregon coastal forests

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Abstract: Swiss needle cast (SNC), an important fungal disease of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), has increased in severity throughout its natural and introduced range over the last half century. The role of climate change and forest management practices in the increase is unclear. We analyzed tree-ring chronologies from six late-successional Douglas-fir stands in the western Oregon Coast Range using time-series intervention analysis (TSIA) to address how climate relates to the impact of SNC on tree growth. Tree-ring chronologies of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), a species not susceptible to the fungus *Phaeocryptopus gaeumannii* (Rhode) Petrak, were used as a climate proxy in the TSIA. We found that growth reductions associated with SNC dated back to the 1590s, the earliest record in our dendritic data. Growth reductions were synchronous across the six sites, indicating that the disease severity was largely influenced by climatic conditions. SNC impact peaked in 1984–1986 at all six study sites, followed by unprecedented disease impacts of 100% in 1996 and 2004 at one site, while decreasing to previous levels at the other five sites. Our SNC index of impact significantly correlated with winter and summer temperatures and summer precipitation. Winter conditions were more strongly associated with disease impact at wetter, cooler sites, whereas summer conditions were more important at less humid, warmer sites. With climate change, SNC impacts are likely to increase in coastal areas where June–July precipitation is much higher than the *P. gaeumannii*-limiting threshold of ~110 mm, and decrease where summer precipitation is at or below the threshold. Warmer winters will increase disease severity at higher elevation, north along the coast from northern Oregon to British Columbia, and at inland sites where current winter temperatures limit fungal growth.

Résumé : La sévérité de la rouille suisse (RS), une maladie cryptogamique du douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco), a augmenté partout dans son aire de répartition naturelle et dans les régions où elle a été introduite au cours du dernier demi-siècle. Le rôle joué par les changements climatiques et les pratiques d'aménagement dans cette augmentation est nébuleux. Nous avons analysé des séries dendrochronologiques dans six peuplements de douglas en fin de succession dans la chaîne côtière de l'Oregon à l'aide de l'analyse d'intervention en séries chronologiques (AISC) dans le but de déterminer de quelle façon le climat influence l'impact de la RS sur la croissance des arbres. Les séries dendrochronologiques de la pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.), une espèce non sensible au champignon *Phaeocryptopus gaeumannii* (Rhode) Petrak, ont été utilisées dans l'AISC comme données indirectes liées au climat. Nous avons trouvé que les réductions de croissance associées à la RS remontaient aux années 1590, la période correspondant aux plus anciennes de nos données dendrométriques. Les réductions de croissance étaient synchrones dans les six stations, indiquant que la sévérité de la maladie était largement influencée par les conditions climatiques. L'impact de la RS a culminé en 1984 à 1986 dans les six stations faisant partie de l'étude, suivi d'impacts sans précédent de la maladie atteignant 100% en 1996 et 2004 dans une station, alors qu'ils diminuaient pour revenir à des niveaux antérieurs dans les cinq autres stations. Notre indice d'impact de la RS était significativement corrélé avec les températures hivernales et estivales et avec la précipitation estivale. Les conditions hivernales étaient plus étroitement associées à l'impact de la maladie dans les stations plus humides et plus fraîches tandis que les conditions estivales étaient plus importantes dans les stations moins humides et plus chaudes. Avec les changements climatiques, les impacts de la RS risquent d'augmenter dans les zones côtières où la précipitation durant les mois de juin et juillet est beaucoup plus élevée que le seuil de ~110 mm, le minimum requis pour le développement de *P. gaeumannii*, et de diminuer dans les endroits où la précipitation estivale est égale ou inférieure à ce seuil. Les hivers plus chauds vont augmenter la sévérité de la maladie à plus haute altitude, au nord le long de la côte allant du nord de l'Oregon à la Colombie-Britannique et dans les endroits situés à l'intérieur des terres où les températures hivernales actuelles limitent la croissance des champignons. [Traduit par la Rédaction]

Introduction

Swiss needle cast (SNC) is an economically important disease of both coastal (*Pseudotsuga menziesii* (Mirb.) Franco) and interior (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) forms of Douglas-fir, as well as bigcone Douglas-fir (*Pseudotsuga macrocarpa* (Vasey) Mayr) in New Zealand (Boyce 1940; Gadgil 2005). SNC disease is caused by the fungus *Phaeocryptopus gaeumannii* (Rhode) Petrak and is widespread throughout the natural and introduced range

of the host, but it is most severe in forests and plantations on the western slopes of the Oregon Coast range within the coastal fog belt (Hansen et al. 2000). Epidemic outbreaks of SNC have been reported in coastal Oregon, Washington, and British Columbia since the mid-1980s, (Hansen et al. 2000; Omdal and Ramsey-Kroll 2010) and have caused widespread symptoms of chlorosis and premature needle loss (Shaw et al. 2011). Thought to be innocuous in western North American forests prior to 1950 (Boyce 1940; Peace 1962; Hood 1982), increased severity since that time is

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uncertain. Evidence suggests that SNC is affected by climate (Manter et al. 2005; Stone et al. 2008b), alone or in combination with forestry practices of the 20th century. Possible causes for the current SNC epidemic include climate change, the introduction of Christmas tree plantations in the mid-1970s (Hadfield and Douglas 1982; Michaels and Chastagner 1984), or the planting of susceptible plantation stock brought from outside the epidemic region (Hood 1982). It is predicted that impending climatic changes in the Pacific Northwest (PNW) will lead to warmer and wetter winters and warmer and drier summers (Mote and Salathé 2010), leading to increased intensity, frequency, and range of SNC disease impacts over the 21st century (Zhao et al. 2011; Watt et al. 2011).

The effects of SNC on its host include chlorosis, decreased needle retention, and reduction in tree height and diameter (Hansen et al. 2000; Maguire et al. 2002; Mainwaring et al. 2005). The disease reduces assimilation of carbon by stomatal occlusion (Manter et al. 2000). Three major phases of the infection cycle of *P. gaeumannii* are relevant to the understanding of the climate–growth relationship (Manter et al. 2005): (1) the fungus reproduces only sexually and pseudothecia (i.e., fruiting bodies) proliferate in winter from December to April; (2) sporulation and initial infection of needles occur from May to July; and (3) needle colonization by internal hyphal growth occurs year round following initial infection. Sporulation occurs in synchrony with bud break and shoot elongation, and only the newly emerged needles are infected (Hood and Kershaw 1975; Stone et al. 2008b). Wet needles in late spring and early summer are necessary for sporulation and hyphal growth into the stomata (Capitano 1999; Stone et al. 2008b).

Disease severity is associated with favorable weather conditions for pathogen development, which includes mild winter temperatures and spring leaf wetness in the North American PNW (Manter et al. 2005; Stone et al. 2008a) and New Zealand (Watt et al. 2011). These climate influences have been verified for *P. gaeumannii* infection based on epidemiological studies of needle retention and the frequency of stomata occluded by pseudothecia (Hansen et al. 2000; Manter et al. 2005; Stone et al. 2008b; Maguire et al. 2011; Zhao et al. 2011). Summer temperature may also affect the severity of the disease because the optimum temperatures for ascospore germination and germ tube growth occur at 18 and 22 °C, respectively (Capitano 1999). At a severely diseased site in northern coastal Oregon, severity based on periodic annual ring-width increment was correlated with current-year temperatures from March through August, but was not correlated with early winter temperature and spring leaf wetness (Black et al. 2010). Similarly in New Zealand, growth loss was most strongly correlated with spring temperature from October to December, whereas spring precipitation was not a limiting factor for infection (Kimberley et al. 2011). The conflicting relationships with climate from epidemiological and dendrochronological studies suggest that the primary environmental factors controlling the degree of pathogen colonization in the PNW (Rosso and Hansen 2003; Manter et al. 2005; Coop and Stone 2007) and New Zealand (Stone et al. 2007; Watt et al. 2010) vary with elevation, aspect, proximity to coast, and site conditions.

The impact of SNC on Douglas-fir growth is further influenced by climatic factors associated with the infection and development of the fungus over multiple years. A delay of several years between climate conditions favorable to reproduction and growth of the fungus and visible symptoms of growth reduction in the trees is expected because the pathogen infects only the newly emerged needles each year (Stone et al. 2008b). Further, needle abscission typically occurs after 50% or more of the stomata are occluded by fruiting bodies (Hansen et al. 2000). Pseudothecia can be commonly found on 4- to 7-year-old needles in the Cascade Mountains of Oregon and Washington, and on 1- to 2-year-old needles in some areas of the Coast Range where more favorable climatic conditions allow the fungus to develop faster (Stone et al. 2008b). Consequently, the proportion of stomata occluded depends upon

current and previous years' climatic conditions associated with inoculum abundance, ascospore dispersal and germination, and pathogen colonization in each needle age class. Douglas-fir trees on the coast typically retain up to 4 years of needles, but may only have current and 1-year-old foliage due to premature needle abscission in severely affected plantations (Hansen et al. 2000; Maguire et al. 2002; Zhao et al. 2011).

Needle retention and fungal fruiting body abundance have routinely been used as indices of disease severity (Hood 1982; Michaels and Chastagner 1984; Hansen et al. 2000; Manter et al. 2005). However, foliar assessment studies of needle retention and stomata occlusion on several needle classes of Douglas-fir are limited in their ability to examine lagged cause–effect relationships beyond the life of the needle. While annual radial growth is the preferred endpoint for understanding the economic and ecological impact of the disease (Maguire et al. 2002; Shaw et al. 2011), such studies are few (Black et al. 2010). Annual tree-ring width data have the ability to examine the effect of current and past climate conditions on SNC but have not been used previously to examine the lagged relationship to climate beyond the previous year (Black et al. 2010). Relating SNC severity with annual growth increment is problematic because weather affects both the growth of the fungus and trees in similar ways — conditions favorable to fungal growth are (usually) also favorable to tree growth.

This paper reconstructs the history of SNC impact at naturally regenerated Douglas-fir stands in coastal Oregon to address the following questions: Did SNC impact growth prior to 1950? How will climate change affect disease severity in the future? We examined the historical impacts of SNC in coastal Oregon by using tree-ring chronologies and weather records for six sites differing in elevation, aspect, and distance from the coast to determine the key climate factors associated with disease severity. Specific objectives of this research were to (1) reconstruct the history of SNC impact on forest growth in coastal Oregon, (2) determine whether the impacts of the current SNC epidemic in Oregon are unprecedented or were similar in the past, (3) examine the climate and site factors associated with SNC that account for reduced radial growth, and (4) examine the delay of several years in the relationship to climate. We used time-series intervention analysis (TSIA) to reconstruct the SNC history as a series of pulse and (or) step changes in growth rates (Druckenbrod 2005). Although there is considerable spatial heterogeneity in disease severity within the western Oregon Coast Range (Hansen et al. 2000), we hypothesized that if climatic variation is an important driver of the fungal disease, the impacts of SNC should be synchronous across the landscape.

Methods

Study sites

The three Douglas-fir chronologies presented in Black et al. (2010) were reanalyzed and three new Douglas-fir chronologies at coastal forest stands in Oregon were constructed for this study. The six study sites (Table 1) are representative of the major forest type consisting of Douglas-fir and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), which account for 52%–100% of the total basal area at these stands. At Tillamook Lower, a severely diseased site, Sitka spruce (*Picea sitchensis* (Bong.) Carrière) is the dominant tree species, accounting for 47% of the total basal area (Black et al. 2010). The sites represent even-aged, naturally regenerated stands of Douglas-fir ranging in age from 90 to 420 years old, although the Horse Creek Trail Lower site in the Siuslaw National Forest (SNF) has two cohorts of Douglas-fir trees (Table 1). All chosen stands had no history of logging or thinning. Site attributes (Table 1) and climate conditions varied between sites (Table 2).

The three reanalyzed sites, Tillamook Lower and Upper (TL and TU) and Euchre Mountain (EM), were located adjacent to younger

Table 1. Site attributes and tree-core-sampling information.

Name	Latitude, longitude	Elevation (m)	Aspect (°)	Slope (%)	Distance to coast/bay (km)	Species	Pith date	No. of trees	Density (stems·ha ⁻¹)
Tillamook Lower	N45°28', W123°41'	260	210 (SSW)	15	22/5	DF	1927	23	242
						WH	1932	21	
Tillamook Upper	N45°28', W123°40'	520	230 (SW)	20	23/6	DF	1931	21	500
						WH	1925	19	
Cascade Head	N45°02', W123°54'	150	80 (E)	19	8	DF	1870	17	241
						WH	1900	6	
Euchre Mountain	N44°51', W123°54'	410	330 (NNW)	15	11	DF	1882	21	300
						WH	1887	19	
Horse Creek Trail Lower	N44°29', W123°54'	280	320 (NW)	29	14	DF	1586/1860	9/8	~300
						WH	1884	13	
Horse Creek Trail Upper	N44°28.5', W123°55'	470	310 (NW)	26	13	DF	1859	16	~300
						WH	1881	5	
Soapgrass Mountain	N44°21', W122°24'	1190	56 (NE)	6	144	DF	1547	29	256

stands that were heavily or moderately affected by SNC; see Black et al. (2010) for a complete description of these sites. Three additional study sites, Horse Creek Trail Lower and Upper (HCTL and HCTU) in the SNF and Cascade Head (CH) in the Cascade Head Experimental Forest, were located at different elevations and latitudes than the reanalyzed sites to extend the regional inferences of climatic factors influencing the impact of SNC on Douglas-fir. TL and TU are located within a 3 km distance along an elevational gradient on southwest-facing slopes of the Coast Range near Tillamook, Oregon (Fig. 1). CH and EM are located within a 22 km distance but at different elevations near Lincoln City, Oregon, and 50–70 km south of the Tillamook sites. The CH site is on an east-facing slope west of the Oregon Coast Range 8.5 km from the Pacific Ocean; see Lee et al. (2007) and Beedlow et al. (2013) for a complete description of the site. The HCTL and HCTU sites are located within a 2 km distance at different elevations on northwest-facing slopes of the Coast Range in the Drift Creek Wilderness Area (SNF) about 62 km south of CH and 13 km from the coast. HCTL was chosen for having a greater density of old-growth Douglas-fir trees than neighboring sites in the SNF, and provided a longer term record of annual stem-growth increments for reconstructing the history of SNC disturbance. There are two cohorts of Douglas-fir trees at this site ranging from 180-year-old trees in the southern half to 420-year-old trees in the northern half. HCTU has a similar density of dominant and codominant 160-year-old Douglas-fir trees, but it is 190 m higher in elevation than HCTL.

We included a reference site, Soapgrass Mountain (SM), at a 1190 m elevation on the west slopes of the Oregon Cascade Range where Douglas-fir trees were limited primarily by summer temperature and less by water as at CH (Beedlow et al. 2013). A west coast marine climate predominates from the Oregon coast to the west slopes of the Cascade Range because of the west-to-east movement of air masses coming from the Pacific Ocean. Consequently, weather changes in a similar manner across the region. Temperature is more moderate at CH than at SM, with mean daily temperatures of 5.4 and 20.0 °C in January and July/August, respectively, at CH versus 1.7 and 23.8 °C, respectively, at SM (Beedlow et al. 2013). Mean annual precipitation is about 2000 mm at the two sites. The chronology of tree ring-width for SM was used as a reference or climate proxy in the reconstruction of the history of SNC disturbances on the coast. Infection was not evident in the 460-year-old Douglas-fir trees at SM likely because winter temperatures were below the threshold of 4 °C for formation of pseudotsuga (Stone et al. 2008a; Kimberley et al. 2011).

Field sampling

Different field-sampling methods and plot sizes were used to sample tree cores from Douglas-fir and western hemlock trees at the six sites depending upon the origin, source, and focus of the

study. Species, diameter, and canopy class were recorded for all trees >10 cm diameter at breast height (DBH; at 1.3 m) at the three study sites chosen by Black et al. (2010) and for trees >20 cm DBH at CH and SM. At TL, TU, and EM, trees were systematically sampled within circular plots of 0.02 ha in area along transects through the forest interior at approximately 20 m intervals (Black et al. 2010). There were 19–23 tree cores of each tree species collected in 2007 and 2008 at these three sites (Table 1).

At CH and SM, trees of each species within a rectangular plot of 0.39 ha in area were selected by stem diameter in proportion to their relative abundance and canopy class (following Avery (1975)). The study trees at CH and SM were selected between the years 1998 and 2000 based on no visible signs of damage or disease (Beedlow et al. 2013). Fruiting bodies of *P. gaumannii* were found on the undersides of needles of Douglas-fir at CH in the mid-2000s, confirming the presence of SNC. One or more tree cores from 19 Douglas-fir and 6 western hemlock at CH and from 29 Douglas-fir at SM were collected between 1999 and 2011. All cores were taken at breast height (1.4 m) using a 5-mm diameter increment borer (Haglöf, Långsele, Sweden).

At HCTL, we attempted to sample all dominant and codominant Douglas-fir (DBH > 180 cm) and western hemlock (DBH > 80 cm) trees within a rectangular plot of approximately 1.1 ha in area in 2011 and 2012, but the trees had varying degrees of heart rot, which made coring difficult. Additional trees were selected by stem diameter in proportion to their abundance and canopy class for a total of 17 Douglas-fir and 13 western hemlock trees. Nine of the 17 Douglas-fir trees were >400 years old. At HCTU, dominant and codominant trees of each species were systematically selected along a 170 m section of the main trail at approximately 15 m intervals and within 25 m to either side of the trail for a total of 16 Douglas-fir and 5 western hemlock trees in 2012. At HCTL and HCTU, one core from each selected tree was collected at breast height using a 5-mm diameter increment borer. At the time of sampling, the presence of SNC appeared minimal as retention of needle age classes up to 6 years was high at both sites.

Dendrochronological methods

Total annual ring widths of tree cores from TL, TU, and EM were measured manually to the nearest 0.002 mm by using a Unislide "TA" system (Velmex, Inc., Bloomfield, New York) (Black et al. 2010). Tree cores from CH, HCTL, and HCTU were processed and optically scanned using an Epson Expression 10000XL color flat-bed scanner attached to a Windows-based personal computer. The digital images were analyzed to measure annual total ring width as well as earlywood and latewood increments to the nearest 0.01 mm using the WinDENDRO 2008g tree-ring measuring system (Regent Instruments Inc., Quebec, Canada). Following measurement, the tree-ring data were cross-dated by tree species and site using the University of Arizona Laboratory of Tree-Ring

Table 2. Canonical correlations (r_c) between the Swiss needle cast index of impact and the current and previous seasonal temperatures, dew-point deficit, and precipitation for six study sites on the western slopes of the Oregon Coast Range.

Site	No. years	Winter temperature			Summer precipitation			Summer dew point deficit			Summer temperature		
		Months, mean \pm SD ($^{\circ}$ C)	Lags (years)	r_c	Months, mean \pm SD (mm)	Lags (years)	r_c	Months, mean \pm SD ($^{\circ}$ C)	Lags (years)	r_c	Months, mean \pm SD ($^{\circ}$ C)	Lags (years)	r_c
Tillamook Lower	28	Jan-Mar, 9.7 \pm 1.4	0-24	0.86*	June-July, 144 \pm 72	1-21	0.69*	June-July, 3.7 \pm 0.5	3-21	-0.81*	July-Sep, 20.8 \pm 0.9	3-24	0.84*
Tillamook Upper	21	Jan-Mar, 8.3 \pm 1.4	0-19	0.50*	June-July, 144 \pm 72	1-25	0.76*	June-July, 3.7 \pm 0.5	4-17	-0.67*	July, 19.5 \pm 1.2	3-22, 12-27	-0.83*, 0.55*
Cascade Head	34	Dec-Feb, 7.6 \pm 1.1	3-25	0.70*	June-July, 121 \pm 62	0-16	0.75*	June-July, 4.2 \pm 0.6	0-22	-0.70*	July-Aug, 19.7 \pm 1.2	0-22	-0.95*
Euchre Mountain	25	Dec-Feb, 7.6 \pm 1.0	3-26	0.53*	June-July, 100 \pm 51	1-10	0.56*	June-July, 4.9 \pm 0.5	1-22	-0.69*	July-Aug, 20.7 \pm 0.9	2-22, 0-26	-0.82*, 0.70*
Horse Creek Trail Lower	34	Dec-Feb, 9.7 \pm 1.2	18-25	0.65*	June-July, 81 \pm 44	1-22	0.78*	June-July, 6.2 \pm 0.8	2-23	-0.57*	July-Aug, 24.1 \pm 1.2	5-23, 18-19	-0.63*, 0.32
Horse Creek Trail Upper	28	Dec-Feb, 8.7 \pm 1.2	3-25	0.56*	June-July, 81 \pm 44	1-12	0.68*	June-July, 6.2 \pm 0.8	15-23	-0.48*	July-Aug, 23.1 \pm 1.2	15-21, 0-28	-0.40*, 0.60*

*Denotes a significant correlation at the 0.05 level of significance.

Research program COFECHA Version 6.06P (Holmes 1983) to confirm that all growth increments were assigned the correct calendar year. Once cross-dated, data were log-transformed, detrended using a cubic spline with a 50% frequency response of 32 years, and averaged across trees to produce a master tree-ring chronology for each species and site. Because the SD and the effects of climate and disease on ring width were proportional to the mean, a log transformation was used to stabilize the variance of ring widths and estimate the relative impacts of SNC over time (Cook 1987; Cook et al. 1990).

Individual trees were detrended using a cubic spline smoother to remove the lower frequency climate signal and preserve and isolate the higher frequency signals associated with disease and climate. At TL, the most severely diseased site, detrending the tree-ring data for Douglas-fir using a cubic spline smoother resulted in an over-adjustment of recent data because many diseased trees were missing multiple rings and displayed significant declines in growth since the mid-1980s as noted by Black et al. (2010). To resolve this issue, we used spline regression to detrend each individual that displayed a linear trend on a log scale since 1983. For these individuals, a cubic spline with a 50% frequency response of 32 years was used to detrend the tree-ring data prior to 1983, whereas data after 1983 were detrended using a fixed mean (a horizontal line) so that the detrended time series was continuous at the join point. For 14 of the 23 Douglas-fir trees at TL, the multidecadal trend in the tree-ring data after 1983 was likely due to historically high levels of SNC severity and, consequently, was not removed. Twelve of these 14 severely diseased trees had 5-14 years of little to no growth after 1983, and the other two trees were missing one or two rings. Once the data were detrended, the median across trees was used to produce a master tree-ring chronology for Douglas-fir. We used the median because it was more robust to extreme values than the mean. On a log scale, the mean was highly influenced by missing rings, which were assigned a value of -3 (i.e., a constant of 0.001 mm was added to the tree-ring data prior to log transformation).

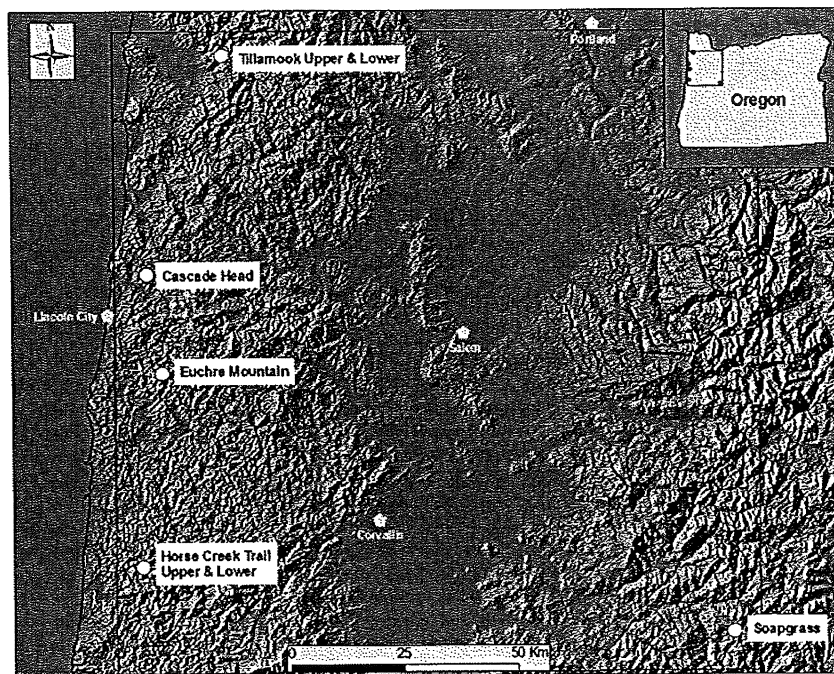
Statistical procedures

TSIA (Box and Tiao 1975; Tsay 1988) was used to reconstruct the history of SNC impact on Douglas-fir relative to nondiseased reference trees. Episodes of SNC suppression and release were identified as a series of pulse changes in annual growth rates of Douglas-fir in the presence of climate factors, trend, and autocorrelation. While detrending removed the long-term variability in the tree-ring data associated with climate and nonclimatic growth, the detrended master chronology of Douglas-fir was further adjusted for the shorter term variability owing to climate by including the detrended master chronology of the reference site as a climate proxy in the structural time-series model. We also included summer temperature as a covariate in the time-series regression model (Beedlow et al. 2013). The following equation describes the mean function for the log of periodic annual ring-width increment of Douglas-fir (Y) as a function of the chronology of log annual ring-width increment of the reference trees (W), summer temperature (X), and trend (T), excluding terms for the intervention pulse events:

$$(1) \quad \mu_t = E(Y_t) = \beta_0 + \beta_1 W_t + \beta_2 X_t + \beta_3 X_t^2 + \beta_4 T_t$$

where X is the mean daily maximum temperature ($^{\circ}$ C) for June and July, $T = \text{Year} - 1980$ for $\text{Year} > 1980$ and 0 otherwise for $t = 1, 2, \dots, N$ years. The model parameters ($\beta_0, \beta_1, \beta_2, \beta_3$, and β_4) are unknown and estimated from the data for each site. Because trend was present in the master chronology of Douglas-fir only at TL, β_4 was set equal to 0 at the other five study sites. To account for autocorrelation (Fritts 1976), the Douglas-fir master chronology of annual ring width was modeled as a third-order autoregressive

Fig. 1. Locations of six study sites in the Oregon Coast Range. Tillamook Upper and Lower are within 3 km of each other, and Horse Creek Trail Upper and Lower are within 2 km of each other. One reference Douglas-fir site, Soapgrass Mountain, is located at about the 1200 m elevation on the western slope of the Cascade Range of Oregon.



process, denoted AR(3), based on the temporal patterns of association identified in the autocorrelation and partial autocorrelation functions (Box and Jenkins 1970) and the Akaike Information Criterion. The AR(3) model for the Douglas-fir master chronology with nonstationary mean has the form

$$(2) \quad (Y_t - \mu_t) = \rho_1(Y_{t-1} - \mu_{t-1}) + \rho_2(Y_{t-2} - \mu_{t-2}) + \rho_3(Y_{t-3} - \mu_{t-3}) + e_t$$

where the autoregressive model parameters (ρ_1 , ρ_2 , and ρ_3) are unknown and satisfy the constraints of stationarity and e_t is a sequence of normally and independently distributed random variables with a mean of 0 and a variance of σ^2 .

The master chronology of local western hemlock was used as the reference in the TSIA for three sites (TL, TU, and EM) and the master chronology of Douglas-fir at SM was used as the reference for the other three sites (CH, HCTL, and HCTU). The western hemlock chronology was not used as a climate proxy at three sites because it did not extend as far in the past as the Douglas-fir chronology. The interspecies correlation was low at CH ($r = 0.21$) and HCTL ($r = 0.26$) relative to the correlations of 0.48 at TL and 0.41 at EM. The correlation between the Douglas-fir chronologies for HCTL and SM was 0.30.

Additive pulse interventions were identified sequentially as significant divergences between the master chronology of Douglas-fir and its mean given in eq. (1). The identification of pulse intervention years is analogous to the detection of outliers from the AR(3) model given in eq. (2). The TSIA model approach assumes the mean function is the sum of a climatic signal given in eq. (1) and an additional component for disease disturbance, following Cook (1987) but implemented using a traditional time-series approach (Box and Tiao 1975; Tsay 1988). When $\beta_1 = 1$, our approach is comparable to commonly used dendroecological approaches that use the difference in chronologies between the dis-

turbed and reference species to test for divergences in growth rates (e.g., Black et al. (2010)). Given that reductions in stem growth owing to SNC range from 25% to 55% in the PNW (Maguire et al. 2002, 2011), pulse interventions were initially defined as a 25% or greater reduction in the master chronology of Douglas-fir adjusted for climatic factors. Years prior to and following a >25% reduction in growth were also identified as interventions when reductions in growth exceeded 10%. Additional pulse events were identified as multiple consecutive years of reduced growth with a peak reduction <25% at less severely diseased sites that were synchronous with growth reductions >25% at the more severely diseased sites. Several reconstructions of forest disturbance history showed an increase in growth rate following a disturbance event (Henry and Swan 1974; Oliver and Stephens 1977). Consequently, candidate years with enhanced growth >10% were identified as pulse interventions associated with release.

Candidate pulse interventions were retained in the TSIA model when the divergences in chronologies between the host and reference chronologies were statistically significant based on the likelihood ratio test at $\alpha = 0.05$. We also retained several negative pulse events that were statistically significant at the 0.10 level and represented a cycle of growth suppression. Maximum likelihood estimation (MLE) was used to fit the structural time-series intervention model with an AR(3) autocorrelation structure and compute the SNC index of impact for each site. The model parameters associated with the years having a significant negative divergence were back-transformed by exponentiation to calculate the SNC index of impact as a percentage reduction in growth. For example, a pulse parameter of -1 corresponds to a $(1 - 10^{-1})100\%$ or 90% growth loss. MLE of the model parameters was performed using the PROC NLIN procedure in SAS/STAT software, Version 9.2 of the SAS System, as described in Fuller (1976).

We cross-correlated the index of SNC disturbance with the seasonal averages of temperature and precipitation for each site.

Monthly temperature, dew-point temperature, and precipitation data were obtained from the PRISM Climate Group at Oregon State University, available at their Web site (<http://prism.oregonstate.edu>). Single grid-point PRISM data (2.5 arcmin) of 1895–2011 mean monthly climate variables were obtained for the specific sample site locations based on latitude and longitude and adjusted for bias to the elevation of interest. Bias in the PRISM temperature data was adjusted for elevation using either local instrument records at CH (Beedlow et al. 2013) or a wet adiabatic lapse rate of $5.5\text{ }^{\circ}\text{C}\cdot\text{km}^{-1}$ when local temperature data were not available. The climate data were summarized as seasonal averages of temperature and precipitation that corresponded to the three major phases of the infection cycle, following Manter et al. (2005): (1) winter (January–March) when proliferation of pseudothecia occurs; (2) spring (May–July) when sporulation and initial infection occur; and (3) summer (August–October) when needle colonization by internal hyphal growth is rapid. Winter temperature was summarized as the average daily maximum temperature for one or more months between December and March. Spring–summer precipitation was summarized as total precipitation for one or more months between May and July. Dew-point deficit (DPD) was calculated as the difference between the mean and dew-point temperature for one or more months between May and July. Precipitation and DPD during the summer months are related to potential leaf wetness, which is difficult to derive from modeled climate data (Manter et al. 2005). Summer temperature was summarized as the average daily maximum temperature for one or more months between June and October. Cross-correlation analysis was used to identify the seasonal averages of current and past temperature and precipitation that were significantly associated with the SNC impact of Douglas-fir.

Because the pathogen infects only the newly emerged needles and coastal Douglas-fir trees retain about four needle classes, the cross-correlations up to 4 years in the past relate the SNC impact with favorable disease conditions associated with the infection and fungal development of the present foliage classes. Lagged relationships prior to 4 years relate the SNC index of impact to favorable disease conditions associated with past generations of the fungus and the infection of past foliage classes. Following cross-correlation analysis, canonical correlation analysis was used to calculate integrated averages of current and previous seasonal temperature and precipitation that optimize the correlation with SNC impact.

Results

Comparisons of growth suppression and release patterns between Douglas-fir and the reference trees indicated that Douglas-fir trees at the coastal sites experienced more frequent cyclical reductions in growth. Douglas-fir had more years of below-average growth (47%–56%) than western hemlock (43%–50%). Reductions in annual ring-width increments of Douglas-fir were more pronounced at lower elevation sites, in particular TL, than at higher elevations (Fig. 2). Significant growth reductions of 25% or greater in Douglas-fir occurred about 29% of the time at TL, 12% at HCTL, and 5% at the other four sites. Significant growth reductions of 10% or greater in Douglas-fir, unadjusted for climate, were most frequent at TL (45%) and least frequent at EM (14%). At TL, more than half of the Douglas-fir trees were missing rings in the years 1984, 1996–1997, and 2004–2005. The growth rates of Douglas-fir for TL declined linearly beginning about 1983 during a period of unprecedented disease impact (Fig. 2A). No other chronologies of Douglas-fir displayed a linear decline in growth rates during the most recent decades. At TU, about 10%–15% of Douglas-fir trees were missing rings in the years 1996–1998 and 2002–2003. Few rings were missing at the other four sites.

Swiss needle cast index

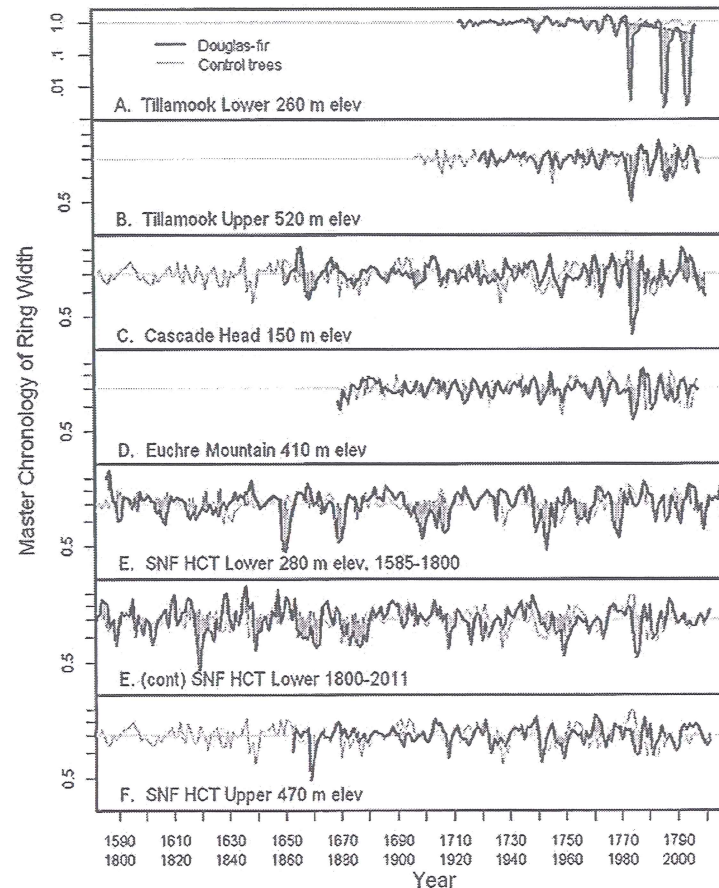
The time-series intervention models accounted for at least 86% of the total variation in the Douglas-fir chronologies for the six study sites. Similar tree-ring-based reconstructions of the SNC impact for each site were obtained by using either the local western hemlock chronology or the Douglas-fir chronology for SM as the reference species. The Douglas-fir chronology for SM was used as a baseline for coastal study sites having host trees that were much older than the western hemlock chronology. The coefficient for the climate proxy (β_1 in eq. (1)) ranged from 0.05 at TL to 0.44 at TU and tended to be greater at the less severely diseased sites. The climate proxy coefficient is indicative of the interspecies difference in climate effects on annual tree-ring width increments relative to disease effects. That is, β_1 should be near one when disease impacts are minimal and both the host and control species' chronologies are climate proxies, and less than one when disease impacts on the host are significant. At TL, the detrended master chronology of Douglas-fir was influenced more strongly by SNC rather than by climate, most notably since 1984 during a period of unprecedented disease impact. The intervention analysis identified cycles of growth release or positive pulse events often immediately following a growth suppression cycle (Fig. 2). The frequency of significant growth reductions owing to SNC ranged from 21% to 27% at the higher elevation sites and from 27% to 33% at the lower elevation sites. Significant growth releases occurred half as often as growth suppressions and were more frequent at lower elevations (15% of the time) than higher elevations (3%–11%). Significant negative divergences between the host and reference species were first observed in 1590 at HCTL, which was about the earliest of the tree-ring record (Fig. 2E).

Average SNC impact ranged from 2%–16% across all years and from 18%–50% across the diseased years. Elevation changes rapidly over short distances in the western Oregon Coast Range as did SNC impact. Growth reductions owing to SNC were considerably greater at TL (average 50% in diseased years) than at TU (21%), which were both located on south-facing slopes within a 3 km distance but at 260 and 520 m elevation, respectively (Figs. 3A and 3B). Further south and more inland, SNC impacts on 120- and 150-year-old Douglas-fir for the years 1984–2011 were greater and more frequent at a lower elevation, east-facing site (CH, average 31% impact in diseased years) than a higher elevation, NNW-facing site (EM, 21% impact) (Figs. 3C and 3D). Similarly, average SNC impacts of 30% and 18% for the disease years 1984–2011 were observed at HCTL (280 m elevation) and HCTU (470 m elevation), respectively, which were located within a 2 km distance on north-facing slopes (Figs. 3E and 3F). The SNC impact for TU, CH, EM, HCTL, and HCTU peaked in 1984–1986, followed by a decline to past levels of disease severity during a period when winter temperature was increasing and spring precipitation was decreasing. The peak in the SNC index of impact for 1984–1986 is a unique signature of the disease at all six study sites.

Cyclical patterns of Swiss needle cast

Spectral analysis of the climate-adjusted SNC index for the common period 1880–2011 identified cyclical patterns of growth suppression represented by sinusoids having periods of about 6 and 12 years at all study sites and longer periods >25 years at CH, HCTL, and HCTU. Unlike a white noise time series whose spectrum is constant at all frequencies, the spectrum of the SNC index of impact for all six study sites displayed primary and secondary peaks in the frequency range between 0.02 and 0.28 cycles·year⁻¹ (Fig. 4). In comparison, the spectra of the master chronologies of the references were more similar to the white noise spectrum and were relatively flat in the frequency range between 0.08 and 0.5 cycles·year⁻¹. The spectrum of the reference Douglas-fir chronology for SM identified a low-frequency signal in the climate proxy represented by a sinusoid having a period of about 20 years. The periodicities of 6, 12, and >25 years found in the SNC indices

Fig. 2. Tree-ring based reconstruction of Swiss needle cast impact on Douglas-fir for six study sites on the west side of the Coast Range in Oregon. Significant negative and positive divergences between the host and control species are indicated by red and blue vertical lines, respectively. The master chronology of the control species (green line) is local western hemlock for Tillamook Lower and Upper and Euchre Mountain and Douglas-fir at Soapgrass Mountain for Cascade Head and Horse Creek Trail (HCT) Lower and Upper. The tree-ring chronology of Douglas-fir for Tillamook Lower was reported on a different scale because reductions in growth were much greater than at the other five sites. SNF, Siuslaw National Forest.



of impact were absent in the reference trees. The primary peaks of the spectrum in the very low and mid-frequency ranges are another identifying signature of the episodic nature of SNC effects on Douglas-fir. The magnitude of the spectrum of the SNC index at the primary frequencies characterized the disease severity and was greatest for TL and least for HCTU (Fig. 4).

Co-spectrum analysis indicated that the SNC indices for all sites were coherent and in phase at the key frequencies (not shown). The synchronization of SNC impact on Douglas-fir across the landscape indicated that there were climate factors, which favored disease conditions at these sites in coastal Oregon (Fig. 3).

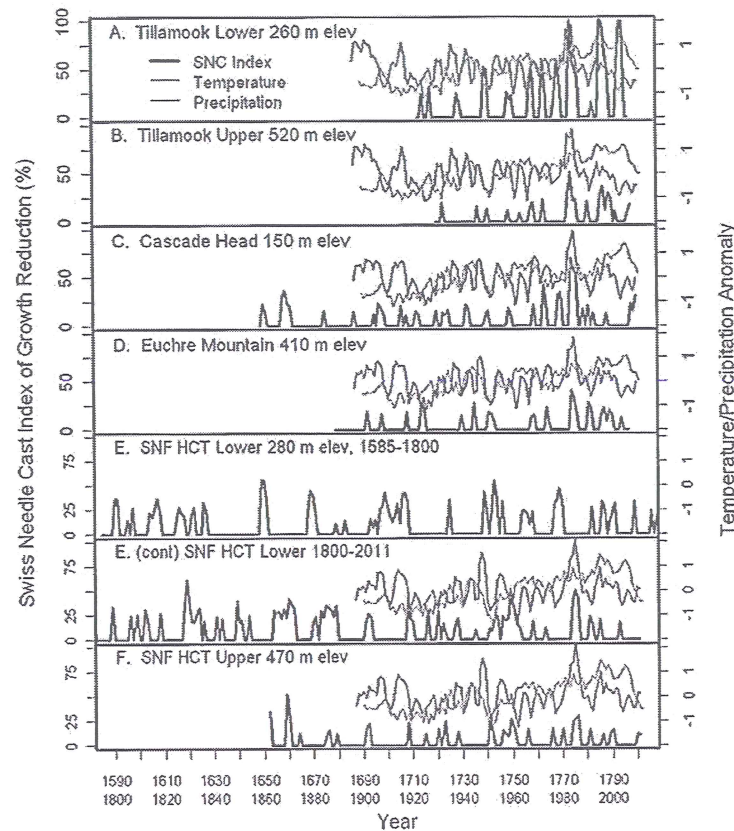
Seasonal climate factors

The climatic factors associated with the SNC index were examined for each site, focusing on the three lower elevation sites where the magnitude and frequency of disease impacts and the statistical power of the test for correlation were greater. The impact of SNC on stem growth lagged the seasonal averages of winter and summer temperatures and summer precipitation and DPD by 1–25 years to varying degrees at all study sites (Fig. 5). A statistically significant cross-correlation represented a past year when growth loss was affected primarily by climatic factors rather than

biotic factors (e.g., abundance of fruiting bodies). A nonsignificant cross-correlation indicated either no linear association between impact and past climate or a potential interaction between biotic and abiotic factors.

The SNC index of impact was generally positively correlated with current and past winter temperatures and summer precipitation and negatively correlated with summer DPD. The SNC index of impact was either positively or negatively correlated with summer temperature depending upon whether summer temperature was above or below the temperature optima of 18 and 22 °C. At TL, the most severely affected site, the SNC index of impact was positively correlated with current and past January–March and July–September temperatures lagged 1–24 years (Figs. 5A and 5C) and past June–July precipitation (not shown), and negatively correlated with past June–July DPD (Fig. 5B). The SNC index of impact for CH and HCTU was positively correlated with past winter temperatures and current and past summer precipitation lagged 1–25 years but, unlike TL, was negatively correlated with most past summer temperatures lagged 1–25 years (Fig. 5). A moderate climate with mild winters and cool, wet summers was also associated with SNC impact at TU, EM, and HCTU (not shown). Summer

Fig. 3. The percentage reduction in annual-tree-ring width increment of Douglas-fir adjusted for temperature and a climate proxy at six study sites in coastal Oregon. The index of Swiss needle cast corresponded to negative pulse intervention events, which indicated low growth relative to a control species. Temperature and precipitation were normalized to a mean of 0 and a variance of 1. The red line is the 5-year running average of mean daily maximum temperature for January and February. The blue line is the 3-year running average of total precipitation for June and July. SNF, Siuslaw National Forest; HCT, Horse Creek Trail.



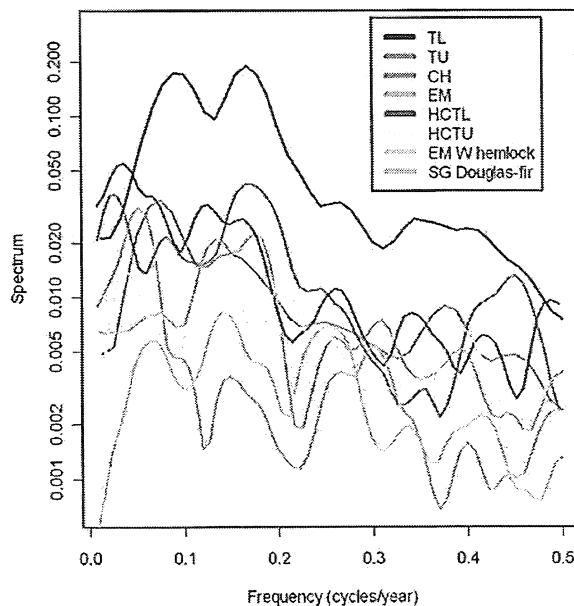
precipitation was the primary limiting factor of disease impacts at HCIL (Figs. 5G–5I) and HCTU (not shown) because the warmer, less humid summers at these sites were likely less favorable conditions for infection and colonization. The interactive effects of SNC and climate factors over several decades were most evident in the cyclical pattern in the cross-correlations between the SNC index and summer precipitation at HCIL (Fig. 5H).

Canonical correlation analysis was used to generate a climate index for each seasonal climate factor and study site based on a weighting scheme of current and previous years to optimize the correlation with the SNC index of impact (Table 2). The canonical factors for summer and winter temperatures and summer precipitation and DPD included only those years having a cross-correlation >0.2 (or <-0.2 for summer temperature and DPD). Much stronger associations between the SNC index and seasonal temperature, precipitation, and DPD were obtained when the climatic variables were averaged across current and past years than for individual years. Overall, canonical correlations with the SNC index were strong and ranged from 0.50 to 0.86 for winter temperature, from 0.68 to 0.78 for summer precipitation, from -0.81 to -0.48 for summer DPD, and from -0.95 to 0.84 for summer temperature. Disease impact related to winter temperature, summer precipitation, and DPD consistently across all study sites. The lagged relationship between SNC impact and summer temperature was complex and varied by the range of local summer tem-

perature in relation to two temperature optima — 18°C for ascospore germination and 22°C for germ-tube growth.

The disease impacts were more highly correlated with winter and summer temperatures at the cooler, wetter sites and with summer precipitation and DPD at the warmer, drier sites. At TL, where DPD was relatively low, the SNC index of impact was associated primarily with winter and summer temperatures and secondarily with summer precipitation and DPD (Fig. 6). The positive relationship between SNC impact and summer temperature at TL indicated that growth loss increased with increasing temperature below 22°C (Fig. 6C). In contrast to TL, the SNC indices for the other five study sites were associated primarily with summer conditions, in particular, summer temperature at TU, CH, and EM and summer precipitation at HCIL and HCTU (Table 2). The SNC index for CH was relatively insensitive to winter temperatures below 7°C and was influenced primarily by summer temperature and precipitation associated with spore germination and colonization (Fig. 7). The negative relationship between SNC severity and summer temperature at CH (Fig. 7C), EM (Fig. 8B), and TU (not shown) indicated that growth loss decreased with increasing summer temperatures above 18°C . The cyclical pattern of positive and negative cross-correlations between the SNC index and past summer temperature at EM is also consistent with a temperature optimum of 22°C for disease severity (Fig. 8). The SNC index for HCIL and HCTU was associated primarily with summer

Fig. 4. Comparison of the cyclical and multidecadal effects of Swiss needle cast (SNC) disease and climate on Douglas-fir and control species based on the spectral analysis of the SNC index of growth reduction for the years 1880–2011 at six Oregon Coast sites. Annual growth suppressions owing to the disease displayed periodicities of about 6 and 12 years at all sites as indicated by the primary and secondary peaks of the SNC spectrum in the frequency range between 0.08 and 0.3 cycles-year⁻¹. The periodicities of 6 and 12 years were unique to the disease because the spectrum of the climate proxies lacked significant peaks in the frequency range between 0.08 and 0.3 cycles-year⁻¹. The disease impacts were greatest at Tillamook Lower and least at Horse Creek Trail Upper as indicated by the amplitude of the primary peaks of the spectrum.



precipitation and less with winter and summer temperatures and summer DPD (Table 2 and Fig. 9). The SNC index for HCTL and HCTU was negatively correlated with summer temperature likely because both temperature optima of 18 and 22 °C were exceeded (Fig. 9C).

Discussion

Using the time-series intervention and spectral analyses of tree-ring data, we identified several patterns of growth suppression and release associated with SNC. Intervention analysis was adapted from econometrics to dendroecology for the decomposition of a tree-ring time series into discrete signals for trend, climate, disturbance, and random error (Cook 1987). Intervention analysis has been shown to be a reliable method for determining whether a nonrandom change has occurred in a manipulated or disturbed ecosystem relative to an undisturbed reference system (McLaughlin et al. 1987; Carpenter et al. 1989; Druckenbrod 2005). Unlike the econometric applications of TSIA to study a system where the intervention events are known, anecdotal and epidemiological arguments must be combined with statistical evidence to infer whether the changes in annual-ring-width data can be attributed to the disturbance of interest.

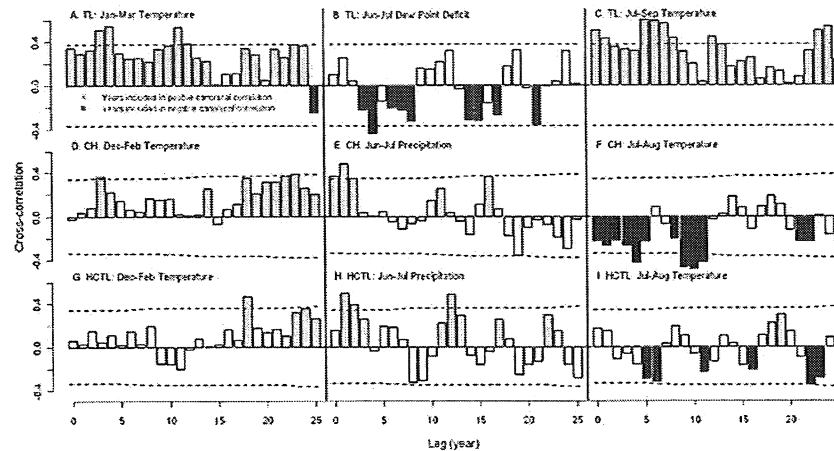
Defoliation owing to SNC was the most likely cause of the significant divergences in chronologies of annual-ring-width increment between coastal Douglas-fir and the reference trees. Evidence from past foliar assessment surveys (Boyce 1940), historical records, epidemiological studies (Maguire et al. 2002), and a

previous study of tree-ring data (Black et al. 2010) also identified SNC disease as the most likely cause of annual growth suppressions of coastal Douglas-fir in Oregon. Regular cyclical patterns of growth suppression having periodicities of 6, 12, and ~25 years were synchronous across study sites and associated with current and past winter and summer conditions, indicative of SNC. The fundamental periodicity of ~25 years and its harmonic periodicities of 6 and 12 years were associated with climate and its effect on the intensification of *P. gaeumannii* abundance over one or more decades. Because *P. gaeumannii* almost exclusively infects the newly emerged needles (Stone et al. 2008b), the 6-year periodicity in the SNC index was likely the result of a delayed growth response to climate conditions favorable to the infection and ensuing pathogen colonization in each needle age class. Close correlations have been found between growth impacts and needle retention, pseudothecia density, and pathogen biomass (Hansen et al. 2000; Manter et al. 2001; Maguire et al. 2002; Winton et al. 2002, 2003), suggesting that the SNC index of impact correlates with these indices. Pathogen abundance likely peaked during a year with severe impact, followed by a decrease to a minimum because of the loss of foliage, and increased in intensity to a peak after one or more decades in synchrony with the SNC index. At the most severely impacted site, the intensification of pathogen abundance was much faster because of the more favorable conditions for pathogen development as evidenced by abundant pseudothecia on 1- and 2-year-old needles in this area (Stone et al. 2008b). This likely explains the lack of a 25-year periodicity in the SNC index at this site.

Our dendrochronological study showed that growth suppression owing to the SNC is not a recent phenomenon on the coast. Mature stands are equally susceptible to the disease (Black et al. 2010). According to our TSIA of dendritic data for 420-year-old Douglas-fir at HCTL, SNC dates back to at least 1590, the earliest of our tree-ring records. Our dendritic reconstruction of SNC disturbance history predates the creation of Douglas-fir plantations in coastal areas and the use of susceptible seed stock from outside the most severely diseased regions in the 20th century. Our history of SNC impact also predates the first observations of *P. gaeumannii* in Douglas-fir plantations in Switzerland and Germany in 1925 and across the range of native Douglas-fir in western North America in the 1930s (Boyce 1940). Disease impacts prior to 1950 were not negligible in the PNW, as suggested by Boyce (1940) and Black et al. (2010), but were significant and displayed cyclical patterns of growth suppression and release. Our data suggest that cyclical patterns of SNC impact represent the interaction between pathogen abundance and short-term climate variability over one or more decades.

While forest management practices of the 20th century increased the abundance of its host Douglas-fir in coastal areas, SNC had a long history, and past epidemic levels were as great or greater as current levels at all but one study site. Disease impacts at TL increased after 1984 because climatic conditions in this Sitka spruce – western hemlock plant association zone (Franklin and Dyrness 1973) were highly favorable conditions for *P. gaeumannii* (Black et al. 2010). Our findings that climate rather than increased host abundance affected SNC symptoms are consistent with model predictions of disease distribution (Rosso and Hansen 2003). Reforestation of the Tillamook burns and introduction of Douglas-fir plantations in the 20th century do not account for the widespread occurrence and long history of the disease in the PNW and elsewhere (Shaw et al. 2011). The average growth reduction owing to SNC for the six study sites ranged from 18% to 50% in the years 1590–2011, which was consistent with the range of growth losses found in Oregon (Maguire et al. 2002; Shaw et al. 2011) and New Zealand (Kimberley et al. 2011). The tree-ring records at all six study sites indicated that SNC intensity peaked in 1984–1986 because of a prior decade of warmer winters and milder, wetter summers, which favored spore dispersal, germination, and needle

Fig. 5. Cross-correlations between the Swiss needle cast index of impact and current and past seasonal temperature, dew-point deficit, and precipitation at (A–C) Tillamook Lower (TL), (D–F) Cascade Head (CH), and (G–I) Horse Creek Trail Lower (HCTL). Growth loss was enhanced by favorable disease conditions in years where significant cross-correlations were found and was likely limited by biotic and abiotic factors in the other years. Correlations above or below the horizontal broken lines are significantly different from zero at $\alpha = 0.05$. Canonical correlation analysis was used to calculate a weighted running average of each seasonal climate factor averaged across the current and past years having either a positive (grey bar) or negative (black bar) cross-correlation >0.2 in absolute value.



colonization. The peak impact of SNC for the six study sites ranged from 31% to 100% in the years 1984–1986, about double the historic average impact at each site. Tree-ring data for HCTL suggested that the SNC impacts in 1984–1986 were unprecedented in the past 170 years, but were greater at various times in the past, notably in 1649–1650, 1743, and 1829. At TL, where disease impact was greatest, there was a significant decline in growth rates of 90-year-old Douglas-fir from 1984 to 2007. The growth reductions at this site over the past three decades may have been site-specific because of a combination of unfavorable climatic and site conditions, which increased the severity of SNC (Black et al. 2010). At the other five study sites, disease severity did not increase from 1984 to 2011, but rather declined to at or below historic levels following the peak in 1984–1986, and was less intense after 1996.

Many pathogens causing needle diseases are sensitive to precipitation, humidity, and temperature, and their rates of reproduction and infection increase when conditions are moist or closer to their temperature optimum (Harvell et al. 2002). Tree-ring records indicate that outbreaks of another fungal disease, *Dothistroma* needle blight caused by the fungus *Dothistroma septosporium* (Dorog.) Morelet, occurred periodically since 1831 in northwestern British Columbia (Welsh et al. 2009) and, in comparison with our findings, were in synchrony with the SNC epidemic in Oregon. Similar to the SNC epidemic in severely diseased areas in Oregon, the *Dothistroma* outbreaks occurred prior to the creation of managed lodgepole pine plantations (*Pinus contorta* var. *latifolia* Dougl. ex Loud.) and have increased in severity in both managed and natural stands since the late 1990s (Woods 2003). The spike in summer precipitation that appeared to cause the 1984–1986 SNC outbreak in Oregon also appeared to cause the 1984–1986 outbreak of *Dothistroma* needle blight in British Columbia (Woods et al. 2005). An increase in the frequency of warm summer rain events since the 1970s was more favorable for pathogen infection and development, indicating that the recent SNC and *Dothistroma* epidemics in the Pacific Northwest were caused primarily by directional changes in climate rather than forest management practices (Woods et al. 2005; Welsh et al. 2009).

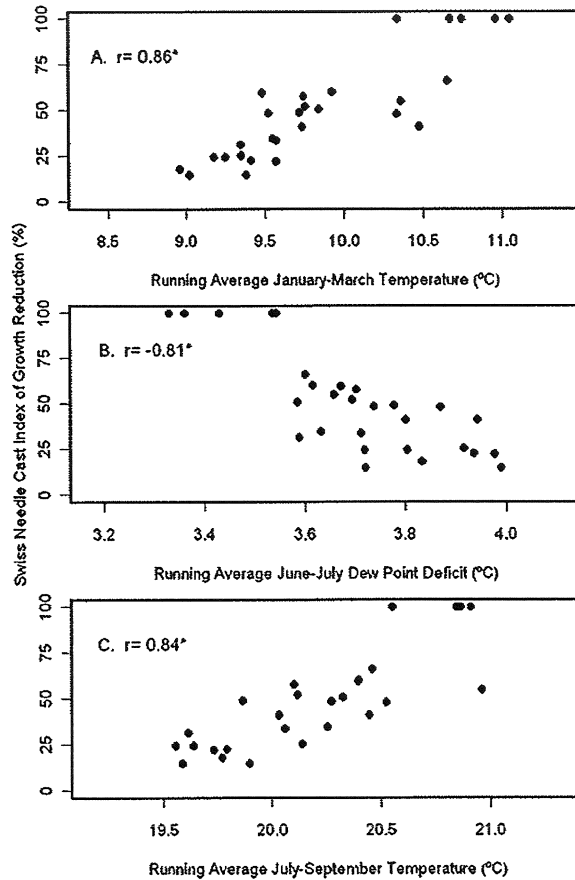
Our dendrochronological study corroborates the findings of greenhouse and field studies that associate SNC severity with winter temperature and spring–summer needle surface wetness (Manter et al. 2005; Stone et al. 2008a) when summer temperature

is relatively low (Rosso and Hansen 2003). Our findings are generally consistent with earlier studies but indicate a more complex site-specific climate–growth relationship between SNC impact and current and previous winter and summer temperatures and summer precipitation having lags of up to 25 years. Unlike previous climate–disease models that associate disease severity and needle retention with current and past winter and summer conditions having lags of up to 4 years (Zhao et al. 2011), our findings indicate a delayed growth response to past climate conditions associated with the intensification of *P. gaeumannii* abundance over several decades. Inferences of these lagged climate–growth relationships are possible with the long time series of tree-ring data but not with laboratory or field studies conducted over a limited number of years.

The impacts caused by SNC varied spatially by elevation, proximity to the coast, and aspect at small to broad spatial scales. In general, SNC impacts were greater and more frequent at lower elevations, nearer the coast, and on south-facing aspects with exposure to coastal fog and summer drizzle (Manter et al. 2003, 2005; Rosso and Hansen 2003). The relative effects of winter and summer temperatures and summer precipitation on annual radial stem growth vary spatially by site condition and interact with biotic factors over time and space (Shaw et al. 2011). Because the temperature optimum of 18 °C for *P. gaeumannii* spore germination is considerably below the optimum of 22 °C for hyphal growth of the pathogen (Capitani 1999), disease severity can respond either positively (Black et al. 2010) or negatively (Zhao et al. 2011) to summer temperature depending upon site conditions in relation to the two optima. The key drivers of SNC impact are winter and summer temperatures associated with fungal colonization at the most severely diseased site, TL, and summer precipitation, dew-point deficit, and temperature associated with ascospore germination of *P. gaeumannii* at the other five sites. Warm winters and warm, wet summers correspond with the greater SNC impact at TL because summer temperature is consistently below the optimum of 22 °C for fungal growth, and germination rates are consistently high despite the higher than optimal temperatures for germination (Black et al. 2010).

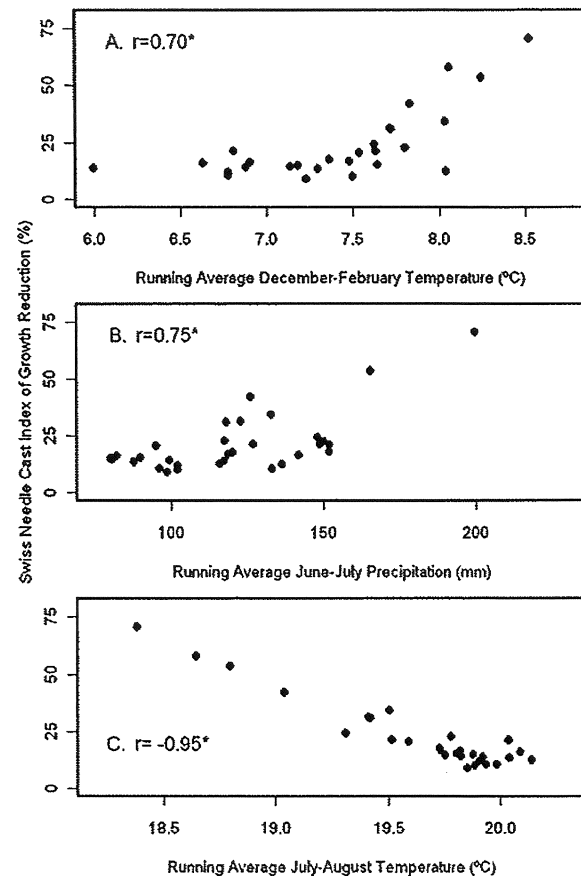
The recent SNC epidemic at the cool, humid TL site was likely due to winter and summer temperatures increasing at a rate of 0.2–0.4 °C/decade⁻¹ (for January–March, slightly higher for the

Fig. 6. Canonical correlations between current-year Swiss needle cast index of impact and (A) the weighted mean daily maximum winter temperature averaged across the previous 2–23 years, (B) the weighted mean summer dew-point deficit averaged across the previous 3–21 years, and (C) the weighted mean daily maximum summer temperature averaged across the previous 3–24 years at Tillamook Lower.



summer) since 1966 (NOAA 2005). The decline in SNC impact at the warmer, drier sites after 1996 was related to summer temperature increasing at a rate of about $0.3\text{ }^{\circ}\text{C}\cdot\text{decade}^{-1}$ and summer precipitation in July decreasing at a rate of about $8\text{ mm}\cdot\text{decade}^{-1}$ since 1970, resulting in less favorable conditions for ascospore germination of *P. gaeumannii*. Our findings are consistent with previous studies that suggest disease severity in young Douglas-fir plantations in coastal Oregon is best explained by climate variables in the summer months, most notably July (Rosso and Hansen 2003; Coop and Stone 2007; Latta et al. 2009). Climate conditions in July correlate best with SNC impact and severity because higher temperature combined with lower moisture in July may be more inhibiting to *P. gaeumannii* development than in other months (Rosso and Hansen 2003). A negative relationship between impact and summer temperature is consistent with the findings of Zhao et al. (2011), who reported a positive effect of summer temperature on foliage retention. Zhao et al. (2011) postulated that warmer summer temperatures are associated with higher vapor pressure deficit and lower water potential within the foliage, which negatively affect fungal development and increase needle retention. Where summer temperature along the Oregon coast exceeds the optimum of $18\text{ }^{\circ}\text{C}$ for spore germination

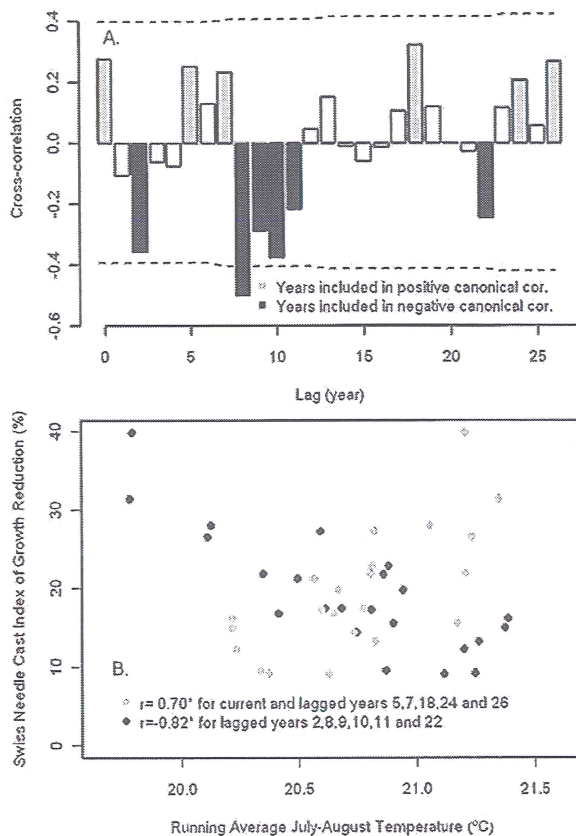
Fig. 7. Canonical correlations between current-year Swiss needle cast index of impact and (A) the weighted mean daily maximum winter temperature averaged across the previous 3–23 years, (B) the weighted mean total summer precipitation averaged across the current and the previous 1–11 years, and (C) the weighted mean daily maximum summer temperature averaged across the current and the previous 1–22 years at Cascade Head. Canonical correlation analysis was used to determine the weighting scheme for each seasonal factor.



(Capitani 1999), we postulate that warmer summer temperature is associated with less SNC impact because the establishment efficiency (i.e., proportion of spores that successfully infect the newly emerged needles) is reduced under warmer, drier conditions.

Whereas disease impact was more strongly correlated with summer conditions than winter conditions at all sites except TL, disease impact was highly sensitive to small changes in winter temperature at all sites. The sensitivity of *P. gaeumannii* to small changes in winter temperature were observed previously from foliar assessment studies (Manter et al. 2005; Stone et al. 2008a). No infection of 1-year-old needles is predicted when mean winter temperature is below about $4\text{ }^{\circ}\text{C}$ (Stone et al. 2008a), which translates to a winter mean daily maximum temperature threshold of about $7\text{ }^{\circ}\text{C}$ based on an offset of $3\text{ }^{\circ}\text{C}$ according to our local meteorological station at CH. In support of a temperature threshold of $7\text{ }^{\circ}\text{C}$, the SNC index of impact responded linearly to winter temperatures above $7\text{ }^{\circ}\text{C}$ but was relatively insensitive to temperature below $7\text{ }^{\circ}\text{C}$ at all six study sites, in particular CH. A temperature threshold of $7\text{ }^{\circ}\text{C}$ is consistent with the spatial shift in the association

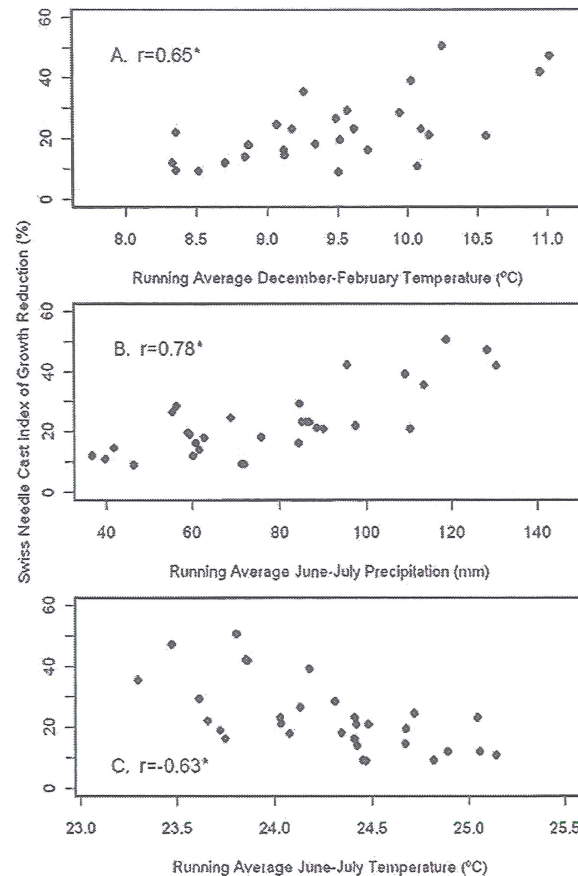
Fig. 8. (A) Cross-correlations between the current-year Swiss needle cast (SNC) index of impact and the current and past July–August temperature at Euchre Mountain. (B) Canonical correlation between the SNC index and the weighted mean daily maximum July–August temperature averaged across current and previous years. SNC impact responds both positively and negatively to summer temperature in alternating cycles because summer temperature exceeds the optimum temperature of 18 °C for germination of 18 °C, but is less than the optimum temperature of 22 °C for fungal growth. The canonical factors for summer temperature were based on the years having a cross-correlation >0.2 (gray bars and symbols) or <−0.2 (black bars and symbols).



between SNC impact and winter temperature in December–February at lower latitudes to January–March at higher latitudes. While January is the coolest month, the January–March period is, on average, warmer than the December–February period.

Our findings suggest that the geographic area affected by severe SNC may expand overall, but the intensity and frequency in coastal Oregon may increase or decrease under future climate conditions. Peak SNC impacts since 1984 were most frequent and severe at TL where the warmer winter and wet summer conditions promoted faster hyphal development in the intercellular spaces of the needle and faster pseudothecia formation (Manter et al. 2005). In some high-severity areas of the Coast Range, pseudothecia are abundant on 1- and 2-year-old needles (Hansen et al. 2000; Stone et al. 2008b) and only current and 1-year-old needles of Douglas-fir are retained in some years (Hansen et al. 2000; Maguire et al. 2002; Zhao et al. 2011). Continued warming during winter and summer will likely increase SNC intensity and frequency in areas within the coastal fog zone where needle wetness is maintained by coastal fog and drizzle. Conversely, continued warming and dry-

Fig. 9. Canonical correlations between the current-year Swiss needle cast index of impact and (A) the weighted mean daily maximum winter temperature averaged across the previous 2–25 years, (B) the weighted mean total summer precipitation averaged across the previous 1–22 years, and (C) the weighted mean daily maximum summer temperature averaged across the previous 4–23 years at Horse Creek Trail Lower.



ing in the summer will likely decrease SNC intensity and frequency in areas where warm, dry summers currently limit ascospore germination. Needle retention is predicted to decrease or increase gradually from 2020 to 2080 under future climate scenarios depending upon whether winter or summer conditions are the primary driver of pathogen development (Zhao et al. 2011). Based on annual area surveys conducted by the Swiss Needle Cast Cooperative at Oregon State University, the spatial extent of infected forests increased from 53 000 ha in 1996 to 210 000 ha in 2012 at a rate of about 3.2 km²·year^{−1} inland. This inland movement of disease was likely due to an expansion of area in the Coast Range where the winter temperature threshold was exceeded and disease conditions became more favorable. The disease will continue to spread inland, north, and to higher elevations in the Coast Range under a projected climate change scenario of warmer winter and summer temperatures, which will become more favorable for fungal germination and development.

Conclusion

Time-series intervention analysis of tree-ring data was used to reconstruct the disease history of Douglas-fir and make regional inferences of the environmental factors associated with disease

symptoms. The impacts of SNC disease were observed as far back as 1590 and occurred frequently with periodicities associated with the life cycle of *P. gaumannii*. The findings based on tree-ring data corroborate the epidemiological studies that indicate disease symptoms are associated with winter and summer temperatures and summer needle wetness. Disease intensity peaked in 1984–1986 at all study sites, followed either by a decline to at or below historic levels at warmer, less-humid study sites owing to decreasing needle wetness in summer, or an increase to unprecedented levels from 1984 to 2007 at a cooler, more humid site owing to increasing winter and summer temperatures. Our findings suggest that the spatial extent of SNC will likely increase, but the impact of the disease on Douglas-fir will vary spatially with site conditions under impending climate changes towards warmer, wetter winters and warmer, drier summers. Under future climate change scenarios, SNC impacts are likely to increase along the coast from northern Oregon to British Columbia, New Zealand, and elsewhere where June–July precipitation is much higher than the *P. gaumannii*-limiting threshold of 110 mm (Hood 1982), and decrease along the coast from California to southern Oregon and elsewhere where summer precipitation is at or below the threshold.

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biometrics

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 Mainwaring, Jon Wehage, and Alan Kanaskie

In coastal forests of the Pacific Northwest, young coniferous plantations typically contain a mixture of planted and natural Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). Swiss needle cast (SNC) disease 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, site characteristics, 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 the SNC growth impact study (GIS), precommercial thinning study (PCT), commercial thinning study (CT), and retrospective commercial thinning study (RCT). Predictor variables represent tree size, competitive position, site characteristics, 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-in. western hemlock tree will exceed the basal area growth of any Douglas-fir tree up to 7.7 in. in DBH. In a relatively healthy stand (foliage retention = 3.0 years) the basal area growth of 6 in. Douglas-fir and western hemlock trees will be approximately equivalent.

Keywords: relative growth, basal area increment, foliage retention, disease severity, thinning guidelines

Young Douglas-fir plantations (≤ 40 years) 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 (*Pseudotsuga menziesii*) 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. 2003, 2005, 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 2012 was 519,375 ac, the highest total since the aerial survey began (Kanaskie and McWilliams 2013). The extent of discoloration is particularly significant given the relatively aggressive conversion of both merchantable and nonmerchantable Douglas-fir stands to nonsusceptible tree species in the most severely impacted areas.

Precommercial thinning is commonly used to achieve management objectives in stands where high stand density limits individual tree growth and reduces vigor to a level that leaves trees more susceptible to insects and disease (Mitchell et al. 1983). Precommercial thinning 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

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indicate that infected stands respond positively to thinning (Mainwaring et al. 2005a, n.d.). However, consistent with unthinned stands (Maguire et al. 2011), Douglas-fir growth in precommercial thinning stands 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 nonsusceptible species and preferential retention of the both planted and naturally regenerated trees of these other species during precommercial thinning.

The SNC problem is mostly limited to the strip of land between the Pacific Ocean and approximately 20 miles inland, with the disease gradually diminishing in intensity from west to east, probably due to climate factors strongly influenced by proximity to the Pacific Coast (Zhao et al. 2011). Natural stands within the narrow *Picea sitchensis* vegetation zone immediately adjacent to the ocean (Franklin and Dryness 1973) have historically contained a mixture of other commercial species, including western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), and red alder (*Alnus rubra*), with much less Douglas-fir than is currently present. Within this zone, conversion of naturally regenerated stands to Douglas-fir plantations during the 1970s is believed to have played a role in the elevation of SNC from endemic to epidemic status (Hansen et al. 2000), but many other climatic and nutritional factors are probably contributing to the emergence of SNC as a serious obstacle to growing Douglas-fir in this coastal band (El-Hajj et al. 2004, Manter et al. 2005, Stone et al. 2008, Zhao et al. 2011).

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 with closer 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 relative 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). In many models, diameter

growth is expressed as a function of tree size, competition effects, and site characteristics (Wykoff 1990, Hann and Hanus 2002, Trasobares and Pukkala 2004, Zhao et al. 2004, Calama and Montero 2005, Uzoh and Oliver 2008, Hartmann et al. 2009). Previous work makes it clear that a distance-independent, individual-tree model structure is flexible enough to predict diameter growth in pure even-aged stands as well as in mixed multiaged stands (Monserud and Sterba 1996, Lhotka and Loewenstein 2011).

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 stands 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

Field Sites

Data for this analysis were compiled from four ongoing studies established on predominately Douglas-fir sites to investigate the influence of SNC on growth losses and response to thinning (Table 1). Plots were established across a range in topographic positions and SNC severity. Latitudes ranged from 43.5°N to 46.22°N, longitudes from 124.06°W to 122.29°W, and elevation from 45 to 1,024 feet (ft) above sea level (Figure 1). Over the last 40 years, the mean January minimum for this region was 32 °F and the mean July maximum was 77 °F. Total annual precipitation averaged 59–118 in., with approximately 70% of the total falling from October to March.

The growth impact study (GIS) was established in the winter and spring of 1998 within 76 Douglas-fir plantations ranging in total age from 10 to 30 years. These plots were established to monitor SNC severity and growth impacts within young stands in the Oregon Coast Range (Maguire et al. 2002, 2011). These plantations were sampled from a population of stands located within 18 miles of the Pacific coast and between the cities of Newport in the south and Astoria in the north.

The precommercial thinning study (PCT) was established in 23 Douglas-fir plantations to assess the effects of precommercial thinning on SNC symptom development and possible growth reduction (Kanaskie et al. 1998). In April and May of 1998, 23 paired plots were established within 29 miles of the Pacific coast and between the cities of Newport and Astoria. One plot in each pair was precommercially thinned to approximately 200 trees per acre in May 1998 (because of initial stocking levels, at two sites the target residual was 100 trees per acre). At five of the 23 locations, an additional plot was thinned to approximately 100 trees per acre. Only the unthinned stands were used in the present study.

The commercial thinning study (CT) was established in 30 stands scheduled for commercial thinning. These stands were older, ranging from 25 to 60 years, and were sampled to test the influence of commercial thinning on tree growth and SNC symptom development (Mainwaring et al. 2004, 2005b). Half of the plots were established prior to the 2002 growing season while the other half were established prior to the 2003 growing season. Prior to thinning, paired 0.5-ac fixed area plots, each with a 33-ft. buffer, were established in each stand. One of the plots was thinned while the other was left unthinned. Plots were chosen to fill a sampling matrix

Table 1. Summary of 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.

Species	Variable	Mean	Std dev	Min	Max	Mean	Std dev	Min	Max
Modeling data set (383 plots)						Validation data set (92 plots)			
Douglas-fir	Age (yr)	27.34	12.31	8.00	75.78	25.57	10.99	12.00	66.51
	FR (yr)	2.50	0.66	1.10	4.63	2.39	0.54	1.01	4.09
	Distance (mile)	14.07	11.39	0.60	87.60	12.49	9.78	0.60	78.20
	BA (ft²/ac)	125.95	52.68	17.20	344.67	121.17	48.90	7.44	256.75
	CCF (ft²/ac)	184.28	72.36	38.00	553.54	177.56	57.02	38.97	305.02
	D40 (in.)	12.23	3.85	3.39	25.59	11.82	3.76	2.19	20.75
	H40 (ft)	65.11	25.41	18.25	157.49	61.21	24.03	13.17	133.63
	TPA (trees/ac)	434.22	301.22	42.00	2099.11	417.54	234.64	72.00	1,094.53
	QMD (in.)	8.56	3.83	2.54	22.70	8.21	3.42	1.62	18.25
	SDI (in.)	249.66	97.88	52.22	783.29	240.70	82.55	28.01	443.96
SI (ft)	139.78	20.60	46.92	205.05	141.06	23.27	45.28	207.02	
Western hemlock	Modeling data set (181 plots)					Validation data set (42 plots)			
	Age (yr)	28.07	12.80	11.00	75.78	26.29	12.54	13.00	66.51
	FR (yr)	2.36	0.67	1.10	4.63	2.37	0.44	1.48	3.30
	Distance (mile)	12.68	13.78	0.60	87.60	10.57	12.59	0.60	78.20
	BA (ft²/ac)	138.81	54.68	25.30	344.67	132.00	49.94	16.24	256.75
	CCF (ft²/ac)	203.49	78.77	62.89	553.54	191.18	52.57	43.16	304.58
	D40 (in.)	12.39	3.72	4.23	23.71	12.03	3.68	4.88	20.75
	H40 (ft)	65.16	24.82	20.75	156.39	60.50	24.57	27.74	133.55
	TPA (trees/ac)	515.59	343.54	42.00	2099.11	481.89	238.45	72.00	1,094.53
	QMD (in.)	8.24	3.63	2.89	22.70	7.81	3.21	3.26	18.25
	SDI (in.)	281.09	107.75	75.73	783.29	266.98	83.23	46.35	443.94
	SI (ft)	136.97	20.50	86.61	198.16	142.55	21.77	104.00	207.02

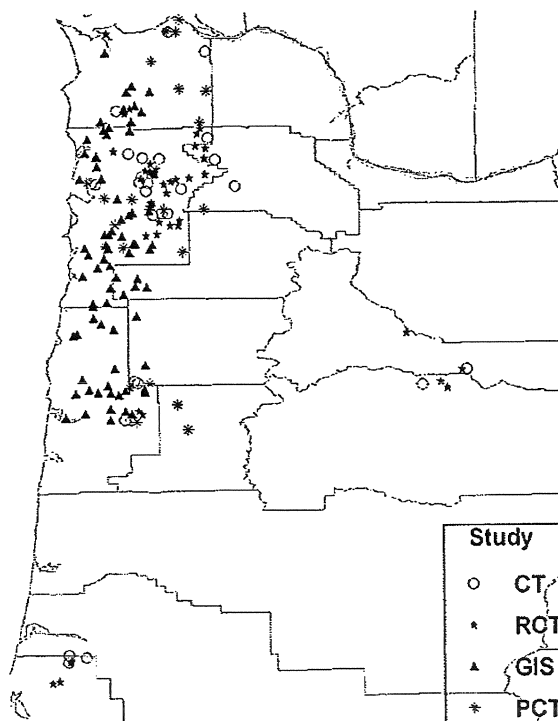


Figure 1. Location of the permanent research installations used in this analysis.

based on three levels of SNC severity (severe, moderate, light) and two levels of Douglas-fir stand density (relative density 20–35 and 35–50 ft²ac⁻¹in^{-0.5}; Curtis 1982). Located on state land managed by the Oregon Department of Forestry, 28 of the stands were in the Oregon Coast Ranges and two were in the western foothills of the

Cascade Mountains. Only the unthinned plots were used in this analysis.

The retrospective commercial thinning study (RCT) was established in 40 Douglas-fir stands that were 30- to 60-years-old and had been commercially thinned 4–10 years prior to plot establishment in 2002. This study was initiated to study the effects of commercial thinning on retrospective stand development under varying levels of current SNC (Mainwaring et al. 2005a).

Plot and Tree Measurements

In the younger GIS and PCT plantations, all trees with diameter at breast height (DBH) ≥ 2 in. (5 cm) were tagged on 0.2 ac (0.08 ha) permanent plots established in 1998. Trees were remeasured in 2000, 2002, 2004, and 2008. DBH was recorded for all trees, and total height (HT) and height to lowest live branch (HLB) were measured on a subsample of Douglas-fir trees across the diameter range. Where small trees (DBH < 2 in.) were abundant, a 0.05 ac (0.02 ha) subplot was established and only these small trees were measured for DBH on this nested subplot. Ten dominant or codominant trees were scored annually in April or May for SNC severity. On each tree, crown length was divided into thirds and foliage retention (FR) estimated visually as the average number of annual needle cohorts. Tree-level foliage retention was computed as the average of all crown thirds and plot-level retention as the average of all 10 sample trees.

In the CT stands, all trees with DBH ≥ 2 in. (5 cm) were tagged on square 0.5 ac (0.2 ha) permanent plots established during the winter prior to the 2002 or 2003 growing seasons. Trees were measured before the growing season of 2002, 2004, and 2006 on the 15 plots established in 2002 and before the growing seasons of 2003, 2005, and 2007 for the 15 plots established in 2003. All tagged trees were measured for DBH and a subsample of 40 Douglas-fir trees was measured for HT and HLB. This subsample included the 10 largest Douglas-fir trees by DBH and the four smallest by DBH, with the remaining 26 distributed evenly across the DBH range within the

Table 2. Summary of tree characteristics in Swiss Needle Cast Cooperative database for modeling individual-tree diameter growth of Douglas-fir and western hemlock in the Oregon Coast Ranges.

Species	Variable	Mean	Std dev	Min	Max	Mean	Std dev	Min	Max
Modeling data set (23,510 trees)					Validation data set (5,763 trees)				
Douglas-fir	DBH (in.)	9.10	4.30	0.12	39.09	8.75	4.05	0.04	38.39
	CR	0.70	0.18	0.07	1.00	0.72	0.17	0.03	1.00
	BAL (ft ² /ac)	77.05	50.82	0.00	331.03	75.92	51.34	0.00	248.93
	CCFL (ft ² /ac)	97.97	63.87	0.00	516.79	97.78	61.60	0.00	304.39
	ΔDBH (in./year)	0.24	0.18	0.00	1.32	0.25	0.18	0.00	1.14
Modeling data set (4,219 trees)					Validation data set (576 trees)				
Western hemlock	DBH (in.)	6.13	3.70	1.93	40.71	6.43	3.71	2.24	21.85
	CR	0.81	0.14	0.19	1.00	0.84	0.11	0.23	1.00
	BAL (ft ² /ac)	120.62	75.85	0.00	340.94	106.44	64.76	0.00	256.68
	CCFL (ft ² /ac)	170.75	115.31	0.00	534.76	135.04	72.97	0.00	276.04
	ΔDBH (in./year)	0.27	0.21	0.00	1.26	0.33	0.23	0.00	1.20

plot. On the largest 10 Douglas-fir trees, breast height ages were also obtained by coring the trees. Due to the height of crowns and associated visibility problems in these older, larger trees, binoculars were used to estimate a single foliage retention on the 5–10 largest trees on each plot.

In the RCT stands, all trees with DBH \geq 2 in. (5 cm) were tagged and measured on square 0.5 ac (0.2 ha) permanent plots established during the winter of 2001–2002. The plots were remeasured just before the growing seasons of 2005 and 2006, and individual tree measurements (DBH, HT, HLB, and foliage retention) were measured the same way as on the CT plots. Breast-height ages were obtained from the 10 largest Douglas-fir trees and foliage retention on the same 10 trees provided an estimate of SNC severity.

Model Development

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, in addition to its logarithmic, inverse, and squared transformations.
2. Competition variables: number of stems, TPA (stems/ac); average diameter of largest 40 trees by DBH, D40 (in.); average height of largest 40 trees by DBH, H40 (ft); quadratic mean diameter of all trees, QMD (in.); stand age, Age (year); total basal area, BA (ft²/ac); crown competition factor, CCF (Krajicek et al. 1961); stand density index, SDI; basal area of trees larger than the subject tree, BAL (ft²/ac); crown competition factor in trees larger than the subject tree (CCFL); and various transformations of these variables. Crown competition factor (CCF, Krajicek et al. 1961) was calculated 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 acre with a quadratic mean diameter of 10 in.
3. Site characteristics: Bruce's site index (Bruce 1981), SI (ft) and distance from coast, DIST (miles), in addition to their squared, logarithmic, and inverse transformations.
4. SNC severity: the number of years of retained foliage, FR, along with its squared, logarithmic, and inverse transformations.

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 with the logarithm of

diameter growth as the response variable 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 combination of methods was used to select the variables and their transformations: (1) stepwise regression; (2) subjective selection based on known drivers of stand dynamics (tree size, competition, site characteristics, and SNC severity); and (3) selection based on a combination of statistical fit and biological interpretability. The linear model was estimated using the maximum likelihood procedures in PROC REG in SAS version 9.2 (SAS Institute, Inc. 2008).

At the second stage, nonlinear diameter increment models were tested using the predictors identified with the log-linear diameter increment models. The nonlinear model was estimated using maximum likelihood by PROC NLIN in SAS version 9.2 (SAS Institute, Inc. 2008). Preliminary analysis indicated that a random plot effect was not suitable in accounting for the repeated measurements across different growth periods, primarily because the random plot effect served in part as a surrogate for plot-level foliage retention. Final models were chosen on the basis of statistical significance of parameter estimates ($\alpha = 0.05$), residual analysis, and biological interpretability.

For selecting the most suitable regression model, it is generally advisable to use some measure of lack of fit in combination with one or more test statistics (Kozak and Kozak 2003). An independent dataset can provide validation of model accuracy (Kariuki 2008). In this study, a random selection of 80% of the data was used for initial model development, and the remaining 20% was set aside to evaluate growth model accuracy (Table 2). 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. A fit index (FI) was computed as an analog to R^2 , in addition to root mean square error (RMSE), mean bias (MB), and absolute mean bias (ABS)

$$FI = 1 - \frac{\sum_{i=0}^n (\Delta DBH - \widehat{\Delta DBH})^2}{\sum_{i=0}^n (\Delta DBH - \overline{\Delta DBH})^2} \quad (1)$$

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

$$MB = \frac{1}{n} \sum_{i=0}^n (\Delta DBH - \widehat{\Delta DBH}) \quad (3)$$

$$AMB = \frac{1}{n} \sum_{i=0}^n (|\Delta DBH - \widehat{\Delta DBH}|) \quad (4)$$

Here n was the number of observations; ΔDBH was the measured diameter increment; $\widehat{\Delta DBH}$ was predicted diameter increment; and $\overline{\Delta DBH}$ was mean measured diameter increment.

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 averages across the entire dataset.

Thinning Guidelines

To illustrate potential application of the models, implied basal area growth was computed assuming that a subject stand had 400 trees/ac (988 trees/ha), including 250 Douglas-fir/ac (618 trees/ha) and 150 western hemlock/ac (370 trees/ha). Western hemlock trees ranged in diameter from 2 to 12 in. (5.1 to 30.5 cm), and Douglas-fir trees ranged in diameter from 0 to 5 in. (0 to 12.7 cm) 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 in. (0 to 12.7 cm) smaller than Douglas-fir. Plantation age was set to 10 years. 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 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 during a thinning to select the leave tree from a pair of adjacent trees of the two species.

Results

A large range of tree sizes was available for both species, with Douglas-fir exhibiting a greater diameter range (Table 2). The following final diameter increment equation for Douglas-fir included variables representing initial tree size, competition, and SNC severity

$$\begin{aligned} \Delta DBH = & \exp(\alpha_0 + \alpha_1 \times DBH + \alpha_2 \times DBH^2 + \alpha_3 \\ & \times \log(\text{Age}) + \alpha_4 \times \frac{BAL^2}{DBH} + \alpha_5/FR \\ & + \alpha_6 \times H40 + \alpha_7 \times \log(BA)) + \varepsilon_1 \end{aligned} \quad (5)$$

where ΔDBH = Periodic annual diameter growth of a Douglas-fir (in./year)

DBH = initial tree diameter (in.)

Age = plantation age (year)

Table 3. Parameter estimates and their standard errors for the Douglas-fir and western hemlock diameter growth models (Equations 5 and 6).

Parameter	Variable	Douglas-fir		Western hemlock	
		Estimate	Standard error	Estimate	Standard error
α_0	Intercept	1.8601	0.0423		
α_1	DBH	0.1297	0.0033		
α_2	DBH ²	-0.0026	0.0001		
α_3	Log(Age)	-0.3702	0.0149		
α_4	BAL ² /DBH	-0.0003	0.0000		
α_5	1/FR	-1.0002	0.0270		
α_6	H40	-0.0092	0.0004		
α_7	Log(BA)	-0.3769	0.0080		
β_0	Intercept			-0.8082	0.0958
β_1	Log(DBH)			0.8632	0.0313
β_2	DBH ²			-0.0006	0.0001
β_3	Log(Age)			0.2710	0.0442
β_4	BAL ² /DBH			-0.0001	0.0000
β_5	1/FR			0.8242	0.0407
β_6	H40			-0.0245	0.0010
β_7	Log(BA)			-0.3461	0.0150

BAL = basal area in trees with larger DBH than subject tree (ft²/ac)

FR = plot mean foliage retention (years)

H40 = average height of largest 40 trees by DBH (ft)

BA = total basal area per acre (ft²/ac)

α_k = parameter to be estimated from the data

ε_1 = random error with $\varepsilon \sim N(0, \sigma_1^2)$

All parameter estimates for Douglas-fir (Table 3) were significantly different from zero at $\alpha=0.05$, the fit index was 0.6177, RMSE was 0.0875, MB was 0.0011, and AMB was 0.0831. Residual plots indicated that the model provided a good fit to the data. Validation using 20% of the plots produced a fit index of 0.5871, RMSE of 0.1147, MB of 0.0028, AMB of 0.0858.

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

$$\begin{aligned} \Delta DBH = & \exp(\beta_0 + \beta_1 \times \log(DBH) + \beta_2 \times DBH^2 + \beta_3 \\ & \times \log(\text{Age}) + \beta_4 \times \frac{BAL^2}{DBH} + \beta_5/FR \\ & + \beta_6 \times H40 + \beta_7 \times \log(BA)) + \varepsilon_2 \end{aligned} \quad (6)$$

where ΔDBH = Periodic annual diameter growth of a western hemlock (in./year); β_k = parameter to be estimated from the data

ε_2 = random error with $\varepsilon \sim N(0, \sigma_2^2)$

and all other variables were defined above.

All parameter estimates for western hemlock (Table 3) were significantly different from zero at $\alpha=0.05$, the fit index was 0.6243, RMSE was 0.1014, MB was -0.0010, and AMB was 0.0954. Residual plots indicated that the model provided a good fit to the data. Validation using 20% plots produce fit index of 0.6470, RMSE of 0.1349, MB of 0.0409, AMB of 0.1033.

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 1.5 years) was only 69% of that expected in a comparable uninfected stand (foliage retention of 3.5 years) (Figure

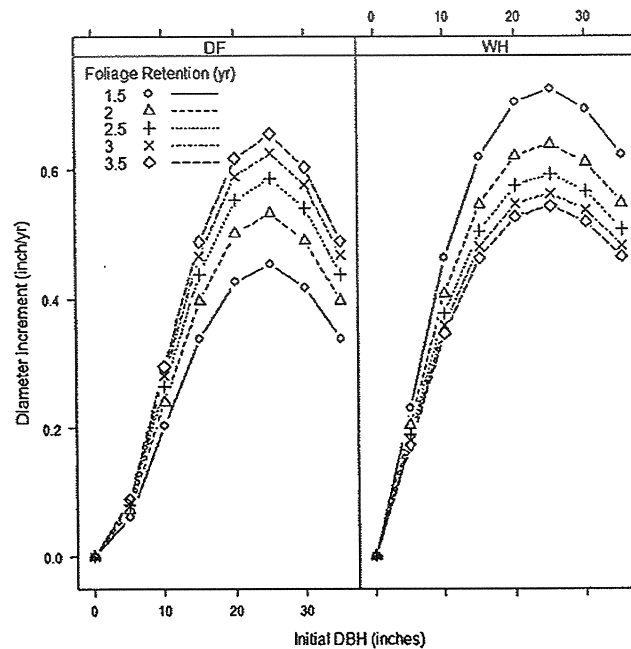


Figure 2. Diameter increment of Douglas-fir and western hemlock for a given initial diameter and SNC severity (foliage retention) in a stand with average age, QMD, TPA, H40, and BA. BAL for Douglas-fir and western hemlock was calculated from BA, DBH, QMD, and H40. Specifically, for Douglas-fir, $BAL = -4.88468 + 0.61475 \cdot BA - 13.85379 \cdot DBH + 9.36785 \cdot QMD + 0.35728 \cdot H40 + 12.11854 \cdot \log(DBH)$, ($R^2 = 0.8448$); for western hemlock, $BAL = 59.14009 + 0.66528 \cdot BA - 5.12461 \cdot DBH + 6.64968 \cdot QMD + 0.50032 \cdot H40 - 56.16876 \cdot \log(DBH)$ ($R^2 = 0.8149$).

Table 4. 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 database (Equation 7).

Parameter	Estimate	Standard Error
γ_1	224.9	6.9582
γ_2	-16.814	0.4839
γ_3	10.1474	2.5272

2). In contrast, western hemlock growing in the same mixed-species stand grew 34% more in diameter where foliage retention in Douglas-fir was only 1 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 components: a set of Douglas-fir with uniform diameters and heights and a set of western hemlock with uniform diameters (and implied equal heights) that were less than or equal to the diameter of the Douglas-fir component. When constructing the field charts, compatibility between DBH and H40 was ensured by fitting the following equation to the dataset (Table 4)

$$H40 = 4.5 + \gamma_1 \cdot \exp(\gamma_2 / D40 + \gamma_3 / BA) + \varepsilon_3 \quad (7)$$

where γ_k = parameter to be estimated from the data
 ε_3 = random error with $\varepsilon \sim N(0, \sigma_3^2)$

Fit index of the above model was 0.8029, and RMSE was 11.19.

The Douglas-fir and western hemlock diameter growth models implied that, as SNC severity increased, successively smaller western hemlock trees are capable of matching or exceeding the basal area growth of Douglas-fir (Figure 3). Under the assumptions made to generate the charts (Figure 3), basal area growth of individual Douglas-fir trees in a healthy stand (foliage retention of about 3.5 years) would always exceed that of western hemlock. Basal area growth ratio between western hemlock and Douglas-fir trees increasing with increasing SNC severity (declining foliage retention). Western hemlock trees with DBH of 2–10 in. can outgrow Douglas-fir of the same size if SNC is sufficiently severe. For western hemlock with DBH larger than 12 in., basal area growth of an equal or larger Douglas-fir would always be greater, regardless of SNC intensity. In stands with severe SNC, (foliage retention of 1.5 years or less), basal area growth of individual western hemlock trees with DBH of approximately 4–6 in. exceeds that of Douglas-fir trees that are up to 2 in. greater in DBH (Figure 3).

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), this conclusion relies on assumptions about relative value. Furthermore, knowledge that

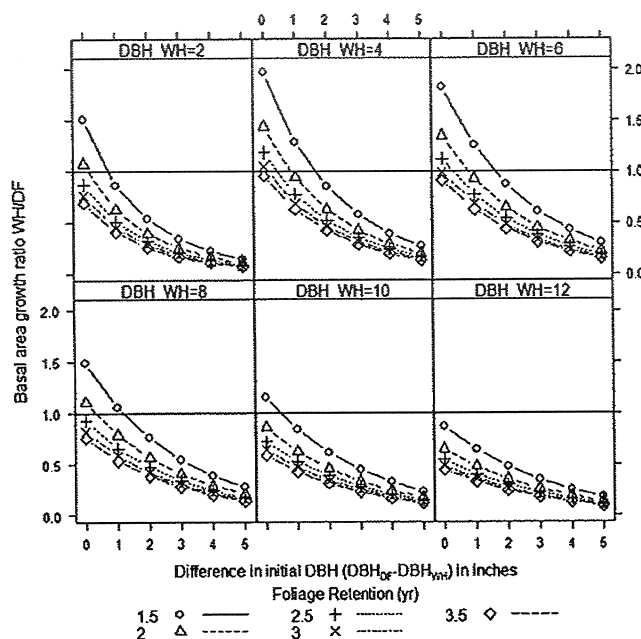


Figure 3. Ratio of western hemlock to Douglas-fir basal area growth as a function of size differential ($DBH_{DF} - DBH_{WH}$) between Douglas-fir and western hemlock under different initial diameters of western hemlock (DBH_{WH}) and SNC severity (foliage retention). Assumptions required to construct these charts were described in the methods section. H40 was calculated using Equation 7 to ensure compatibility with DBH.

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 Pacific Northwest 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 only in areas of moderate infection, not where disease intensity is high (Filip et al. 2000). Managers must consider including greater proportions of nonsusceptible 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; Figures 2 and 3). In healthy stands with a foliage retention of 3.5, the relative basal area growth of western hemlock with the same size initial DBH ($i = 0$) declines as tree diameter increases from 2 to 12 in., due to natural differentiation patterns of the species mix rather than to relative 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 outperforms individual Douglas-fir trees that are 1–2 in. larger in diameter depending in part on the initial diameter of the western hemlock (Figure 3). This difference would almost certainly be larger at lower foliage retention, although where foliage retention has remained at such a low level, optimal

selection of residual trees in a thinning operation becomes considerably more obvious. To illustrate general application of the graphs, assume that a 6-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 7.7 in. 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 and represents the average growth pattern observed in plots from set of Swiss Needle Cast Corporative (SNCC) studies, including the GIS, PCT, CT, and RCT. 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 but also in maximum potential stand density, e.g., McArdle et al. (1961) versus Barnes (1962)), the relative value of the two species, and other stand management objectives besides timber production or maximization of economic return. Note also that under moderate to severe SNC the act of removing the adjacent Douglas-fir will produce a proportionately greater release effect on the growth of the residual western hemlock than removal of the western hemlock would have on the Douglas-fir. In other words, the charts developed from the growth equations (Figure 3) depict the current relative growth rates under current stand conditions, but differences in growth potential between the two trees are dynamic and will be even greater after thinning.

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 northwest Oregon was \$530/mbf

and \$455/mbf, respectively, or a difference of \$75/mbf. These prices during the same quarter 5 and 10 years earlier were approximately \$580/mbf and \$385/mbf, or a difference of \$195.¹ During precommercial thinning operations, current log prices are not as important as long-term projections, so continued market fluctuations underscore the appeal of also considering relative growth potential of individual trees and corresponding stand-level differences in potential productivity.

Finally, the growth equations developed for this specific set of SNC-impacted stands provide insights into the altered stand dynamics of the specific subject population. They were developed to yield precommercial thinning guidelines for a relatively narrow geographic range, over a relatively short portion of a Douglas-fir rotation, and for a relatively narrow range in stand conditions. Long-term stand dynamics under SNC intensities that vary spatially and fluctuate temporally are largely unknown. Analyses using these equations can be complemented with predictions from more comprehensive regional growth models and other sources of information to confirm or modify developed guidelines and to compare the possible long-term consequences of alternative decisions about precommercial thinning in these stands. Although such projections must be recognized as gross extrapolations and interpreted with the same level of caution as the short-term implications of the equations developed here, the more information that can be brought to bear on decisions about managing these mixed-species, SNC-impacted stands, the more likely it is that stand management objectives will be met. We, therefore, strongly advocate that: (1) foresters apply the diameter growth equations in creative ways to develop guidelines for meeting their own stand management objectives for their own current stand conditions (i.e., Figure 3 is intended as only one very specific and simplified application); and (2) foresters combine the information from these equations with other lines of evidence to design strategies for stand management that will have the highest probability of achieving their objectives under uncertain future conditions.

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 years, western hemlock trees will grow more in basal area than Douglas-fir tree that are 1–2 in. 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 under the objective of providing comparable basal area growth over the short-term. In this approach, “ x ” would be selected as a function of SNC intensity as measured by foliage retention.

Endnote

1. Data obtained from www.oregon.gov/ODF/STATE_FORESTS/TIMBER_SALES/logpage.shtml.

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