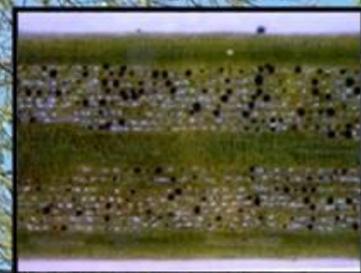


# Swiss Needle Cast Cooperative

## Annual Report 2010





# SNCC

## Swiss Needle Cast Cooperative Annual Report 2010



Edited by Robin Mulvey & David Shaw

**Oregon State**  
UNIVERSITY | College of Forestry



## SNCC Income Sources and Expenditures: 2010

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### Income

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Membership dues	70,000
Oregon State Legislature	76,712
Carry-over	<u>51,472</u>
Total 2009 Budget	<b>\$198,184</b>

### Expenditures

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Salaries and wages	95,288
Travel	4,328
Operating expenses	1,575
Contract Work	13,633
Materials and Supplies	8,884
Indirect Costs	<u>12,931</u>
Total 2010 Expenditures	<b>\$136,639</b>





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November 17, 2010

SNCC Membership,

Thank you for your continued support of the Swiss Needle Cast Cooperative in 2010. We also had support in 2010 from the College of Forestry and the state of Oregon, which makes this cooperative unique and our stakeholders diverse. In June of 2010, Robin Mulvey (MS Forest Pathology, Dept. of Botany & Plant Pathology, Oregon State University) joined the coop as a permanent Faculty Research Assistant. She has been very effective in her duties and is a huge asset to the program. She has reviewed all of the research done on nutrients and Swiss needle cast, taken the lead on the nutrient studies we are doing this year, managed numerous hourly employees, and edited this entire Annual Report. Travis Woolley continues to help the coop by handling budgets and conducting data analysis.

We have made incredible progress in our understanding of Swiss needle cast and the causal agent of this disease. The publication list associated with this Annual Report has over 40 publications, representing a huge body of work! However, the disease continues to intensify on the coast and is not abating. In fact, 2010 was our highest year ever for total acreage of SNC symptoms identified by the aerial survey; almost 400,000 acres. Our recent dendrochronology study (Black et al. 2010) supports the hypothesis that SNC is intensifying and is a more recent historical development on the coast, becoming an evident problem in this region in the late 1980s. The SNCC has completed a suite of research projects concerning disease management, and the final question that remains unanswered is, "What is the relationship between nutrients, especially nitrogen and calcium, and the susceptibility of Douglas-fir to disease?" Two of our current projects are focused on this issue, and some results are presented in this Annual Report.

The SNCC has all of the elements in place for the long-term management of the largest foliage disease epidemic in North America. This has evolved into an Integrated Pest Management (IPM) strategy that we are now promoting with a new publication in the Journal of Forestry (due out March 2011). We are hopeful that we can use this article to endorse the IPM strategy, which will rely on a monitoring program that uses the aerial detection survey to understand the general pattern and intensity of disease in the coast range, as well as permanent plots in the Cascade Range (measured at 5 yr intervals), to provide insight into disease patterns inside and outside the current epidemic area. The Maguire et al. growth impact plot network supports the disease detection surveys, by providing quantitative data on the growth impacts of disease over time.

I'd like to thank those that have contributed to this annual report. We have an additional article from Len Coop and Jeff Stone that summarizes some of their work funded by the Western Wildland Environmental Threat Assessment Center (USFS/PNW Research Station) based in Prineville, Oregon. We are also pleased to have a climate-modeling contribution from Junhui Zhao (et al.), the post-doc scholar working with Doug Maguire. Lastly, there is a synthesis table in the Appendix that was compiled by Robin Mulvey that summarizes all of the SNCC nutrient studies to date.

David Shaw, Director of the Swiss Needle Cast Cooperative



## **Key Features of the SNCC Monitoring, Research & Management Program**

- Aerial Survey & Permanent Monitoring Plots
- Epidemiology
- Silviculture
- Tree Improvement
- Forest Biology
- Integrated Pest Management of Swiss needle cast

## **2010 Projects**

1. Aerial Survey. Alan Kanasie, ODF
2. Tree Improvement: Nehalem Progeny Test Site Remeasurement. K. Jayawickrama, D. Shaw, R. Mulvey
3. Fertilizer influence on SNC disease severity across a gradient of disease: The Beyond N study. D. Shaw, R. Mulvey, D. Maguire, D. Mainwaring
4. Nitrogen influence on seedling susceptibility to SNC. R. Mulvey, R. Rose, D. Shaw, D. Mainwaring.
5. Fertilizer influence on mycorrhizae. D. Luoma.
6. Tree crown distribution of disease across environmental gradients. D. Shaw, T. Woolley, M. Huso



## **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.

# Swiss Needle Cast Aerial Survey, 2010

Alan Kanaskie and Michael McWilliams, Oregon Department of Forestry

## Abstract

Aerial surveys to detect and map the distribution of Swiss needle cast damage have been flown annually since 1996. Although the fungus that causes Swiss needle cast, *Phaeocryptopus gaeumannii*, occurs throughout the range of Douglas-fir, damage is most severe in the forests on the west slopes of the Coast Range. The 2010 survey mapped 393,923 acres of Douglas-fir forest with obvious Swiss needle cast symptoms; this was the largest area with damage since the survey began. Although most damage occurred within 18 miles of the coast, it extended up to 28 miles inland in some areas.

## Introduction

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

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

## Methods

The 2010 Oregon Coast Range survey was flown on May 13 & 14 and June 3, 7, & 8, and covered approximately 4 million acres of forest. The observation plane flew at 1,500 to 2,000 feet above the terrain, following north-south lines separated by 2 miles. Observers looked for areas of Douglas-fir forest with obvious yellow to yellow-brown foliage, a symptom of SNC. Patches of forest with these symptoms (patches are referred to as polygons) were sketched onto computer touch screens displaying topographic maps or ortho-photos and the position of the aircraft. Each polygon was classified for degree of discoloration as either “S” (severe) or “M” (moderate). Polygons classified as “S” had very sparse crowns and brownish foliage, while those classified as “M” were predominantly yellow to yellow-brown foliage with slightly denser crowns than those classified as “S”. The survey area extended from the Columbia River south to Brookings near the California border and from the coastline eastward until obvious symptoms were no longer visible. The Cascade Range was not surveyed in 2010, but SNC occurs in that region and causes damage to trees in several areas.

## **Results and Discussion**

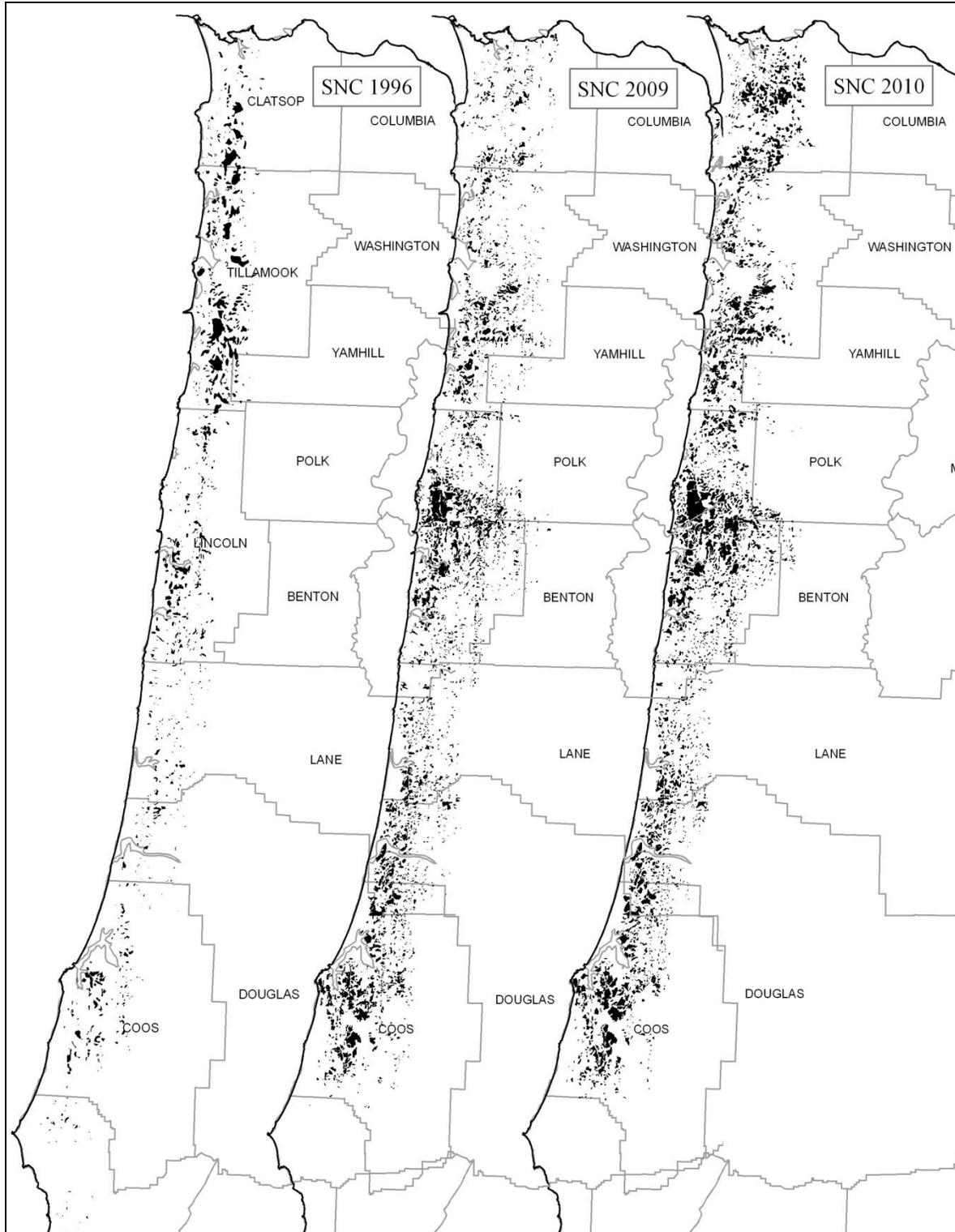
The 2010 survey showed an increase in the area of forest with symptoms of SNC compared to the previous three years, reaching an all-time high. The aerial survey mapped 393,923 acres of Douglas-fir forest with obvious symptoms of SNC (Fig. 1). As has been the case for the past several years, the eastern-most area with obvious SNC symptoms was approximately 28 miles inland from the coast in the Highway 20 corridor, but most of the area with symptoms occurred within 18 miles of the coast. Figure 2 shows the overall trend in damage from 1996 through 2010. Figure 3 shows damage trends in the north and south half of the Coast Range. SNC damage continues at very high levels despite a shift by many landowners to forest management practices aimed at ameliorating disease impacts.

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

[http://oregon.gov/ODF/PRIVATE\\_FORESTS/fh.shtml#Survey\\_Maps\\_\\_\\_Data](http://oregon.gov/ODF/PRIVATE_FORESTS/fh.shtml#Survey_Maps___Data)

## **Acknowledgements**

The 2010 survey was conducted by the Oregon Department of Forestry Insect & Disease and Air Operations sections, and was funded by the Oregon State University Swiss Needle Cast Cooperative, the USDA Forest Service Forest Health Monitoring Program, and the Oregon Department of Forestry. Trevor Courtney (ODF) piloted the plane. Mike McWilliams (ODF) is the survey coordinator and primary aerial observer. Ben Smith (USFS) and Rob Flowers (ODF) were the other aerial observers.



*Figure 1. Swiss needle cast (SNC) aerial survey: areas of Douglas-fir forest with symptoms of SNC detected in the 1996, 2009 and 2010 surveys. Solid black polygons (blotches) depict areas with severe or moderate damage from SNC.*

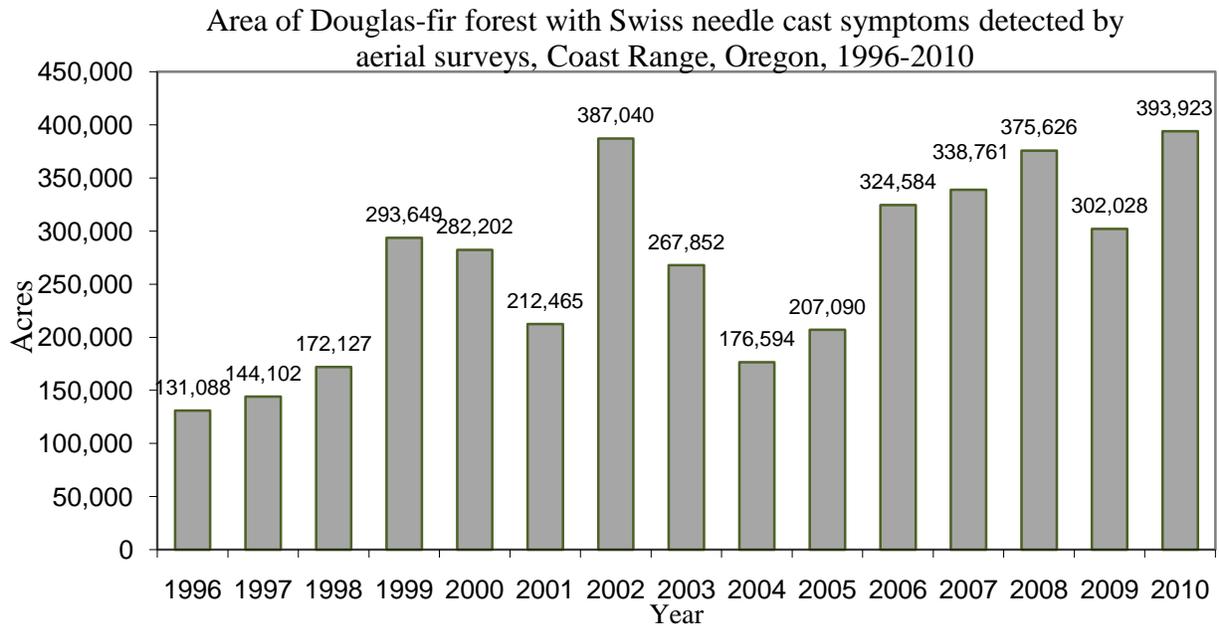


Figure 2. Trend in area of Douglas-fir forest in western Oregon with symptoms of Swiss needle cast detected during aerial surveys in April and May, 1996-2010. Results for 2008 were estimated by extrapolating from 3 sample survey blocks.

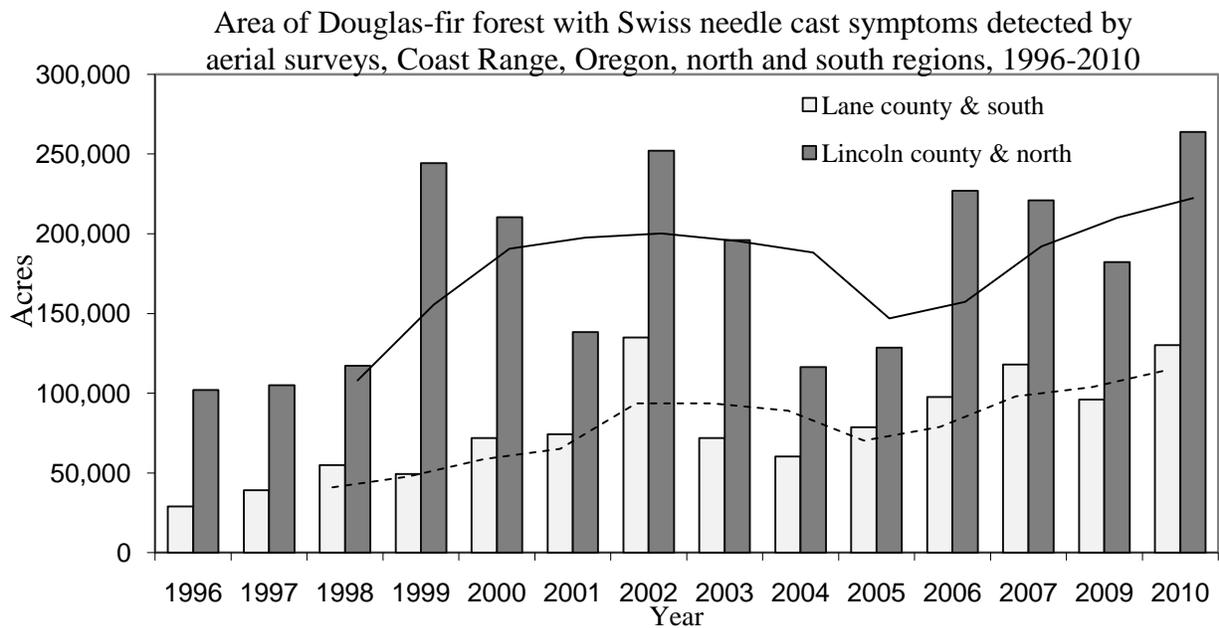


Figure 3. Trend in area of Douglas-fir forest in western Oregon with symptoms of Swiss needle cast detected during aerial surveys in April and May, 1996-2010. North region = Lincoln county & north; South region = Lane county & south. Trend lines are 3-year rolling averages.

# Response of Swiss Needle Cast Infected Trees to Pre-Commercial Thinning in Coastal Oregon

Doug Mainwaring and Doug Maguire, Dept. of Forest Engineering, Resources and Management, College of Forestry, Oregon State University  
Alan Kanaskie, Oregon Department of Forestry

## Abstract

In 1998, twenty-three sets of plots were installed in 5-16 yr old operational Douglas-fir plantations in the northern Oregon Coast Range to test the effects of pre-commercial thinning in Swiss needle cast-diseased stands. Previously identified trends of increasing foliage retention in the lower crowns of trees in thinned stands were determined to depend on initial foliage retention. Increases in foliage retention following thinning were most apparent in lower crowns of healthy trees. In the first six years after thinning, there was no evidence that foliage retention increased within any part of the crown of residual trees in the most heavily infected thinned stands (initial foliage retention < 2 yrs). Volume periodic annual increment in thinned stands was most responsive in the most heavily infected stands, because the stands were thinned from below and residual trees were probably the most tolerant of Swiss needle cast.

## Introduction

Many Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands in western Oregon are suffering from Swiss needle cast (SNC), a foliage disease caused by the fungus *Phaeocryptopus gaumannii* (T. Rohde) Petr. (Hansen et al. 2000). Although this fungus is endemic throughout the native range of Douglas-fir (Boyce 1940), increases in fungal presence, disease-related defoliation, and associated negative growth impacts have been apparent in coastal Douglas-fir stands since at least the 1990s (Maguire et al. 2002).

Reduction of stand density is commonly used in stands where low vigor limits individual tree growth or makes trees susceptible to pests (Mitchell et al. 1983). SNC-induced foliage losses are concentrated in the upper crown (Hansen et al. 2000), where physical factors, such as wind and rain, may induce casting of loosely held foliage. Although stands with wider spacing experience greater wind speeds and turbulence (Gardiner et al. 1997), research has shown that SNC-diseased trees carry a greater proportion of their foliage low in the crown, where older needle cohorts are retained longer (Weiskittel et al. 2006). Density reduction enables tree crowns to expand and elongate. Therefore, it is hoped that thinning will increase crown length, canopy depth, and subsequent foliage area per tree, thereby improving individual tree growth and increasing the likelihood that trees will reach merchantable size. Furthermore, because stands show differential levels of SNC disease-tolerance (Johnson 2002), thinning from below will presumably remove the trees that are performing poorest in the presence of SNC.

Previous analysis of data from the SNC pre-commercial thinning (PCT) plots suggested a trend of increased foliage retention in the middle and lower crown-thirds of trees on thinned plots compared to unthinned plots (Kanaskie and Maguire 2004). However, because initial

foliage retention was not taken into account, it was not apparent whether or not initial infection-level had any influence on this trend.

The first objective of this analysis was to determine whether the trend for increased foliage retention in the lower crowns of trees in pre-commercially thinned stands depends on initial disease-level (initial foliage retention). The second objective was to analyze the growth data over the ten year period since plot establishment, while statistically accounting for repeated measures.

## Methods

### *Study sites*

In the late winter/early spring of 1998, 23 sets of plots were established in 5-16 yr old stands distributed across a range of SNC severity (Fig. 1). One of the plots at each site was randomly chosen for pre-commercial thinning, generally to 200 trees per acre (TPA), while the other was not thinned. Stand densities were already low on two installations, so the thinned plots at these sites were prescribed a lower target residual density of 100 TPA. At five of the 22 sites, a third plot was established that had a target residual density of 100 TPA. All control plots and 200-TPA plots were square and covered 0.2-ac, except for 100 TPA thinned plots, which were 0.4 ac in size.

### *Measurements*

On each measurement plot, all trees were tagged and measured for diameter at breast height (dbh). At least 40 Douglas-fir trees on each plot were also measured for total height and height to crown base. The treated plots were thinned before the growing season started in 1998. After two, four, six, and ten growing seasons (after the 1998-99, 2000-01, 2002-03, and 2004-07 growth periods), all trees were remeasured for dbh, and all trees from the original height subsample were remeasured for total height and height to crown base.

In April and May of each year (1998-2004), ten codominant or dominant trees in each plot were assessed for damage from SNC. Sample trees were permanently tagged so that the same trees could be assessed each year. Foliage retention was estimated by ground crews for each third of the live crown (upper, middle, lower) by examining secondary lateral branches in the middle of each crown-third, and estimating the average number of annual needle compliments present (note: a *secondary lateral* is a branch that originates on the side of the main lateral branch). Sample branches were chosen to represent the average condition in each third of the crown. The number of annual needle compliments present for each third of the live crown was estimated to the nearest 0.1 year. Full crown foliage retention was calculated as the average of all crown-thirds.

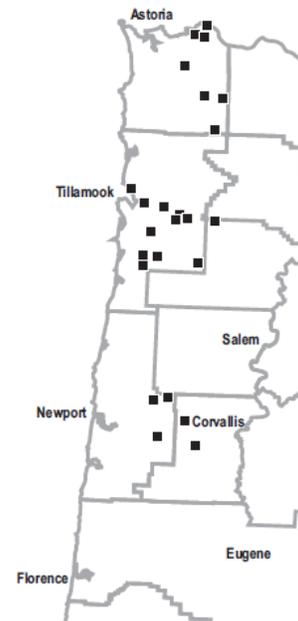


Figure 1. Locations of the 23 sets of plots.

## *Analysis*

The effect of thinning on foliage retention was analyzed for the crown as a whole, as well as for individual crown-thirds using a randomized complete block design. Comparisons were made between the 200 TPA thinning and the control. This analysis was applied to each year of data between 1998 and 2004.

In order to determine the effect of thinning on foliage retention at different levels of SNC intensity, foliage retention was used as the dependent variable and sites were differentiated using categorical variables based on average foliage retention. Sites with average foliage retention of 1-2 yrs were coded as 1, sites with an average foliage retention of 2-3 yrs were coded as 2, and sites with average foliage retention greater than 3 yrs were coded as 3.

$$[1] \text{ folret} = \text{TRT} + \text{FRCODE} * \text{TRT}$$

Where folret	= foliage retention (whole crown or by crown-third)
TRT	= class variable representing thin or control
FRCODE	= class variable: 1, 2, or 3 corresponding to the level of initial folret

For the growth analysis, a mixed effects model was fit to the data for sites thinned to 200 TPA, assuming random effects of both plot and period.

$$[2] \text{ PAI} = \text{IBA} + \text{lfolret} + \text{T200} + \text{lfolret} * \text{T200} + \text{PERIOD} + \text{PERIOD} * \text{T200} + \varepsilon_1$$

Where IPAI	= ln(periodic annual increment) in m <sup>3</sup>
IBA	= is the covariate for ln(plot level basal area of DF)
lfolret	= is the covariate for ln(foliage retention)
T200	= 1 if the plot was thinned to 200 TPA, 0 otherwise
PERIOD	= set of indicator variables for the four growth periods
$\varepsilon_1$	= random error term with $\varepsilon_1 \sim N(0, \sigma_1^2)$

## **Results and Discussion**

### *Foliage retention*

In control plots, average whole crown foliage retention increased between 1998 and 2004, from a low of 2.42 yrs in 1998 to 2.71 yrs in 2004. During the same period, foliage retention on plots thinned to 200 TPA increased from 2.46 yrs in 1998 to 2.88 yrs in 2004. From 1998 to 2001, there were no statistically significant differences in foliage retention attributable to thinning. However, treatment related differences in foliage retention were apparent starting in 2002, increasing from 0.1 yrs in 2002 to 0.16 yrs in 2004 (Fig. 2). Significant treatment-related differences were apparent in the mid- and lower-crown, but not in the upper-crown.

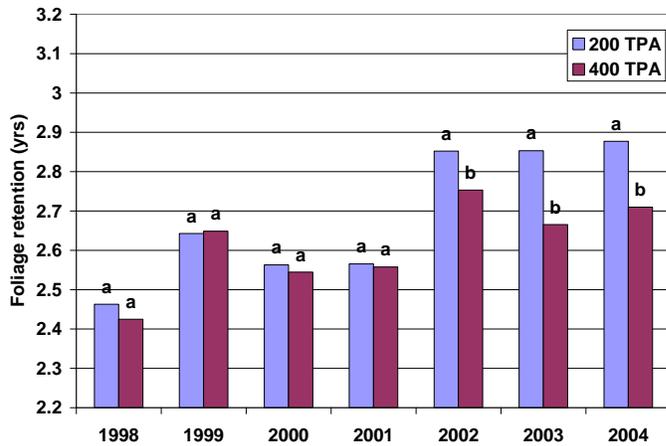


Figure 2. Average whole crown foliage retention by treatment.

After accounting for initial SNC intensity, significant increases in foliage retention following thinning were apparently confined to the healthiest stands with initial foliage retentions greater than three years. Stands with foliage retention between two and three years showed an upward trend in foliage retention since 2002, while heavily infected stands with less than two years of foliage showed no change (Figures 3-5). In healthy stands, foliage retention improvements after thinning were most pronounced at greater crown-depths. Five years after thinning, significant increases were apparent in all crown-thirds, amounting to an average foliage retention increase of 0.3 yrs in the upper crown-third (Fig. 3), and an average increase of 0.45 yrs in the middle (Fig. 4) and lower crown-thirds (Fig. 5). During the same period, stands with an initial average foliage retention between two and three years experienced a ~0.2 yr increase in foliage retention in the middle and lower crown-thirds. Stands with an initial average foliage retention less than two years demonstrated no change in foliage retention attributable to thinning, regardless of crown-third.

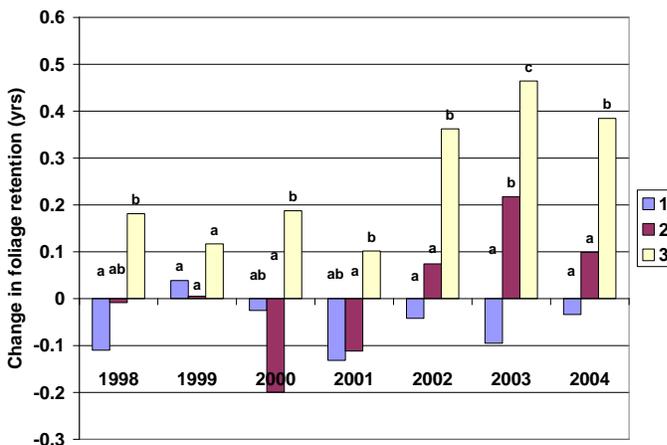


Figure 3. Change in average foliage retention in the upper crown-third attributable to thinning (200TPA).

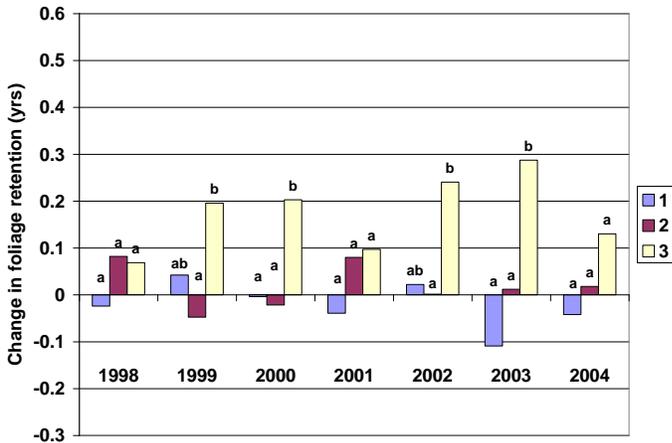


Figure 4. Change in average foliage retention in the middle crown-third attributable to thinning (200TPA).

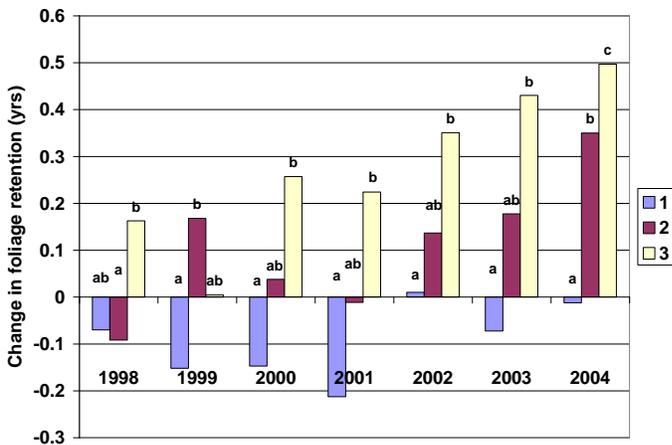


Figure 5. Change in average foliage retention in the lower crown-third attributable to thinning (200TPA).

### Growth

The effect of PCT on volume growth was dependent on both growth period and foliage retention. Volume periodic annual increment (PAI) per unit basal area was much more positively affected by thinning in low foliage retention stands than in healthy stands (Fig. 6). Although volume PAI was greater in healthy stands than in heavily diseased stands, the improvement in residual growth that resulted from thinning increased with SNC disease-level. In the first two year period following thinning, volume PAI in the most symptomatic stands was slightly below that of the thinned stands (Fig. 7), but by growth period 4 (7-10 yrs post-thinning), volume PAI in infected plots had surpassed that of unthinned control stands (Fig. 8). The

implied relationship between foliage retention and PAI in thinned and unthinned stands indicates that, compared to a healthy stand (foliage retention= 3.7 yrs), the most heavily infected thinned stands experienced a 41% volume growth loss, while the most heavily infected control stands experienced a 66% volume growth loss (Figures 7 and 8). In other words, severely diseased stands that were thinned experienced less growth loss than severely diseased stands that were not thinned.

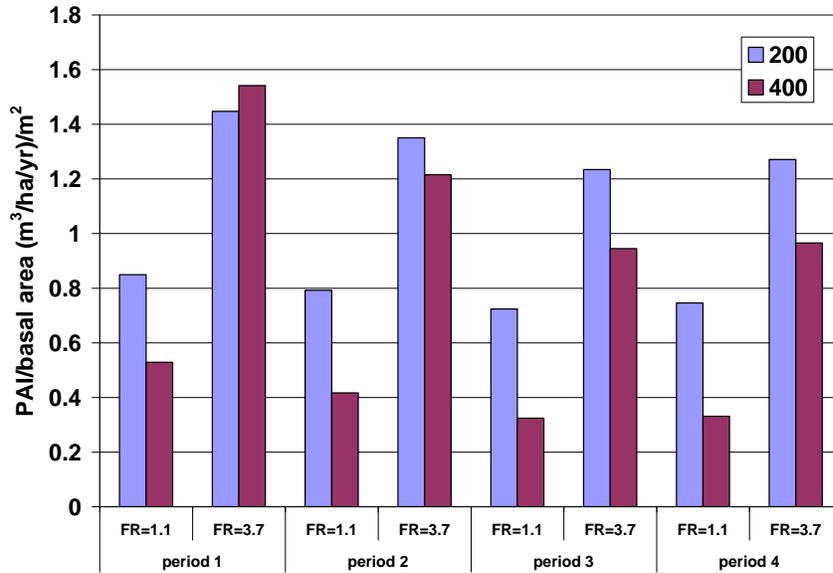


Figure 6. Implied volume PAI per unit basal area by treatment.

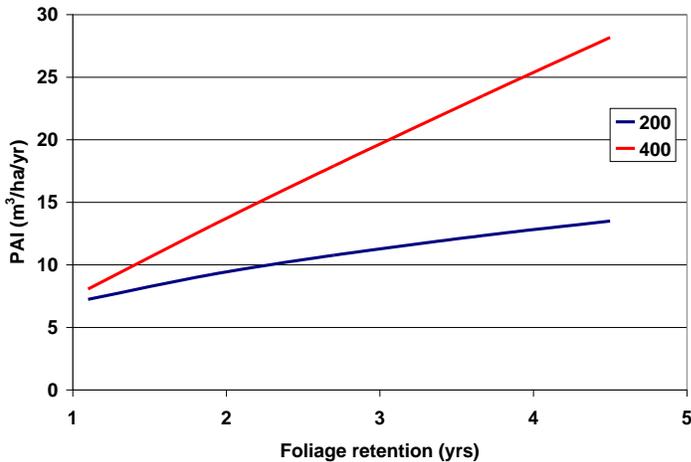


Figure 7. Period 1 (2 yrs post-thinning) PAI by thinning treatment and foliage retention. Based on average Douglas-fir basal area (200 TPA= 8.5 m²/ha; 400 TPA=15.3 m²/ha).

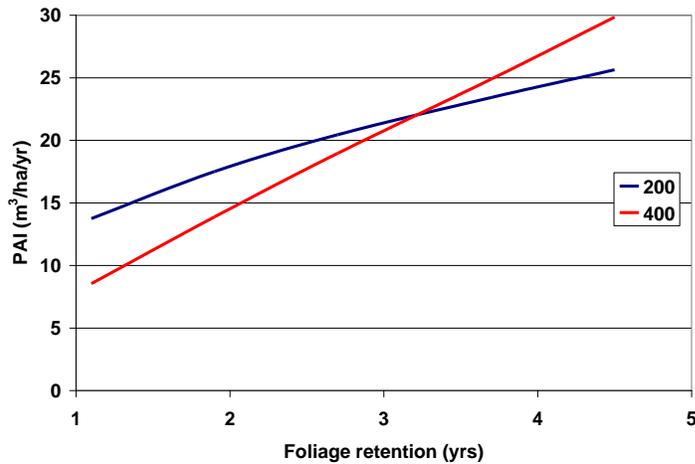


Figure 8. Period 4 (7-10 yrs post-thinning) PAI by thinning treatment and foliage retention. Based on average Douglas-fir basal area (200 TPA= 8.5 m<sup>2</sup>/ha; 400 TPA=15.3 m<sup>2</sup>/ha).

## Conclusion

The improvement in performance following thinning in infected stands is probably the result of numerous factors. Needle loss associated with SNC disease and exposure to wind and weather is greatest in the upper crown, while lower portions of the crown still retain significant foliage. Exposure of this foliage following thinning improves light interception and tree growth. In addition, stands of this age in this region have grown in the presence of SNC since they were established, which indicates that their size distribution at time of thinning reflects their level of SNC-tolerance. These stands were pre-commercially thinned from below; therefore, stocking was reserved for the trees that demonstrated the ability to grow best in the presence of SNC.

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# **The Long-Term Relationship between Foliage Retention and Growth Losses in Douglas-fir Stands Experiencing a Range in Swiss Needle Cast Severity**

Douglas A. Maguire and Douglas B. Mainwaring, Dept. of Forest Engineering, Resources and Management, College of Forestry, Oregon State University  
Alan Kanaskie, Oregon Department of Forestry

## **Abstract**

Swiss needle cast severity continues to be most commonly measured by foliage retention, which is the average number of annual needle age classes held by trees. Growth losses can be estimated from average foliage retention within a stand of Douglas-fir, and evidence to date suggests that the relationship between foliage retention and growth loss has been stable in Douglas-fir plantations in north coastal Oregon since plots to assess growth impacts were installed in 1998. Periodic annual increment ( $\text{ft}^3/\text{ac}/\text{yr}$ ) was measured for three 2-yr growth periods and one 4-yr growth period over the last ten years on permanent plots established as part of the Swiss Needle Cast Cooperative Growth Impact Study. Mixed-effects regression models did not detect any significant differences in the relationship between foliage retention and relative stand-level increments among the four growth periods. As estimated from the retrospective phase of the Growth Impact Study and four subsequent growth periods on the permanent plots, growth losses ranged from just over 50% in stands with the lowest needle retention (approximately 1 year) to 0% in stands with maximum needle retention (approximately 3.9 years). These cubic volume growth losses reflected the marginal effects of foliage retention after accounting for standard effects of initial Douglas-fir growing stock, site quality, stand age, and competition from other coniferous species, as well as yearly fluctuations in regional productivity attributable to climatic factors directly influencing tree growth.

## **Introduction**

The amount of foliage on a tree or in a forest stand indicates its photosynthetic capacity and potential productivity. However, environmental constraints can prevent stands with a given amount of foliage from achieving their potential productivity, with water availability being one key limitation in Douglas-fir (Brix and Mitchell 1986). Likewise, differential photosynthetic efficiencies among needle age classes (Woodman 1971, Ethier et al. 2006) can cause productivity to vary with shifts in needle age class distribution, even with no accompanying change in total foliage amount. Defoliation by several defoliating insects has been shown to cause growth reductions, with the amount of growth loss depending on degree of defoliation and number of years of defoliation (Blais 1958, Williams 1967, Piene 1989, Alfaro and Shepherd 1991, Ostaff and MacLean 1995). Spruce budworm consumes foliage of progressively older age classes, so by removing young needles with greater photosynthetic efficiency, this insect should have a more deleterious growth effect for a given amount of foliage loss than agents like *Phaeocryptopus gaeumannii* that cause premature loss of older foliage (Hansen et al. 2000). Growth losses under severe Swiss needle cast (SNC) disease approach 50% of stem volume

increment (Maguire et al. 2002). In the case of SNC, additional growth losses are imposed by inhibition of gas exchange on surviving foliage through stomatal occlusion by pseudothecia, the fruiting bodies of the causal fungus (Manter et al. 2000).

Foliage retention provides an indirect index of SNC severity because it does not necessarily measure the quantity of foliage lost, the quantity of foliage remaining or the frequency of stomatal inclusion. However, foliage retention can be estimated operationally in stands  $\leq 40$ -50 years of age, and has consistently served as a reliable and practical index of growth loss in Douglas-fir plantations (Maguire et al. 2002). Because stands that have expressed severe SNC for multiple years have also experienced substantial cumulative growth loss, it is uncertain whether the quantitative relationship between foliage retention and growth loss has shifted over time. The objectives of this analysis were to quantify the relationship between foliage retention and stem volume growth loss, and to test the stability of this relationship over a ten-year period. The target population was the collection of 10- to 40-yr-old plantations in north coastal Oregon, where SNC has become a severe impediment to growing Douglas-fir.

## **Methods**

### ***Field Work***

A network of 76 permanent plots was established in the late winter/early spring of 1998 across north coastal Oregon. Sampled stands were randomly selected from the population of 10- to 30-yr-old stands between Astoria and Newport that were within 18 miles of the Pacific Coast. Plots were square, 0.2 ac in area (104 x 104 ft), and centered on the fifth point of the ODF (Oregon Department of Forestry) transect established in Spring 1997 (Phase I plots were centered on the third point). On each measurement plot, all trees with diameter at breast height (dbh) greater than 4cm were tagged at a height of 4.5 feet, and at least 40 Douglas-fir were measured for total height and height to crown base at time of plot establishment. After two, four, six, and ten growing seasons, all trees were remeasured for dbh, and all trees from the original height subsample were remeasured for total height and height to crown base. Trees on each plot were also scored for SNC at time of plot establishment in 1998, and just prior to bud break in years 1999-2004. On ten dominant or codominant trees per plot, the crown was vertically divided into thirds, and the average number of years that foliage was retained in each third was visually estimated to the nearest 0.1 year. Plot ratings were computed as the average of all crown thirds from all ten trees.

### ***Statistical Analysis***

Missing height and height to crown base data for Douglas-fir trees were estimated as a function of dbh by fitting regression models specific to each plot and growth period. Cubic stem volumes of Douglas-fir were estimated with equations presented by Bruce and DeMars (1974). The growth rate of primary interest was the plot-level periodic annual increment (PAI) of Douglas-fir trees that survived through the corresponding growth period. The following equation describes the basic growth model for predicting PAI as a function of initial Douglas-fir basal area, initial breast height age, site quality, foliage retention, and basal area of competing conifer and hardwood species:

$$[1] \quad \ln[\text{PAI}] = \beta_0 + \beta_1 \ln(\text{BA}_{\text{DF}}) + \beta_2 \ln(\text{AGE}_{\text{BH}}) + \beta_3 \ln(\text{SI}) + \beta_4 \text{BA}_{\text{OC}} + \beta_5 \text{BA}_{\text{HARD}} + \beta_6 \ln(\text{FR}-0.5) + \varepsilon_1$$

where	$\text{BA}_{\text{DF}}$	=	Initial Douglas-fir basal area ( $\text{m}^2/\text{ha}$ )
	$\text{AGE}_{\text{BH}}$	=	Initial age at breast height (years)
	SI	=	Bruce's site index (m at 50 years)
	$\text{BA}_{\text{OC}}$	=	Initial basal area in other conifers ( $\text{m}^2/\text{ha}$ )
	$\text{BA}_{\text{HARD}}$	=	Initial basal area in hardwood species ( $\text{m}^2/\text{ha}$ )
	FR	=	Foliage retention (years)
	$\varepsilon_1$	=	Random error term with $\varepsilon_1 \sim N(0, \sigma_1^2)$
	$\beta_i$	=	Parameter estimated from the data

The plot PAIs represented repeated measures over time, and tree growth is widely recognized to fluctuate with annual climatic conditions. Therefore, the error structure of the model was potentially more complicated than indicated by the distribution of  $\varepsilon_1$  in Model [1]. The net result of this departure from the specified distribution of  $\varepsilon_1$  is that the variance estimates are biased, and the intended  $\alpha$ -levels for tests of significance are not maintained. To ensure correct inferences about the significance of foliage retention to PAI, mixed-effects models were fitted to the data under several different assumptions. These assumptions included a random plot effect, a random year effect, both random plot and random year effects, and a compound symmetric structure that recognized covariance among observations within a plot. Model comparisons were based on Akaike's Information Criterion (AIC), which is a function of the maximum likelihood and number of parameters in the model (Burnham and Anderson 2002).

## Results and Discussion

The trends in PAI over four growth periods showed strong plot effects, and to a lesser extent, annual weather effects (Fig. 1). These trends graphically corroborated results from the fitted statistical models described below. Over the range of plantation ages sampled in 1998 (10- to 30-years old), PAI depicted the expected trend for increased growth potential as tree age increased (Fig. 2). Trends in AIC over the full set of fitted models underscored the importance of alternative assumptions about the error structure of the model (Table 1). The compound symmetric error structure was most appealing due to the probable covariance of observations over time from a single plot. In fact, models assuming this error structure were far superior to other models, and led to slightly different conclusions than models that assumed simple random plot or year effects. One key difference between models that assumed these two types of error structure were the apparent effects of non-Douglas-fir tree species on Douglas-fir growth. Under the compound symmetric error structure, the effects of other conifers became non-significant, and the effects of hardwoods alone became only marginally significant (Table 1).

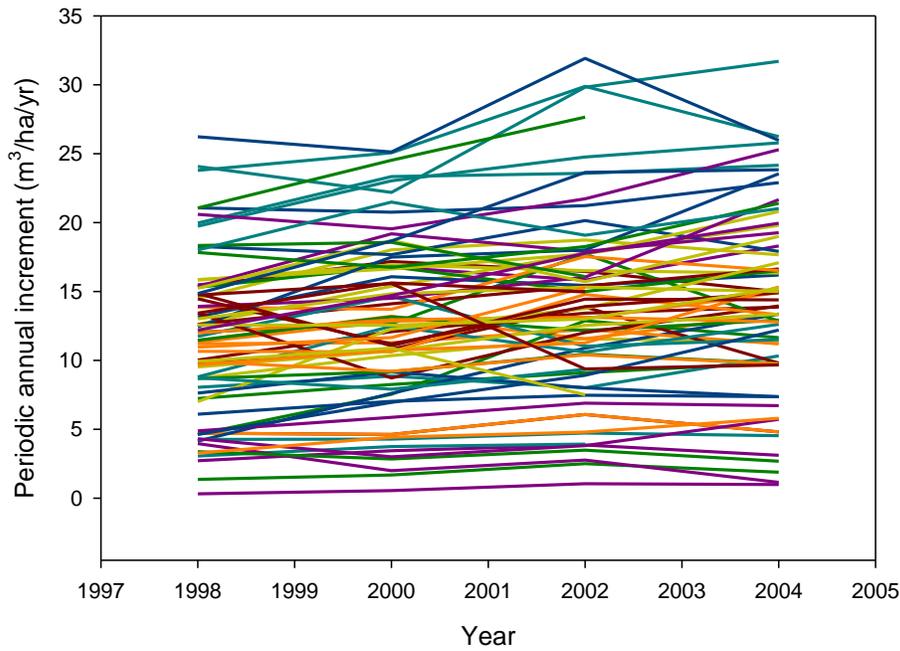


Figure 1. Trends in periodic annual increment of Douglas-fir trees surviving on each Growth Impact Study plot over three 2-yr and one 4-yr growth periods.

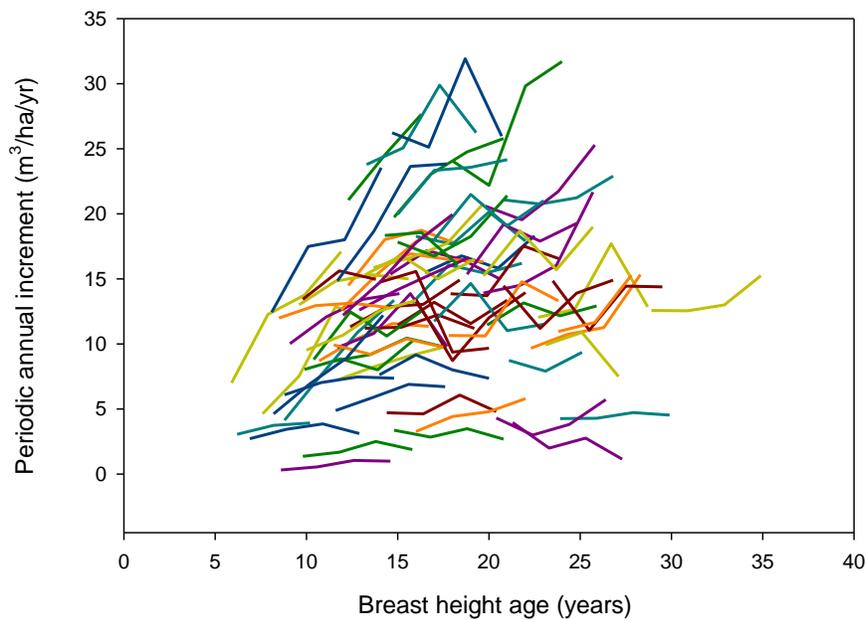


Figure 2. Trends in periodic annual increment over initial breast height age for all surviving Douglas-fir on each Growth Impact Study plot.

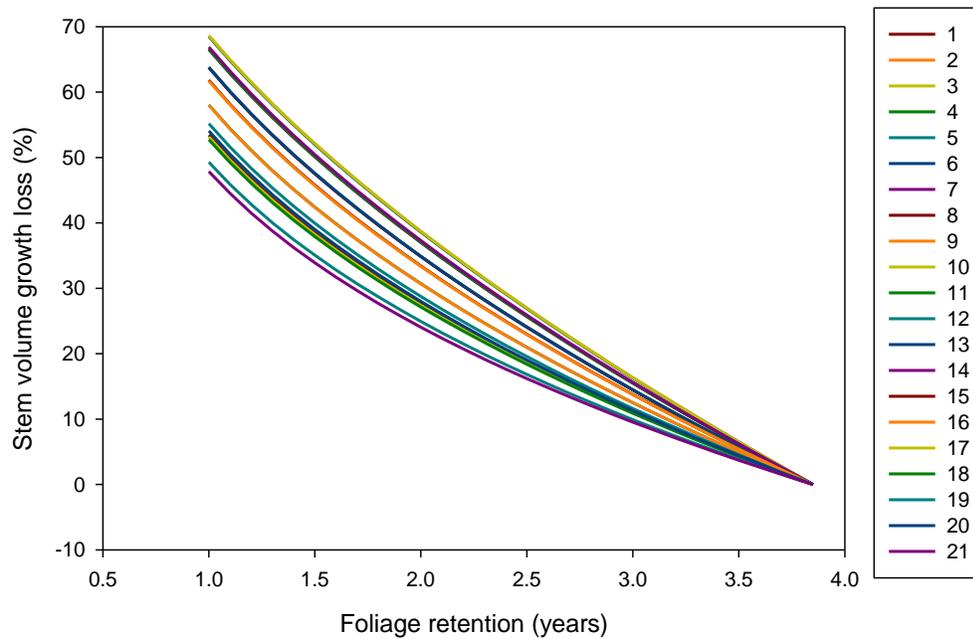


Figure 3. Trends in PAI growth loss over foliage retention as estimated by each of the 21 models in Table 1.

Foliage retention was consistently a very strong predictor of stem volume growth increment. In the model selected as “best” (model 15 in Table 1), growth losses were predicted to reach just over 50% at very low needle retention (1.1 years) and declined to zero impact as needle retention approached 3.9 years. All models recognizing the compound symmetric error structure (models [15]-[20]) predicted very similar trends in growth loss, reaching maxima of slightly less than to slightly greater than 50% (Fig. 3). A rough indication of the reliability of growth loss estimates are provided by plotting out the expected growth loss based on the parameter estimate associated with  $\ln(\text{FR})$  in model [15] and the losses implied by adding and subtracting two standard errors on the parameter estimate (Fig. 4).

Table 1. Models tested for predicting periodic annual stem volume increment of 76 permanent plots installed as part of the SNCC Growth Impact Study. *Italicized variables are marginally significant ( $0.05 < p < 0.10$ ) and underlined variables are not significant ( $p > 0.10$ ). ( $lbadf = \ln(BA_{DF})$ ,  $lsib = \ln(SI)$ ,  $lage = \ln(AGE_{BH})$ ,  $baoc = BA_{OC}$ ,  $bahard = BA_{HARD}$ ,  $lret = \ln(FR)$ )*

Model	Symbols of included variables	Error Structure	AIC
1	$lbadf$ , $lsib$ , $lretm$	random plot	435.1
2	$lbadf$ , $lsib$ , $lret$ , $lage$	random plot	358.7
3	$lbadf$ , $lsib$ , $lret$ , $lage$ , $baoc$	random plot	329.4
4	$lbadf$ , $lsib$ , $lret$ , $lage$ , $baoc$ , $bahard$	random plot	322.9
5	$lbadf$ , $lsib$ , $lret$	random year	416.5
6	$lbadf$ , $lsib$ , $lret$ , $lage$	random year	361.4
7	$lbadf$ , $lsib$ , $lret$ , $lage$ , $baoc$	random year	336.2
8	$lbadf$ , $lsib$ , $lret$ , $lage$ , $baoc$ , $bahard$	random year	330.3
9	$lbadf$ , $lsib$ , $lret$	random plot, year	418.3
10	$lbadf$ , $lsib$ , $lret$ , $lage$	random plot, year	358.7
11	$lbadf$ , $lsib$ , $lret$ , $lage$ , $baoc$	random plot, year	329.4
12	$lbadf$ , $lsib$ , $lret$ , $baoc$	random plot, year	396.9
13	$lbadf$ , $lsib$ , $lret$ , $lage$ , $baoc$ , $hard$	random plot, year	322.9
14	$lbadf$ , $lsib$ , $lret$	compound symmetry	87.8
15	$lbadf$ , $lsib$ , $lret$ , $lage$	compound symmetry	26.4
16	$lbadf$ , $lsib$ , $lret$ , $lage$ , <i><math>bahard</math></i>	compound symmetry	32.2
17	$lbadf$ , $lsib$ , $lret$ , $lage$ , <u><math>baoc</math></u>	compound symmetry	37.5
18	$lbadf$ , $lsib$ , $lret$ , $lage$ , <u><math>baoc</math></u> , <i><math>bahard</math></i>	compound symmetry	41.2
19	$lbadf$ , $lsib$ , $lret$ , $lage$ , $bhage$	compound symmetry	27.4
20	$lbadf$ , $lsib$ , $lret$ , $lage$ , $badf$	compound symmetry	31.5
21	$lbadf$ , $lsib$ , $lret$ , $lage$ , $sib$	compound symmetry	11.3

Growth losses have been very consistent for the range of years and growth periods examined in this permanent plot phase of the Swiss Needle Cast Cooperative Growth Impact Study. Likewise, the losses associated with a given level of initial foliage retention in these four growth periods have been very consistent with the retrospective phase of the Growth Impact study, which examined growth trends prior to 1997 (Maguire et al. 2002). To our knowledge no other links between foliage retention and growth loss have been quantified in other regions of the world where Douglas-fir is grown. Douglas-fir in New Zealand experienced a growth decline attributed to *Phaeocryptopus gaeumannii* starting in 1963, and comparison of pre-1963 to post-1963 growth suggested a growth loss of 26-40%, but foliage retention was not reported (Manley 1985). Cameron et al. (1978) observed that infected trees in Hanmer Forest in New Zealand generally retained 20-30% less foliage than uninfected trees, with 7-yr-old infected trees at Rotorua holding 95%, 43%, 8%, and 0% of 1-4-yr-old needles, respectively.

The trend in declining growth loss over increasing foliage retention has only slight curvature, indicating relatively steady marginal gains in growth per unit increase in foliage retention. Therefore, the curvature is not sufficient to suggest a specific threshold of foliage retention at which growth loss is no longer occurring.

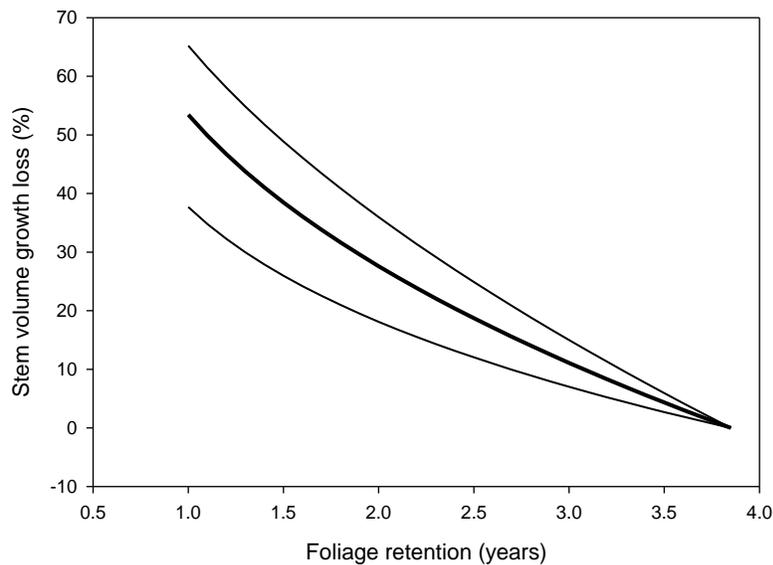


Figure 4. Trends in PAI growth loss predicted from the  $\ln(FR)$  parameter estimate in model [15] (dark line), with bounds on loss implied by adding and subtracting 2 standard errors of the parameter estimate.

Other factors, such as inherent site fertility (Schoettle 1990) and fertilization (Balster and Marshall 2000), have been found to influence needle retention, with needle retention or needle longevity declining with enhanced growth either on more fertile sites or following fertilization (cf. Pensa et al. 2007). Given the opposite trend in growth over foliage retention in north coastal Oregon, it is probably safe to conclude that SNC is the dominant controlling factor on Douglas-fir foliage retention over the relatively narrow age and geographic range sampled.

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# **Three-Year Growth Response of Young Douglas-fir to Nitrogen, Calcium, Phosphorus, and Blended Fertilization Treatments in Oregon and Washington**

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## **Abstract**

Management of forest nutrition in Douglas-fir plantations has predominantly addressed nitrogen limitations, yet growth of Douglas-fir is often unresponsive to nitrogen fertilization. High soil nitrogen availability and harvesting of second and third generation stands has raised the potential for other nutrient limitations, and nutrient imbalances have been hypothesized to predispose young Douglas-fir to Swiss needle cast. Six fertilizer treatments were tested for their ability to improve the growth of dominant and co-dominant trees within young Douglas-fir plantations in western Oregon and Washington. Treatments included a control and applications of urea, lime, calcium chloride, or mono-sodium phosphate on 16 experimental installations. Two additional site-specific blends (Fenn and Kinsey) were applied at 12 of the 16 the installations. Stem volume growth responded positively to urea, lime, and phosphorus treatments. There was no evidence of regional differences in the effect of the blended fertilizers, although marginal regional effects were observed at two of the 12 sites. Volume growth response to nitrogen was negatively correlated with site index and positively correlated with the ratio of soil calcium to soil nitrogen. Growth response to lime was negatively correlated with both initial foliar calcium concentration and soil pH, and growth response to phosphorus was negatively correlated with initial foliar phosphorus concentration and positively with soil pH. Refinements in managing nutrition of Douglas-fir plantations can boost or maintain production, but the viability of specific fertilization regimes will depend on economic and environmental performance.

## **Introduction**

Since the early 1970s, many field trials have been implemented in western North America to assess the benefits of fertilizing Douglas-fir with nitrogen (Miller and Pienaar 1973, Miller and Fight 1979, Peterson et al. 1984, Heath and Chappell 1989, Stegemoeller and Chappell 1990). On average, Douglas-fir responds positively to nitrogen fertilization (Peterson and Hazard 1990), but the magnitude of response depends on such factors as the current site productivity (Edmonds and Hsiang 1987, Miller et al. 1989), the availability of nitrogen (Hopmans and Chappell 1994, Petersen et al. 1984), the degree of crown closure (Barclay and Brix 1985, Stegemoeller and Chappell 1989), the combination of crown size and foliar density (Brix and Ebell 1969, Brix 1983), and the species composition (Miller et al. 1986).

Although the results of this research have motivated nitrogen fertilization of nearly 40,000 ha of timberland each year in Oregon through the 1990s, nutrient pools and availability in intensively managed Douglas-fir plantations have been impacted by harvesting, site preparation,

and other activities that remove biomass, change soil structure, enhance leaching, or promote nutrient volatilization. These activities may lead to large shifts in the relative availability of nutrients, and to tree nutrient imbalances that were not detectable in first generation plantations established after harvesting old-growth, or in naturally regenerated second-growth. These imbalances may predispose trees to various pathogens (Lambert 1986, Turner and Lambert 1986); for example, it has been hypothesized that high nitrogen levels relative to other nutrients may be partially responsible for the current Swiss needle cast (SNC) epidemic along the Pacific Northwest coast (Perakis et al. 2006).

SNC is a foliar disease caused by the endemic fungus *Phaeocryptopus gaeumannii*. Since 1990, SNC has caused significant growth losses, estimated at 400,000 m<sup>3</sup> in 1996 for 10-30 year old plantations in north coastal Oregon (Maguire et al. 2002). Trials conducted to test the efficacy of fertilizer treatments in ameliorating SNC symptoms have used nitrogen fertilizer or fertilizer blends that included nitrogen, and have generally yielded no treatment effect (Weiskittel et al. 2004, Mainwaring et al. 2004, Mainwaring et al. 2005a). The hypothesis that relatively high availability of nitrogen has facilitated the emergence of SNC is supported by the fact that excess nitrogen within needles is often stored as free amino acids (FAA; Turner and Lambert 1986, Näsholm and Ericsson 1990, Ericsson et al. 1995, Kätzel and Löffler 1997), and that these FAA may serve as a primary nutritional source for many foliar fungi (Lambert 1986, Turner and Lambert 1986, Jennings 1995). When Douglas-fir trees with relatively low levels of foliar nitrogen were fertilized with isotopically-labeled urea, *P. gaeumannii* responded to the elevated nitrogen levels with increased fungal fruiting, leading to an increase in disease severity (El-Hajj et al. 2004). Urea nitrogen fertilization continues to be the standard regime in second and third rotation plantations; therefore, research that suggests that excess nitrogen fertilization may exacerbate SNC has prompted reassessment of fertilization regimes (Talbert and Marshall 2005). There is particular interest in attaining balanced nutrition among all macro- and micro-nutrients.

The hypothesis that soil nutrient imbalances cause or contribute to the recent SNC epidemic (Maguire et al. 2000), coupled with the almost exclusive attention given to nitrogen limitations during the last forty years of Douglas-fir fertilization research, has motivated regional managers to re-examine the possibility of other nutrient limitations. In the most recent review of Douglas-fir nutrient research, Walker and Gessel (1991) noted that work on other nutrients is limited and merits further attention.

One study investigating the relationship between SNC symptoms and foliar and soil chemistry along a gradient of SNC disease severity identified consistent positive correlation between foliar retention and foliar calcium, and a negative correlation between foliar retention and foliar nitrogen (Maguire et al. 2000). In the Oregon Coast Range, where SNC severity reaches its peak, soil calcium and nitrogen levels exhibit an inverse relationship, perhaps because naturally high levels of soil nitrogen have resulted in excessive nitrate leaching of base cations (Perakis et al. 2006). Leaching of coastal soils in the Douglas-fir region has contributed to relatively low base saturation, low soil pH, and an abundance of soil aluminum (Meurisse 1972). Management practices that encourage continued accumulation of nitrogen, such as expanding the area of nitrogen-fixing red alder, reducing broadcast burning, and fertilizing Douglas-fir stands with nitrogen, are common, widespread and unlikely to change for the foreseeable future. Because naturally established forests of the Oregon Coast Ranges were already relatively nitrogen-rich systems (Remillard 2000), base cation leaching may be exacerbated by continued

accumulation of N, implying that benefits may be gained from nutrient amendments that counteract this process.

An abundance of aluminum interferes with calcium uptake and transport within plants, causing similarities between symptoms of aluminum toxicity and calcium deficiency (Rengel 1992). Aluminum has been identified as a major inhibitor of forest growth in acidic soils (Cronan et al. 1989), and aluminum-caused calcium deficiency has been a factor linked to the decline of red spruce in the eastern United States (Shortle and Smith 1988). Increases in the ratio of calcium to aluminum ions in soil solution have been found to reduce aluminum toxicity in numerous plant species (Rengel 1992). Similarly, studies on young Douglas-fir seedlings have shown that, under conditions of high aluminum concentration in the growing media, addition of calcium resulted in both increases in root development and root calcium concentration (Ryan et al. 1986, Porada 1987). Calcium fertilization has the potential to ameliorate nutrient imbalances of coastal soils in the Pacific Northwest (PNW) by increasing base cation concentrations, counteracting aluminum toxicity, and increasing soil pH to reduce aluminum solubility.

Increasing soil pH with lime may, under the proper conditions, also increase the quantity of available phosphorus (Haynes 1982). Aluminum has a strong affinity for phosphorus, and the low solubility of aluminum phosphates makes phosphorus less available to plants when aluminum is abundant (McLean 1976). Partly due to the relative abundance of aluminum throughout the Douglas-fir region, regional soils tend to have high phosphorus fixation rates (Meurisse 1972). Such conditions may result in phosphorus limitations to tree growth and reduce the efficacy of phosphorus fertilization. Studies looking at the growth response of Douglas-fir seedlings growing in aluminum rich coastal soils have found a positive response to spot-applied phosphorus fertilizers (Heilman and Ekuan 1980, Porada 1987).

Nitrate-coupled leaching of other nutrients, such as Fe, Mn, Zn, and Cu can also occur where high native soil nitrogen or urea fertilization results in significant nitrification (Otchere-Boateng and Ballard 1981). In addition, high concentrations of aluminum have been found to negatively affect Douglas-fir root morphology (Curt et al. 2001) and successfully outcompete Ca, P, Mg, Fe, and Zn at adsorption sites, thereby limiting uptake of these nutrients (Foy 1984). Relative root growth and root nutrient concentrations of Al, Ca, Mg, Fe, Mn, and Cu declined in Douglas-fir seedlings as pH decreased from five to 3, suggesting that these nutrients may be limiting to growth under acidic conditions (Porada 1987).

Declines in pH due to nitrate-coupled leaching of base cations and associated increases in aluminum interference may be an important mechanism to consider in intensively managed Douglas-fir plantations. A fertilization trial was initiated in 2006, hereafter referred to as the 'Beyond N' fertilization trial, to test the effects of nutrient amendments (including nitrogen fertilization) on sites where nitrogen was presumably not a limiting nutrient. Tree growth and foliage retention (number of annual age classes retained) were the treatment responses of greatest interest. The former response tested the potential of nutrient amendments to enhance growth of young Douglas-fir stands. The latter response tested whether specific nutritional amendments would be effective in diminishing or offsetting the foliar symptoms of SNC.

The specific objectives of this study were to test the following null hypotheses: (1) volume growth does not respond to any of the six nutrient amendments designed to test possible nutrient limitations in Douglas-fir; (2) volume growth response cannot be predicted from initial soil and/or foliar chemistry; (3) response to fertilization is not related to SNC; and (4) nutrient amendments do not change stem form in young Douglas-fir trees.

## Methods

### Study sites

Sixteen study sites were distributed across a range in elevation, aspect, and SNC disease severity in the Oregon and Washington Coast Ranges and west slope of the Cascade Mountains (43.28° to 46.60° N and 122.05° to 124.25° W; Fig. 1). Target stands were 20 years of age, contained 300 (+/- 100) trees per acre, and received no previous thinning or fertilization treatments (Table 1). Because sites were chosen to avoid nitrogen deficiency, site productivity was generally high.



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

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

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

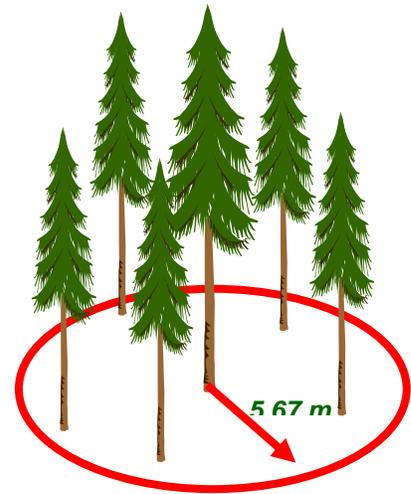


Figure 3. Schematic of the individual tree plot.

## Measurements

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

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

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

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

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

Treatment	Material	Material application rate (kg/ha)	Elemental application rate (kg/ha)
Control	-	0	0
Nitrogen	Urea: (NH <sub>2</sub> ) <sub>2</sub> CO	493	225
Lime	CaCO <sub>3</sub>	2915	1020
Calcium chloride	CaCl <sub>2</sub>	291	105
Phosphorus	Mono-sodium phosphate: NaH <sub>2</sub> PO <sub>4</sub>	2240	580
Kinsey	see Table 3	see Table 3	
Fenn	see Table 4	see Table 4	

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

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

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

Material	WF	CTC	HAGR	STR	GDE	GDH	PB	OSU	ODF	MNN	MNS	HAK	Mean
<b>Fertilizer application rates (kg/ha)</b>													
ESN (slow release N)	534	33	190	155	334	334	190	67	67	601	785	190	290
Potassium magnesium sulfate	637		382	382	764	764	382	255	255	448	240	382	
Gypsum			280	117	700	700	280	351	351	84	534	280	408
Ammonium sulfate		467	47				47					47	51
ZnSO <sub>4</sub>										307	157		
<b>Elemental application rates (kg/ha)</b>													
N	203	111	82	59	127	127	82	25	25	228	298	82	121
K	117	0	70	70	140	140	70	47	47	82	44	70	75
S	140	112	148	106	301	301	148	123	123	176	185	148	168
Ca	0	0	64	27	161	161	64	81	81	19	123	64	70
Mg	70	0	42	42	84	84	42	28	28	49	26	42	45
Zn	0	0	0	0	0	0	0	0	0	124	64	0	17

### Analysis

Four different response variables were analyzed to assess fertilizer treatment effects: 1) three-year basal area growth; 2) three-year height growth; 3) three-year volume growth (Bruce and Demars 1974) and 4) three-year change in form quotient (defined as the ratio of diameter outside bark at a height of 5.5 m to diameter outside bark at 1.3 m). Treatment effects were first tested by analysis of variance under a generalized randomized complete block design. Regression analyses were also performed to correct for several covariates related to initial tree size and local stand density. These covariates included diameter, height, crown ratio, crown base sapwood area, and plot-level basal area. Sapwood area at breast height was computed by assuming a circular stem cross-section, and diameter inside the bark was estimated from diameter outside bark (Larsen and Hann 1985). Sapwood area at crown base was then estimated from an existing sapwood taper function (Maguire and Batista 1996). Tests were considered statistically significant at  $\alpha=0.05$ , and variables were included in the final regression models at this same  $\alpha$ -level. In some cases, where noted, variables with marginal significance ( $0.05 < \alpha < 0.10$ ) were retained in the regression models.

Treatment effects on volume growth were first tested at the regional level. Significant treatment effects were further explored by separately testing for differences in basal area growth, height growth, and form quotient among treatments. The basic statistical model was as follows:

$$[1] \quad Y = \alpha_0 + \alpha_1 I_N + \alpha_2 I_{LIME} + \alpha_3 I_{CaCl} + \alpha_4 I_P + \alpha_5 I_K + \alpha_6 I_F + \alpha_7 X_1 + \alpha_8 X_2 + \dots + \alpha_k X_k + \delta_1 + \varepsilon_1$$

where  $Y$  = stem volume growth, basal area growth, height growth, or change in form quotient  
 $I_N$  = 1 if urea treatment, 0 otherwise  
 $I_{LIME}$  = 1 if lime treatment, 0 otherwise  
 $I_{CaCl}$  = 1 if  $CaCl_2$  treatment, 0 otherwise  
 $I_P$  = 1 if phosphorus treatment, 0 otherwise  
 $I_K$  = 1 in Kinsey regime, 0 otherwise  
 $I_F$  = 1 if Fenn blend, 0 otherwise  
 $X_k$  = kth tree covariate (initial dbh, height, crown ratio, sapwood area, plot basal area)  
 $\alpha_k$  = kth parameter to be estimated from the data  
 $\delta_1$  = random site (block) effect with  $\delta_1 \sim N(0, \sigma_\delta^2)$ .  
 $\varepsilon_1$  = random error term with  $\varepsilon_1 \sim N(0, \sigma_1^2)$ .

All 16 sites were included to test for urea, lime, calcium chloride, and phosphorus fertilization effects, but only 12 sites were available for testing the Kinsey regime and Fenn blend. Replication within sites allowed for identification of site-specific treatment effects. The form of the statistical model was the same as equation [1] above with the random site effect removed. When significant treatment effects are identified at the regional level, but these effects vary among sites, it is helpful to develop a system for discriminating among responding and non-responding sites. Stated differently, greater efficiencies in forest management can be gained by developing site-specific silvicultural prescriptions. Toward this end, additional regional analysis was performed on volume growth responses by replacing site or block effects with attributes that can be measured or estimated at a given site, for example, site index, soil variables or foliar nutrient status. The following statistical model was applied to each of the specific treatments separately to identify important predictors of response to fertilization:

$$[2] \quad \Delta V = \beta_0 + \beta_1 I_f + \beta_2 X_1 + \beta_3 X_2 + \dots + \beta_k X_k + \beta_{k+1} Z_1 + \beta_{k+2} Z_2 + \dots + \beta_{k+j} Z_m + \varepsilon_2$$

where  $Y$  = stem volume growth, basal area growth, height growth, or change in form quotient  
 $I_f$  = 1 if fertilized treatment, 0 otherwise  
 $X_k$  = kth tree covariate (initial dbh, height, crown ratio, sapwood area, plot basal area, etc.)  
 $Z_{k+j}$  = jth site covariate (site index, soil variable, foliar chemistry, etc.)  
 $\beta_k$  = kth parameter to be estimated from the data  
 $\varepsilon_2$  = random error term with  $\varepsilon_2 \sim N(0, \sigma_2^2)$ .

As one final step in the analysis, the random block effect was tested after developing the best possible regression model based on site-level covariates. This test assessed the efficacy of covariates in accounting for block or site effects, and the potential for site variables to predict the magnitude of the response to fertilization. As indicated in the following equation, this final model simply re-introduced the random site or block effects into equation [2]:

$$[3] \Delta V = \gamma_0 + \gamma_1 I_f + \gamma_2 X_1 + \gamma_3 X_2 + \dots + \gamma_k X_k + \gamma_{k+1} Z_1 + \gamma_{k+2} Z_2 + \dots + \gamma_{k+j} Z_m + \delta_3 + \varepsilon_3$$

- where
- Y = stem volume growth, basal area growth, height growth, or change in form quotient
  - I<sub>f</sub> = 1 if fertilized treatment, 0 otherwise
  - X<sub>k</sub> = kth tree covariate (initial dbh, height, crown ratio, sapwood area, plot basal area, etc.)
  - Z<sub>k+j</sub> = jth site covariate (site index, soil variable, foliar chemistry, etc.)
  - γ<sub>k</sub> = kth parameter to be estimated from the data
  - δ<sub>3</sub> = random site (block) effect with  $\delta_3 \sim N(0, \sigma_{\delta_3}^2)$ .
  - ε<sub>3</sub> = random error term with  $\varepsilon_3 \sim N(0, \sigma_{\varepsilon_3}^2)$ .

## Results

### *Regional volume growth*

When data from all sixteen sites were analyzed under a generalized randomized complete block experiment, the treatment effect on regional volume growth was marginally significant (p=0.0578). Site or block effects were highly significant (p<0.0001), indicating significant variation in stem volume growth among the 16 sites. Multiple comparisons indicated that volume production was significantly improved by urea (p=0.0065), lime (p=0.017), and phosphorus fertilization (p=0.033), and was marginally greater after application of calcium chloride (p=0.084). On the twelve sites receiving a site-specific Kinsey regime or Fenn blend, no treatment effects were detected (p=0.79).

When tree-level covariates (dbh, crown ratio, height, and plot basal area) were added to the volume growth analysis, stem volume growth increases following urea (p=0.0829) and lime (p=0.0948) were marginally significant, though phosphorus treatment effects were not (p=0.139). For urea and lime, these marginal responses corresponded to an average volume growth increase of 3.5 and 3.3% respectively (Fig. 3).

Block x treatment interaction effects were not statistically significant (p=0.48), though there was site-specificity in responses to at least some of the treatments. Site specific analysis of covariance tests indicated that volume growth increased significantly following nitrogen treatment at two sites (CTC, WW), calcium chloride treatment at one site (WE), and phosphorus treatment at three sites (CTC, MNS, and WE) (Table 5).

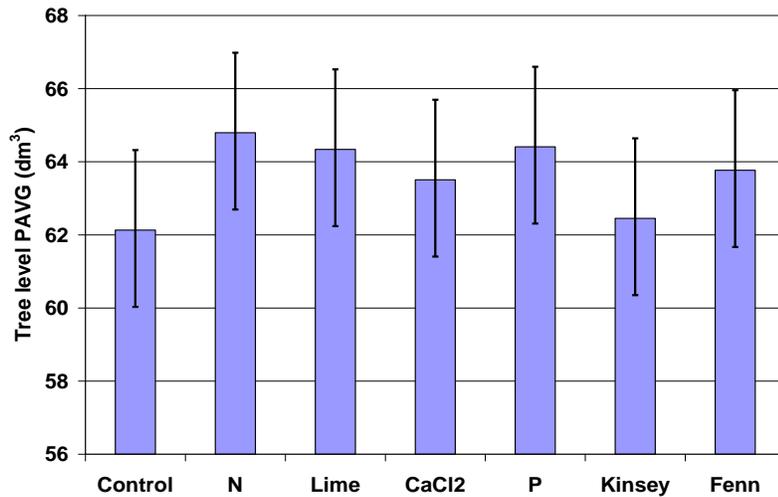


Figure 3. Mean tree-level periodic annual volume increment, assuming mean values for diameter, height, crown ratio and plot basal area.

Table 5 Volume growth response to fertilizer treatments. Dark shaded boxes refer to significant ( $p < 0.05$ ) responses. Light shaded boxes refer to marginally significant responses ( $0.05 < p < 0.10$ ).

	N	Lime	CaCl <sub>2</sub>	Phos	Kinsey	Fenn	R <sup>2</sup>
<b>CTC</b>	<b>32</b>	9	14.7	<b>18.9</b>	12.5	2.3	0.54
<b>GDE</b>	12.4	4.7	11.7	-4.9	4	<b>15.7</b>	0.68
<b>GDH</b>	-11.3	4.4	-3.8	-8.5	-7.3	-10.1	0.58
<b>GPH</b>	6.1	3.2	7.3	3.9			0.48
<b>HAGR</b>	-3.7	0.8	-11.7	3.7	-1.6	1	0.54
<b>HAK</b>	-1.1	-5.2	4.9	-1.4	-0.8	1.9	0.6
<b>LRT</b>	0.2	-1.5	-8.4	-3.4			0.63
<b>MNN</b>	-7.6	8.1	6.8	1.8	-11.9	0.5	0.53
<b>MNS</b>	7.1	12.6	-10	<b>18.5</b>	5.7	8.7	0.59
<b>ODF</b>	-1.9	-1.5	-5.3	<b>12.5</b>	7.3	6.6	0.54
<b>OSU</b>	0.1	7.5	7.1	6.6	6.4	8.1	0.54
<b>PB</b>	-5.6	-0.5	5.8	7.3	-2.5	1.9	0.43
<b>STR</b>	0.7	-10.7	-3.6	3.6	-8	-5.7	0.67
<b>WE</b>	3.5	<b>16.2</b>	<b>20</b>	<b>22.7</b>			0.62
<b>WF</b>	5.9	-8.9	-10.4	-7.3	5.7	4.1	0.52
<b>WW</b>	<b>23.9</b>	16.7	10.8	-2.2			0.58

### **Regional basal area growth**

When data from all sixteen sites were analyzed under a generalized randomized complete block experiment, the treatment effect on regional basal area growth was significant ( $p=0.0098$ ). Site or block effects were highly significant ( $p<0.0001$ ), indicating substantial variation in basal area growth among the 16 sites. Multiple comparisons indicated that basal area growth was significantly improved by urea ( $p=0.0007$ ), lime ( $p=0.01$ ), and phosphorus fertilization ( $p=0.01$ ), and was marginally greater after application of calcium chloride ( $p=0.085$ ) and the Fenn blend ( $p=0.067$ ).

The regional basal area growth analysis that included tree-level covariates (dbh, crown ratio, height, and plot basal area) suggested that basal area growth was significantly improved by urea ( $p=0.0024$ ), and marginally improved by lime ( $p=0.065$ ) and phosphorus ( $p=0.063$ ), corresponding to an average basal area growth increases of 8.1, 5.1, and 5.2%, respectively.

Block x treatment interaction effects were not statistically significant ( $p=0.74$ ), although there was site-specificity in responses to at least some of the treatments. Site specific analysis of covariance tests indicated that basal area growth increased significantly following nitrogen treatment at two sites (CTC, WW), phosphorus treatment at one site (MNS), Kinsey treatment at one site (WF), and Fenn treatment at one site (GDE) (Table 6).

*Table 6. Basal area growth response to fertilizer treatments (%). Bold text refers to significant responses ( $p < 0.05$ ). Italicized text refers to marginally significant responses ( $0.05 < p < 0.10$ ).*

	<b>N</b>	<b>Lime</b>	<b>CaCl<sub>2</sub></b>	<b>Phos</b>	<b>Kinsey</b>	<b>Fenn</b>	<b>R<sup>2</sup></b>
<b>CTC</b>	<b>29</b>	18.4	<b>21.2</b>	8.9	4.9	15.3	0.31
<b>GDE</b>	20.8	6.6	14.1	7.6	7.1	<b>30</b>	0.55
<b>GDH</b>	-5.4	5.3	7	-5.9	-3.9	-20.5	0.43
<b>GPH</b>	17.2	5.6	12.8	5.2			0.46
<b>HAGR</b>	7.8	16	-3.6	15.9	9.5	-2.3	0.5
<b>HAK</b>	-1.3	-7.5	3.7	-4.6	-6.9	5.6	0.36
<b>LRT</b>	3.1	-7.6	-11.8	-3.1			0.51
<b>MNN</b>	-0.9	4.1	6.7	12	-8	-5.8	0.37
<b>MNS</b>	13.2	21.1	<b>-19.7</b>	<b>31.4</b>	5.1	9.3	0.46
<b>ODF</b>	7.3	-1.9	-8.1	<b>22.6</b>	10.5	8.2	0.39
<b>OSU</b>	4.8	11.2	11	9.2	12.9	10.4	0.34
<b>PB</b>	3.7	1	12.3	-1.9	-4.5	8.1	0.36
<b>STR</b>	0.1	-11.2	-7.8	-4.9	-11.4	-5.7	0.4
<b>WE</b>	8.2	12.3	<b>22</b>	15.8			0.39
<b>WF</b>	8.8	-7.7	-10	-9.4	<b>24.1</b>	1.4	0.47
<b>WW</b>	<b>28</b>	11.5	6.6	-10.6			0.32

### **Regional height growth**

When data from all sixteen sites were analyzed under a generalized randomized complete block experiment, the treatment effect on regional height growth was not significant ( $p=0.81$ ). Site or block effects were highly significant ( $p<0.0001$ ), indicating considerable variation in height growth among the 16 sites. Treatment differences remained insignificant after the addition of tree-level covariates.

Block x treatment interaction effects were statistically significant ( $p=0.04$ ), indicating that there was site-specificity in responses to at least some of the treatments. Site specific analysis of covariance tests indicated that height growth increased significantly following nitrogen treatment at two sites (CTC, WW), phosphorus treatment at two sites (CTC and WE), and Kinsey treatment at one site (CTC) (Table 7).

*Table 7. Height growth response to fertilizer treatments (%). Dark shaded boxes refer to significant ( $p < 0.05$ ) responses. Light shaded boxes refer to marginally significant responses ( $0.05 < p < 0.10$ ).*

	<b>N</b>	<b>Lime</b>	<b>CaCl<sub>2</sub></b>	<b>Phos</b>	<b>Kinsey</b>	<b>Fenn</b>	<b>R<sup>2</sup></b>
<b>CTC</b>	<b>39.4</b>	11.9	12	<b>37.8</b>	<b>33.6</b>	-6.4	0.2
<b>GDE</b>	5.5	7	15.2	-12.2	4.1	6.8	0.15
<b>GDH</b>	-15.9	3.4	-8	-13	-1.6	-1.3	0.1
<b>GPH</b>	-6.3	0	-0.3	2.9			0.03
<b>HAGR</b>	<b>-13.2</b>	-11.1	-15.5	-3.9	-8.8	2.6	0.09
<b>HAK</b>	-7	-6.4	1.1	-8.8	-4.3	-2.4	0.14
<b>LRT</b>	0	6.8	-5.9	-0.6			0.04
<b>MNN</b>	-7.8	6.6	4.3	-10.8	-18	6.3	0.15
<b>MNS</b>	2.2	2.6	-2.7	2.8	5.5	3.7	0.02
<b>ODF</b>	-9.5	-2.2	-2.3	-3.2	3.3	9.5	0.14
<b>OSU</b>	-3.8	0.4	0.6	0.4	-4.2	4.3	0.05
<b>PB</b>	-19.3	-2	-12.8	17.4	1.1	-3.2	0.12
<b>STR</b>	-0.4	-7.5	-2.3	4	-7.9	<b>-14.1</b>	0.1
<b>WE</b>	2.5	<b>16.5</b>	13.7	<b>21.2</b>			0.14
<b>WF</b>	0.2	-7.9	<b>-13.7</b>	-8	-10.7	2.6	0.11
<b>WW</b>	<b>23.8</b>	6.1	<b>9.7</b>	-1.8			0.17

### **Regional change in form quotient**

When data from all sixteen sites were analyzed under a generalized randomized complete block experiment, the treatment effect on form quotient was not significant ( $p=0.3$ ), but site effects were highly significant ( $p<0.0001$ ). Multiple comparisons indicated that the change in form quotient was marginally lower following phosphorus treatment ( $p=0.06$ ). After addition of tree level covariates (height, crown ratio), the change in form quotient following phosphorus fertilization ( $p=0.027$ ) was significant and negative.

Block x treatment interaction effects were not statistically significant ( $p=0.60$ ), although there was site-specificity in responses to at least some of the treatments. Site specific analysis of covariance tests indicated that the change in form quotient decreased significantly following phosphorus treatment at one site (ODF, Table 8).

Table 8. Change in form quotient by fertilizer treatment.

	N	Lime	CaCl <sub>2</sub>	Phos	Kinsey	Fenn	R <sup>2</sup>
<b>CTC</b>	-0.0052	-0.0058	0.0079	-0.0006	0.0069	0.0058	0.22
<b>GDH</b>	0.001	<b>-0.0101</b>	-0.0094	-0.0127	0.0042	0.0001	0.2
<b>GPH</b>	-0.0069	-0.0064	-0.0015	-0.0052			0.09
<b>HAGR</b>	0.0111	0.0115	0.0026	0.0069	0.0063	0.0131	0.07
<b>HAK</b>	0.0037	-0.0017	-0.0048	-0.0042	0.0013	-0.0009	0.06
<b>LRT</b>	-0.0037	0.0045	0.0137	-0.0081			0.32
<b>MNN</b>	-0.011	-0.0051	0.0008	0.0037	-0.0016	0.0004	0.31
<b>MNS</b>	0.0009	0.0084	0.0027	-0.0026	-0.006	-0.006	0.17
<b>ODF</b>	-0.0098	-0.0066	<b>-0.0113</b>	<b>-0.0221</b>	<b>-0.0117</b>	-0.0091	0.32
<b>OSU</b>	0.0025	-0.0007	-0.0042	-0.0028	-0.0003	-0.0006	0.14
<b>PB</b>	-0.0032	-0.0069	-0.0093	0.0023	0.0096	-0.0081	0.2
<b>STR</b>	-0.0074	0.0026	0.0012	-0.0016	-0.0022	0.0022	0.2
<b>WE</b>	-0.0013	-0.0033	-0.0091	<b>-0.017</b>			0.21
<b>WF</b>	-0.0027	0.0081	0.0038	0.0031	-0.0029	0.0073	0.14
<b>WW</b>	-0.0072	0.0065	-0.0044	-0.0029			0.14

### Volume growth as characterized by site

When interactions between volume response site factors, such as site index and variables representing various soil and foliar nutrient concentrations, were tested using equation [2], the significance of explanatory variables depended on treatment type.

The regional response to nitrogen treatment was found to depend on either the soil calcium: soil nitrogen ratio (sCa/sN) ( $R^2=0.748$ , Fig. 4) or site index ( $R^2=0.709$ , Fig. 5). After accounting for the effects of initial diameter, height, and crown-base sapwood area, and site index, growth response to nitrogen fertilization was negligible or even negative if the soil calcium: nitrogen ratio was  $\leq 0.6$ . At sites with high soil calcium: nitrogen ratio, the maximum volume growth response was  $\sim 15\%$ . Average volume growth response to nitrogen fertilization was positive until site index exceeded 49 m in 50 years (Fig. 5).

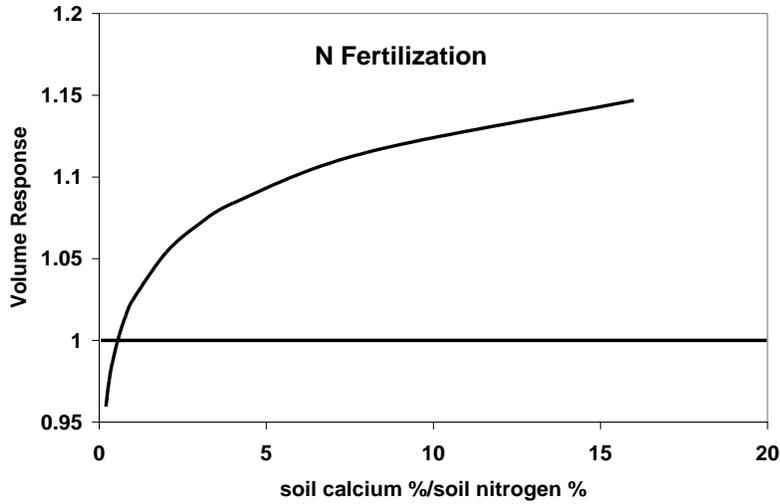


Figure 4. Volume response to nitrogen fertilization versus soil calcium: nitrogen ratio.

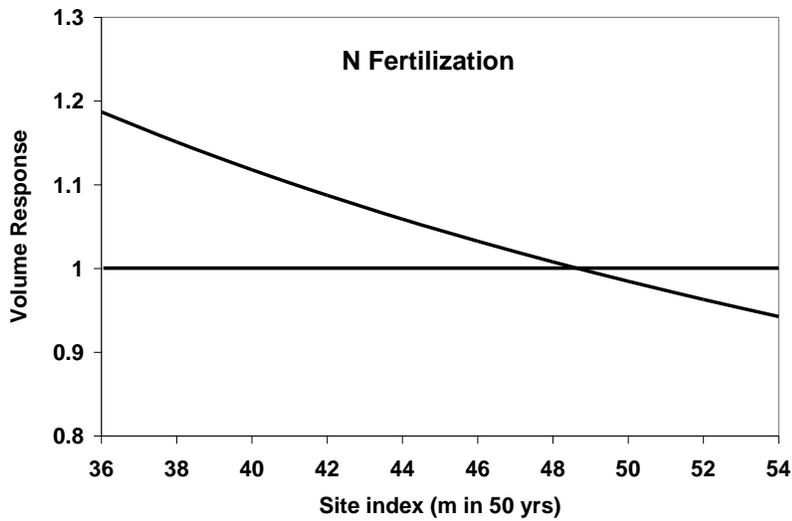


Figure 5. Volume response to nitrogen fertilization versus site index.

Volume growth response to lime application was positively correlated with initial soil pH and negatively correlated with initial foliar calcium concentration (Fig. 6). A model that included these variables, in addition to tree diameter, height, crown-base sapwood area, site index and soil Ca/N, explained approximately 75% of the variation in response to lime application ( $R^2=0.759$ ). Volume response to calcium chloride was also positively associated with pH and negatively correlated with soil Ca/N ( $R^2=0.743$ , Fig. 7).

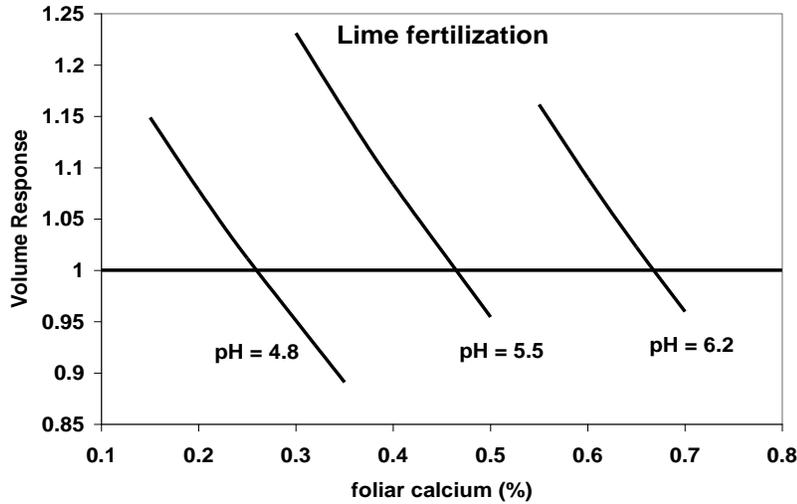


Figure 6. Volume response to lime application at various levels of initial soil pH.

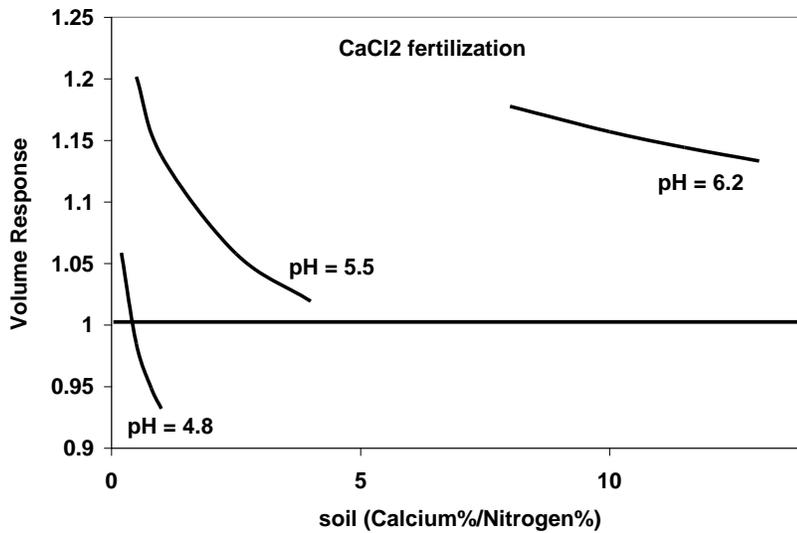


Figure 7. Volume response to  $CaCl_2$  fertilization versus foliar calcium: nitrogen ratios at various levels of initial soil pH.

Volume response to phosphorus fertilization increased as initial foliar phosphorus concentration declined and as soil pH increased (Fig. 8). The regression model that included these variables, in addition to dbh, height, crown-base sapwood area, site index, and initial foliar calcium, explained 74% of the variation in volume growth response ( $R^2=0.741$ ). The interaction between soil pH and foliar phosphorus suggested that growth response fell to negligible levels when foliage phosphorus concentration exceeded 0.18%, at all levels of soil pH (Fig. 8).

Volume response to the Kinsey treatment also depended on foliar phosphorus, soil pH, and their interaction in a model that included dbh, height, crown-base sapwood area, site index, and soil Ca/N ( $R^2=0.633$ ). As with the phosphorus fertilization, the increase in volume growth response over initial soil pH increased rapidly as foliar phosphorus decreased (Fig. 9). On these study sites, it was inferred that growth responses were near zero when initial foliar phosphorus exceeded approximately 0.17%, regardless of initial soil pH.

There was a marginally significant volume growth response to the Fenn treatment ( $p=0.0805$ ) after accounting for diameter, crown-base sapwood area, site index, foliar calcium concentration, and soil calcium: nitrogen ratio ( $R^2=0.607$ ). However, the implied volume growth response was 4.6%.

Addition of the random block effect to these regional regressions (equation [3]) increased the amount of variation explained by the model and generally made the site-level covariates insignificant, suggesting a multicollinearity between explanatory variables. Extra sums of squares F-tests revealed that the full models were better fits to the data.

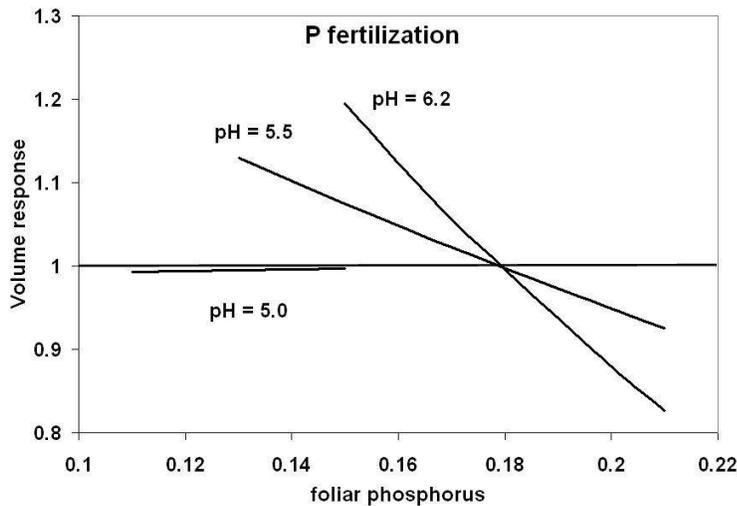


Figure 8. Volume response to Phosphorous fertilization versus foliar phosphorus at various levels of initial soil pH.

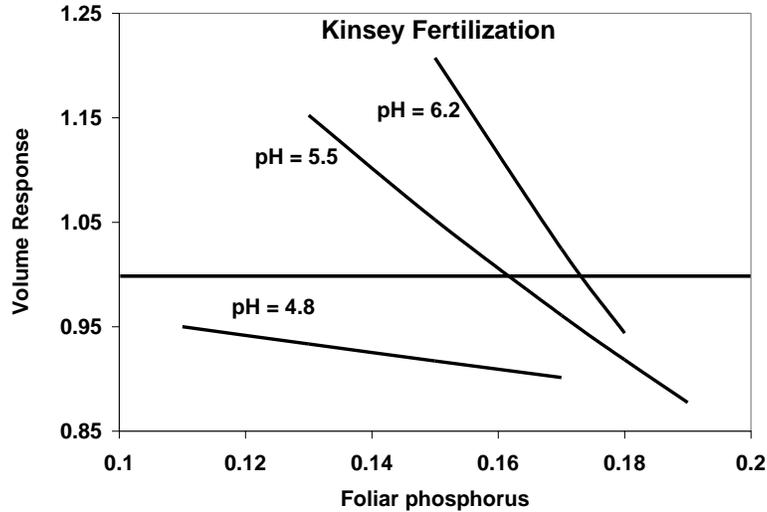


Figure 9. Volume response to Kinsey fertilization versus foliar phosphorus at various levels of initial soil pH.

## Discussion

In western Oregon and Washington, growth responses of Douglas-fir to nitrogen fertilization have been shown to average about 4 m<sup>3</sup>/ha/yr for 4 years after application (Peterson and Hazard 1990). The Beyond N fertilization trials targeted stands with relatively high nitrogen availability, and, therefore, reasonable potential for limitations in other nutrients. Regardless, volume growth responded most strongly to nitrogen fertilization, but also to lime and phosphorus additions. Height growth and basal area growth responses were inconsistent, perhaps due to site or stand structural differences. Of the sites that received nitrogen, only two sites (CTC and WW) exhibited both height and basal area growth responses that were significant over the initial 3-yr growth period. All other volume growth responses resulted from either significant height growth response or significant basal area growth response, and apparently not from the combination of height and basal area growth response.

Although all of the sites in this study were chosen to be relatively nitrogen-rich to determine which nutrients may be limiting when nitrogen is abundant, the WW site was an exception by having low initial foliar nitrogen concentration averaging 1.16%. The other site that experienced significant growth response (CTC) had an average initial foliar nitrogen concentration of 1.31%. The threshold concentration of nitrogen deficiency for Douglas-fir has been identified as 1.45% (Ballard and Carter 1986), and nine of the 16 sites had nitrogen concentrations below this level (av. =1.28%). Nevertheless, while foliar N% has been a useful predictor of response to nitrogen fertilization in some cases (Hopmans and Chappell 1994, Carter et al. 1998), significant variation in response remains at a given foliar nitrogen concentration, perhaps because nitrogen concentration does not incorporate other metrics of plant performance, such as leaf area index (LAI) or total canopy nitrogen (Brix 1983, Vose and Allen 1988, Albaugh et al. 1998).

Site index has previously been correlated with response to nitrogen fertilization (Miller et al. 1989, Carter et al. 1998), leading to the general conclusion that growth response to

fertilization is greatest on sites of low to medium productivity (Heath and Chappell 1989, Peterson and Hazard 1990). With the exception of one site with severe SNC, the sites that experienced the greatest volume growth response to nitrogen fertilization in the Beyond N study had the lowest site indices of all sites (36.2 and 41.8 m in 50 yrs). Site indices are based on tree height at age 50, and it is likely that the severely diseased site that did not respond to fertilization had an artificially low site index due to height growth losses associated with disease. Nevertheless, regionally, these site indices would not be considered low.

An inverse relationship was previously identified between soil calcium and soil nitrogen in the Oregon Coast Range (Perakis et al. 2006). This negative correlation was attributed to inherently high 0-10 cm soil nitrogen concentrations (avg. soil N=0.56%) and relatively rapid nitrate leaching that can result in low base cation concentrations and a low soil calcium: nitrogen ratio. The same inverse relationship between soil calcium and nitrogen was observed across the Beyond N study sites, and sites farther from the coast (> 30km) had lower levels of soil nitrogen (avg. 0.23% ;stdev=0.07). However, the greatest increase in volume growth response across the gradient of soil Ca/N occurred near the coast, where the soil nitrogen gradient was steepest. Nevertheless, soil nitrogen alone was not a significant predictor of stem volume growth response to nitrogen fertilization.

Douglas-fir stands on sites with low soil calcium: nitrogen ratios tend to have more severe SNC symptoms (Maguire et al. 2000). Of the two sites exhibiting a significant volume response to nitrogen treatment, one had low 2006 foliage retention (2.28 yrs), suggesting significant impacts from SNC. However, the two year old needles from this site show little evidence of stomatal occlusion by pseudothecia, so the low foliage retention at this site may have been related to the high water table and poor drainage class of the soil (Bond-Lamberty et al. 2002).

Previous studies with Douglas-fir seedlings have shown a positive growth response to liming (Heilman and Ekuan 1973, Littke and Zabowski 2007). Results from the Beyond N trials indicate that at a given pH, volume growth response to liming is expected to be greater for a tree with a low foliar calcium concentration. Likewise, for a given foliar calcium concentration, average growth response to calcium addition increases with soil pH. Because calcium availability generally increases with pH, the low calcium concentration at a relatively high pH suggests that some sites have inherently low soil calcium availability. At low pH levels, the increased volume growth response at low foliar calcium concentrations may be related less to calcium deficiency and more to mitigation of aluminum toxicity, as shown by Porada (1987) in Douglas-fir seedlings, particularly given the similarity in the symptoms (Rengel 1992).

In the case of calcium chloride application, growth response also depended on soil pH, but in combination with soil calcium: nitrogen ratio, rather than foliar calcium concentration. This response requires a slightly different explanation than the mechanism driving response to liming, though soil Ca/N and foliar calcium were highly correlated ( $R^2=0.89$ ). The implied negative response to calcium application as pH decreased, whether the calcium was applied as lime or calcium chloride, is particularly vexing. In prior studies, though not necessarily in Douglas-fir, it has been proposed that this phenomenon may be due to reduced uptake of other nutrients such as metals (Brallier et al. 1996, Ljungstrom and Nihlgard 1995, Islam et al. 1980), to adverse changes in soil chemistry in the period immediately after lime application (Ingerslev 1997), or to negative effects on fine root growth (Perrson and Ahlstrom 1990). Because these negative effects are primarily the result of changes in pH, they should apply only to the lime treatment. Nevertheless, the positive linear relationship between volume growth response to

lime and volume growth response to calcium chloride suggests that the mechanisms driving these growth responses may be similar (Fig. 10). The additional implication that, where calcium deficiencies exist, short term growth may be improved with calcium applications other than lime, is operationally preferable due to the smaller quantity of material applied. However, long-term effects of the two treatments are unlikely to be similar.

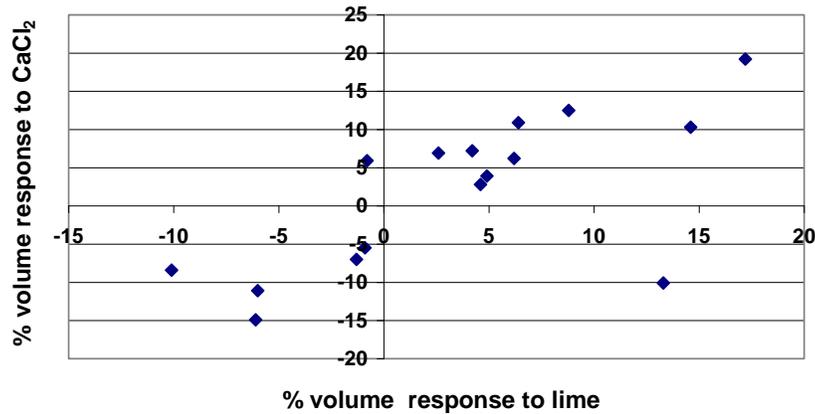


Figure 10. Correlation between volume growth response to lime and response to calcium chloride.

The implied responsiveness of trees with high initial foliar calcium to calcium fertilization was unexpected. The lowest calcium concentration found in the Beyond N dataset was 0.14%, suggesting a slight to moderate deficiency according to standards established by Ballard and Carter (1986) and by Walker and Gessels (1991). However, it may be significant that these deficiency thresholds were partially based on seedling studies (Ballard and Carter 1986). Also, calcium is known to be relatively immobile in plants (Marschner 1995), and, in mature trees, is concentrated in older foliage deep in the crown (Lavender and Carmichael 1966, Mainwaring and Maguire 2008). In contrast, foliage samples for the Beyond N study were collected from young needles relatively high in the crown. Comparisons between sampled foliage concentrations and published deficiency levels for a nutrient with such high within-crown variability are problematic.

In studies looking at Douglas-fir response to added P, positive responses have been common for seedlings (Heilman and Ekuan 1980, Van Den Driessche 1984) but generally not for larger trees (Radwan et al. 1991). In the case of the larger trees studied by Radwan et al. (1991), the initial foliar P concentration (0.12%) was less than the threshold for deficiency (P=0.15% (Ballard and Carter 1986), but the initial soil pH was less than five. The lack of growth response to phosphorus fertilization observed in the Beyond N trials agrees with the lack of response observed by Radwan et al. (1991). A similar lack of stem growth response to phosphorus fertilization was recorded for nitrogen and phosphorus fertilized trees in the Washington Cascade Range (Steinbrenner 1981), but initial foliar phosphorus and soil pH were not provided.

Over the range of data in the Beyond N trials, the growth response to phosphorus fertilization at a given pH improved as initial foliar phosphorus concentration decreased. Positive growth responses to phosphorus, however, were limited to plots where the soil pH exceeded five. Phosphorus becomes increasingly unavailable as pH decreases (Brady 1990), and

results from the Beyond N trials indicate that large additions of phosphorus were not sufficient to overcome low phosphorus availability at low soil pH. At higher initial soil pH, low foliar phosphorus concentrations suggest that phosphorus uptake is limited more by low soil phosphorus content than by low availability induced by soil acidity. Positive growth response to phosphorus fertilization can also result from the precipitation of aluminum and the associated reduction in aluminum toxicity (Haynes 1982).

Parameter estimates in the regression equation describing the volume growth response to the Kinsey treatment were nearly identical to those in the equation for phosphorus growth response, with all interactions behaving similarly. In the short term, therefore, response to the Kinsey treatments may be driven by an increase in phosphorus availability from phosphorus added as a component of the blend, by an increase in phosphorus made available by the lime-fueled increase in pH, or by a decrease in aluminum toxicity after phosphorus-induced precipitation of aluminum. The volume growth response to phosphorus fertilization at low initial foliar concentrations of phosphorus (0.12%) was nearly identical for the Kinsey and phosphorus treatments. Short-term responses to the Kinsey regime likely depended on more than just the added P, as evidenced by the notable difference in the quantities of phosphorus added in the Kinsey regime versus the phosphorus fertilization. The large quantity of phosphorus used in the phosphorus fertilization treatment (580 kg/ha) was designed to ensure that the massive dose of phosphorus could overcome the phosphorus-binding capability of these soils and be made available to the tree. Furthermore, broadcast application of the relatively fine-textured monosodium phosphate by hand resulted in some patchiness that imitated banding application, which is common practice in agricultural applications. In contrast, each of the Kinsey applications entailed 280 kg/ha of mono-ammonium phosphate (75 kg/ha of P) which was relatively easy to spread evenly. These results suggest that growth response to phosphorus fertilization on soils of pH > five may be achievable with significantly less phosphorus than was applied in the phosphorus treatment. However, for soils with pH < 5.0, it remains unclear whether higher levels of phosphorus addition (> 580 kg P / ha) are needed to overcome sorption and elicit a tree growth response.

Growth responses to the Fenn blend were not correlated with any specific site factors, and amounted to a marginally significant 4.6% growth increase. This small magnitude of a response and marginal significance lends only weak appeal to this treatment. A larger growth response of significant duration would be necessary to make the Kinsey or Fenn treatments economically viable. These treatments are relatively expensive due to the costs associated with determining site-specific prescriptions, mixing relatively small amounts of these prescribed blends, and applying large quantities of material per unit area. On the other hand, more time may be necessary to observe the full growth responses and economic returns on these treatments.

In general, foliage retention was not a significant covariate in the regression models. When retention was significant, the parameter estimate almost always indicated diminished growth response with greater initial foliage retention. This trend was consistent with a decline in foliage longevity along gradients of increasing fertility (Li et al. 2006, Pensa et al. 2007), and after nitrogen fertilization (Brix 1981, Balster and Marshall 2000). In areas with severe SNC symptoms, these trends are reversed by premature loss of foliage, the primary symptom of the disease, and associated growth losses (Maguire et al. 2002). Therefore, regional volume growth responses were not dependent on foliage retention as a symptom of SNC in the dominant trees serving as experimental units in the Beyond N trials. However, the strong negative correlation between foliage retention and foliage nitrogen concentrations in regions impacted by SNC argues

strongly against the use of nitrogen fertilization as an amelioration measure for SNC. Alternatively, calcium or phosphorus fertilization may be beneficial where the combination of foliar nutrient concentrations, soil pH or soil calcium: nitrogen ratio suggests potential for a positive response. The potential benefits of these fertilization treatments for ameliorating SNC are unknown, although, in the short term, the negative correlation between soil pH and SNC severity suggests limited potential. In the short term, Douglas-fir was not responsive to either calcium or phosphorus fertilization on sites with low pH, but if pH increases over the long term in response to these treatments, the long term growth responses may also change.

Previous studies looking at the effect of fertilization on taper have reported results similar to those found in the Beyond N study, including nitrogen- and phosphorus- fertilized slash pine (Jokkela et al. 1989), nitrogen-, phosphorus-, and blend-fertilized Norway spruce (Mead and Tamm 1988), and nitrogen-fertilized Douglas-fir (Mitchell and Kellogg 1972). Declines in taper have been reported for nitrogen-fertilized Scots pine (Valinger 1992) and sulfur-treated and blend-fertilized Douglas-fir (Younger 2008). In another study, in which nitrogen fertilization resulted in significant increases in leaf area and volume growth, no effect of fertilization on taper was detected (Brix 1993). Nearly all of the treatments exhibiting a significant volume growth response in the present study followed this latter pattern. In general, treatment effects on stem form depend on stand age, density, and time since treatment (Larson 1963). The significant negative effect of phosphorus on form quotient suggests that the marginally positive volume growth associated with phosphorus fertilization may be more apparent than real. If the form quotient is decreasing, dbh growth is relatively greater than upper stem growth, implying that diameter growth is occurring low in the stem, but not necessarily high in the stem.

In the absence of other silvicultural treatments, the effect of fertilization on stem form is primarily the result of changes in foliar quantity and distribution (Brix and Ebell 1969, Brix 1981, Kershaw and Maguire 1995), changes in crown geometry (Kershaw and Maguire 1995, Weiskittel et al. 2007), and shifts in photosynthate allocation patterns. Fertilization may induce the same effects as higher site quality, with reduced investment in belowground components due to greater nutrient availability (Keyes and Grier 1981, Gower and Vitousek 1989). Alternatively, stem form may change in a way that allows the tree to deal with new biomechanical stresses caused by greater foliage mass (Petty and Swain 1985, Morgan and Cannell 1994, Dean et al. 2002). The relative effect of each of these factors will depend upon the time since treatment, initial stand structure, and the duration of direct treatment effects. Most studies assessing the effect of silvicultural treatment on tree taper focus on thinning. Decreases in stand density result in increased wind speed and tree sway, which cause responsive reallocation of photosynthate towards stem thickening near the base (Larson 1965, Mitchell 2000). While such stand density reductions did not take place in this study, positive responses to fertilization are, to a large extent, a result of increases in crown densification and foliar mass (Brix and Ebell 1969, Brix 1981), which also result in increased tree sway, bending moment, and stem growth (Dean 2004). Any such increases in foliar mass might be especially important in SNC-diseased stands, where tree crowns would initially be most sparse (Maguire and Kanaskie 2002). This response of foliage mass may explain why changes in form quotient were negative following lime,  $\text{CaCl}_2$ , and phosphorus treatments at the most heavily SNC-diseased site (GDH).

Studies conducted in young Douglas-fir stands using a thinning/nitrogen fertilization factorial design have concluded that increases in needle mass are greatest in the top half of the crown with fertilization, and in the bottom half of the crown with thinning (Brix 1992).

However, needle loss from SNC is typically most severe in the top of the crown, where infection dynamics and physical factors make needle loss more prevalent (Hansen et al. 2000). Even in the most heavily impacted stands, needle retention may be relatively high in the lower canopy due to the fact that it is relatively protected from wind and that canopy light penetration is improved due to sparse upper crowns, enabling shade intolerant Douglas-fir needles to persist in the lower crown. If densification of the crown following fertilization of SNC-diseased trees is primarily limited to the lower portions of the crown, it is likely to exacerbate the tendency of infected trees to produce significant taper (Weiskittel et al. 2007).

## **Conclusions**

- 1) On the regional level, average response to nitrogen was the greatest among all of the fertilizers used in this study, though this response was primarily driven by a small number of the sixteen sites. Site-level covariates suggest that the most effective returns from nitrogen fertilization are on sites with moderate site indices and where the soil Ca: nitrogen ratio exceeds five.
- 2) Phosphorus fertilizers can be effective in increasing the growth of Douglas-fir in stands where there is a combination of low foliar phosphorus (<0.18%) and soil pH greater than five. The relationship between phosphorus response and pH suggests that calcium-based phosphorus fertilizers may be most appropriate.
- 3) Three years into this study, these fertilization treatments do not appear to have improved the growth of SNC-diseased trees. Likewise, it is possible that SNC disease and associated foliage loss prevents trees from responding positively to nutrients that might otherwise limit growth. Results from this study suggest that Douglas-fir does not generally respond to these fertilizers where soils are high in nitrogen or low in calcium or pH, all common characteristics of the soils where SNC is especially a problem. Whether such soil conditions are themselves an exacerbating factor of SNC is unknown.
- 4) The positive correlations found between response to fertilization and pH suggests that treatments that increase soil pH may have positive benefits for Douglas-fir. Because increasing soil pH is a slow process, additional time will be necessary to determine the efficacy of the lime and Kinsey treatments.

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# Prediction of foliage retention from climate variables

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## Abstract

Douglas-fir needle retention along the Oregon and SW Washington coasts is directly related to tree productivity, and also reflects the severity of Swiss needle cast. Previous research has shown that foliage retention can be predicted from specific climate variables, but in these regression analyses, only a limited number of climate variables were considered. For this analysis, we tested numerous monthly climate variables, as well as site variables. The model was developed from average foliage retention in GIS and PCT control plots from 1996 to 2005; commercial thinning plots measured between 2002 and 2007 were used for validation. With the best model, foliage retention was reasonably predicted by precipitation in October, precipitation in July, maximum temperature in January, minimum temperature in August, and average fog index in May.

## Introduction

Swiss needle cast (SNC) is a major foliar disease of Douglas-fir, caused by *Phaeocryptopus gaeumannii* (T. Rohde) Petr., in coastal areas of Oregon and Washington (Hansen et al. 2000). The disease causes occlusion of the stomates, resulting in carbon starvation and subsequent foliage loss (Manter et al. 2003). Douglas-fir needle retention along the Oregon and SW Washington coasts is negatively correlated with disease-induced tree growth losses, and also reflects the severity of SNC (Maguire et al. 2002). Climatic variability can greatly affect the amount of retained foliage (Xiao 2003). A landscape map of climate-based predictions of foliage retention would be useful to land managers. Latta et al. (2009) used mean January temperature and a Climate Moisture Index (CMI) to predict foliage retention. Coop and Stone (2007) based their predictions of foliage retention on winter temperature and spring leaf wetness. Stone et al. (2007) used a colonization index (CI) as the response variable, with predictions based on average temperature in June.

The objective of this study was to develop a precise and biologically reasonable foliage retention model by testing all potential climate and site variables. The results from this analysis could improve forecasting of SNC distribution along coastal areas of Oregon and Washington.

## **Methods**

### ***Study Area***

In general, plots were established across a range in stand age, topographic position, and SNC severity. Latitude ranged from 43.5°N to 46.16°N, longitude from 124.06°W to 122.31°W, and elevation from 30 to 800 m above sea level. Over the last 40 years, the mean January minimum for this region was 0 °C and the mean July maximum was 25 °C. Total annual precipitation averaged 150–300 cm, with approximately 70% of the total precipitation occurring from October to March.

### ***Fieldwork***

Foliage retention was estimated on ten dominant trees per plot by dividing the tree crown into thirds and visually estimating average retention on representative branches, ignoring the main axis of the primary branch. Distance from the coast, longitude, latitude, elevation, slope, and aspect were recorded for each plot.

### ***Plots Data***

Data for this study was compiled from four ongoing studies established to investigate growth losses and the effect of thinning under varying influence of SNC. These studies included the Growth Impact Study (GIS), the Precommercial Thinning study (PCT), the Paired Permanent commercial thinning plots (PP), and the Retrospective Commercial Thinning Study (RCT) (Kanaskie and Maguire 2001, Maguire et al. 2002, Mainwaring et al. 2008).

The GIS was established in 1998 to monitor SNC symptoms and tree growth in 10- to 30-yr-old Douglas-fir plantations. The PCT, also established in 1998, was designed to test the effect of thinning and initial SNC severity on symptom development and growth response. Spring (April-May) foliage retention was annually estimated at each of these study sites during the ten years from 1996 to 2005. The foliage retention model produced by this analysis was based on climate variables estimated for the 77 GIS plots and 23 PCT control plots.

PP and RCT stands were 30 to 60 years of age, contained at least 75% Douglas-fir by basal area, and were either thinned at the time of establishment (PP), or had undergone commercial thinning four to ten years prior to establishment (RCT). Plots were distributed across a range of disease severity classes and residual stand densities, and included different aspects and slopes. Foliage retention was visually estimated from the ground on ten dominant trees per plot (Mainwaring et al. 2005). Forty-five RCT plots were established during the winters of 2002 and 2003, and re-measured four years later. Thirty PP plot pairs were established during the winters of 2002 and 2003, and re-measured two and four years later.

### ***Independent Variables***

Model fitting was done with both site and climate data. Site data included standard variables, such as latitude, longitude and distance from coast, as well as slope, aspect, elevation, and the interacting effects of aspect and slope (Stage 1976, Stage and Salas 2007). In addition, to attempt to quantitatively describe differences in near-ocean topography directly west of each plot, a variable was created that summed up the product of distance from coast in 100 m

increments (stepid) and elevation at that incremental point, adjusted by different exponential powers (Table 1).

Climate data for each site was based on monthly minimum, maximum, and dewpoint temperatures, along with precipitation data for the period 1996-2005, produced by the Parameter-elevation Regressions on Independent Slopes Model (PRISM, Latta et al., 2009). Elevational interpolation of this data to a 90 m grid was conducted as described by Latta et al. (2009). Seven additional climate variables were used: solar radiation, evapotranspiration (ET), and Climate Moisture Index (CMI), which were calculated using the methods described in Latta et al. (2009); mean temperature; and minimum, maximum, and average fog index, the last three of which were calculated as the difference between the minimum, maximum or average temperature and the dewpoint temperature.

### ***Data Analysis***

GIS and PCT plots were used to develop the foliage retention model, while PP and RCT plots were used for validation. Both site and climate variables were used to develop a foliage retention model. In addition, five topographic indexes (swdp1, swd, swd2, swd5, and swd15) were tested. Table 1 shows the definitions and units of symbols used in this paper.

For this analysis, the foliage retention model was developed in five steps:

- 1) develop a foliage retention model using climate variables,
- 2) develop a foliage retention model using site variables,
- 3) develop a foliage retention model using both climate and site variables,
- 4) refit Coop & Stone's and Latta's model,
- 5) develop a foliage retention model by climate and site variables plus variables from Coop & Stone's (2007) and Latta's (2009) models.
- 6) select and validate the best foliage retention model

Linear regression was used to develop the foliage retention model. For step 1, 3, and 5, forward selection regression was conducted for variable screening. Variables identified by the forward selection procedure were used to do all subsets regression. The Variance Inflation Factor (VIF) was used to measure the impact of collinearity among the variables. Model evaluation was assessed with  $R^2$ , adjusted  $R^2$ , AIC, and MSE.

Table 1. Definitions and units of symbols used in this paper.

category	symbol	definition	unit
<b>Dependent variable</b>	folret	foliage retention	years
<b>site</b>	long	longitude	degree
	lat	latitude	degree
	distm	distance from the coast	meters
	elev	elevation	meters
	slope	slope of plot	degree
	asp	aspect of plot	degree
	slsinasp	slope*sin(asp)	
	slcosasp	slope*cos(asp)	
	swd1	(stepid <sup>0.1</sup> )*elev/1000;	
	Swd5	(stepid <sup>0.5</sup> )*elev/1000;	
	swd	(stepid)*elev/1000;	
swd15	(stepid <sup>1.5</sup> )*elev/1000;		
swd2	(stepid <sup>2</sup> )*elev/1000;		
<b>climate</b>	rad1-12	monthly solar radiation in months 1-12	MJ/m <sup>2</sup> /month
	pre1-12	monthly precipitation in months 1-12	cm
	tmax1-12	monthly maximum temperature in months 1-12	°C
	tm1-12	monthly mean temperature in months 1-12	°C
	tmin1-12	monthly minimum temperature in months 1-12	°C
	tdm1-12	monthly dewpoint temperature in months 1-12	°C
	ET1-12	evaporative transpiration index for months 1-12	mm/day
	CMI1-12	climate moisture index for months 1-12	cm
	fogmax1-12	maximum temperature-dewpoint temperature	°C
	fogav1-12	mean temperature-dewpoint temperature	°C
	fogmin1-12	minimum temperature-dewpoint temperature	°C

## Result and Discussion

### *Developing a foliage retention model with climate variables: Forward selection regression*

The foliage retention model was developed by using all 11 groups of climate variables listed in Table 1. Based on both  $R^2$  and AIC, the best model consisted of 45 variables (Fig. 1). The foliage retention model was then developed by using all 45 climate variables selected from the forward selection procedure. Models containing 5-8 significant variables without collinearity problems are listed in Table 2.

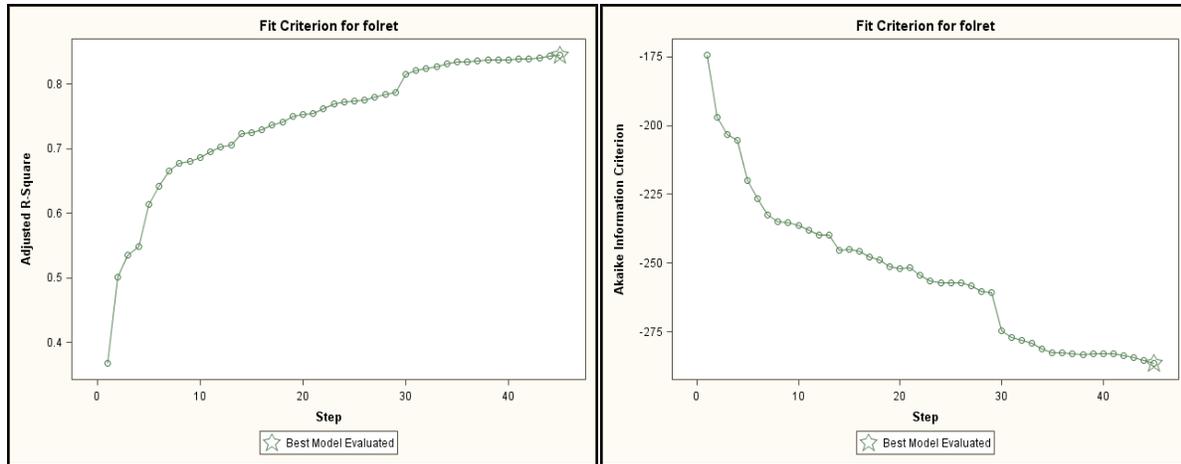


Figure 1. Foliage retention model using forward selection with all climate variables.

Table 2. Selected foliage retention models as function of climate variables.

Model	R2	Adjusted R2	AIC	MSE	Variables in Model*
[1]	0.669	0.651	-229.980	0.095	<b>pre10</b> pre7 tmax1 <b>tmin8</b> fogav5
[2]	0.660	0.642	-227.300	0.097	<b>pre10</b> pre7 <b>tmin8</b> tmin12 fogav8
[3]	0.659	0.641	-227.055	0.097	pre8 <b>pre10</b> tmax1 <b>tmin8</b> fogav8
[4]	0.657	0.639	-226.635	0.098	<b>pre10</b> pre7 <b>tmin8</b> fogav5 tm12
[5]	0.657	0.639	-226.602	0.098	<b>pre10</b> pre7 tmax1 <b>tmin8</b> fogav8
[6]	0.657	0.639	-226.468	0.098	pre8 <b>pre10</b> <b>tmin8</b> tm10 fogav8
[7]	0.682	0.661	-232.030	0.092	<b>tm7</b> pre8 <b>pre10</b> fogav6 tmin12 fogmin7

\*Note: Bold indicate positive value, while non-bold indicate negative value

### Developing a foliage retention model with site variables: Forward selection regression

A foliage retention model was developed by using all 13 site variables listed in Table 1. Models containing 5-8 significant variables without collinearity problems are listed in Table 3.

Table 3. Selected foliage retention models as function of site variables

Model	R2	Adjusted R2	AIC	MSE	Variables in Model*
[8]	0.569	0.546	-203.688	0.123	<b>Long</b> lat <b>elev</b> slope swd5
[9]	0.567	0.544	-203.157	0.124	<b>Long</b> lat <b>elev</b> slope swd
[10]	0.564	0.541	-202.603	0.124	<b>Long</b> lat <b>elev</b> slope swd15

\*Note: Bold indicate positive value, while non-bold indicate negative value

*Developing a foliage retention model with climate and site variables: Forward selection regression*

The foliage retention model was developed by using all 11 groups of climate variables and all 13 site variables listed in Table 1. Based on both  $R^2$  and AIC, the best model consisted of 43 variables (Fig. 2).

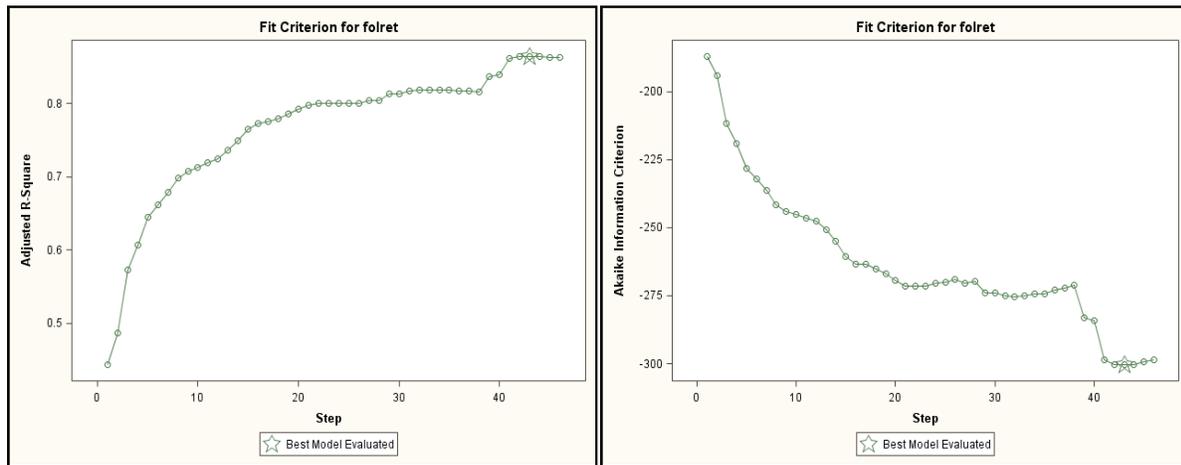


Figure 2. Foliage retention model using forward selection with all climate and site variables.

*All subsets regression*

The foliage retention model was then developed using all 43 climate and site variables selected from the forward selection procedure. Models containing 5-8 significant variables without collinearity problems are listed in Table 4.

Table 4. Selected foliage retention models as function of climate and site variables.

Model	R2	Adjusted R2	AIC	MSE	Variables in Model*
[11]	0.680	0.663	-233.362	0.091	pre8 <b>pre10 long tmin8</b> slope
[12]	0.676	0.658	-232.098	0.093	<b>fogav8 tmin11 tmin7 swdp1</b> tdm1
[13]	0.670	0.653	-230.481	0.094	<b>tmin11 tmin7 swdp1 fogav7</b> tdm1
[14]	0.670	0.652	-230.392	0.094	pre8 <b>pre10 fogav8 tmin7</b> tm1
[15]	0.697	0.677	-236.828	0.088	pre8 <b>pre10 long tmin8</b> slope <b>fogmin1</b>
[16]	0.697	0.677	-236.818	0.088	<b>fogav8 fogmin1 tmin11 tmin7 swdp1</b> tdm1
[17]	0.696	0.677	-236.704	0.088	<b>pre10 long</b> slope <b>tmin11 elev</b>
[18]	0.696	0.676	-236.551	0.088	<b>pre10 tmin8</b> slope <b>fogav8</b> pre7 tdm12
[19]	0.720	0.699	-242.847	0.082	pre8 <b>pre10 long tmin8</b> slope <b>fogav8 fogmin1</b>
[20]	0.719	0.698	-242.507	0.082	pre8 <b>pre10 long tmin8</b> slope <b>fogmin1 fogav7</b>

\*Note: Bold indicate positive value, while non-bold indicate negative value

### ***Refitting Coop & Stone's and Latta's model: Coop & Stone's model***

Coop and Stone (2007) developed a foliage retention model using relative humidity in July (RH7), winter degree days (dds) (3°C threshold), and aspect. RH7 was calculated using standard dewpoint and temperature conversions to RH for July, while dds was calculated based on monthly temperatures:  $((t_{max} + t_{min})/2) - \text{threshold}$ , summed for January & December. Aspect (90m resolution) was converted to a range of 0-2 where 2=SW, 0=NE and 1=NW and SE, with flat (neutral) areas also set to 1.

Coop & Stone's model was refit using GIS and PCT control plots. The result is as follows:

[21]  $\text{Folret} = 6.305 - 0.084 * \text{dds} - 0.047 * \text{RH7} - 0.137 * \text{aspect}$   
R2=0.389, Adj R2=0.370, MSE=0.171, AIC= -172.838.

We also fit Coop & Stone's model using asp in degrees. The result is as follows:

[22]  $\text{Folret} = 6.533 - 0.074 * \text{dds} - 0.050 * \text{RH7} - 0.001 * \text{asp}$   
R2=0.407, Adj R2=0.389, MSE=0.166, AIC= -175.861.

### ***Refitting Coop & Stone's and Latta's model: Latta's model***

Latta et al. (2009) developed a foliage retention model using average temperature in January (tm1) and climate moisture index in July (CMI7). We refit this model using GIS and PCT control plots. The result is as follows:

[23]  $\text{Folret} = 2.653 - 0.2486 * \text{tm1} - 0.1033 * \text{CMI7}$   
R2=0.363, Adj R2=0.350, MSE=0.17618, AIC= -170.668.

### ***Developing a model including variables from previous research***

The significant variables from Coop & Stone's and Latta's model that had not been used in our modeling efforts were added to the independent variables shown in Table 1 for significance testing. One exception was the Coop and Stone aspect variable, which, shown to be inferior to asp, was not used. The resultant foliage retention model was refit using all 11 groups of climate variables and all 13 site variables listed in Table 1, and also included dds & RH7. The result is the same as foliage retention model as a function of climate and site variables, shown in models [8-10].

### ***Selecting and validating the best foliage retention model***

A good foliage retention model should have higher precision with fewer predictors, and also make biological sense. Among the above 23 models, only Model [1] has five predictors, all climate variables, and can predict foliage retention reasonably. Thus, Model [1] was selected as the best model. Parameters of the best model are listed in Table 5. Validation of Model [1] using PP and RCT plots produced the following output: R2=0.412, Adj R2=0.406, MSE=0.452, AIC= -80.674. The precision is lower, but reasonable (Fig. 3).

Table 5. Parameters of the best foliage retention model.

Variable	Estimate	Std. Error	t Value	Pr >  t
<b>Intercept</b>	-3.14647	1.32871	-2.37	0.0199
<b>pre10</b>	0.06684	0.01949	3.43	0.0009
<b>pre7</b>	-0.74027	0.13957	-5.30	<.0001
<b>tmax1</b>	-0.18031	0.03230	-5.58	<.0001
<b>tmin8</b>	0.50260	0.09381	5.36	<.0001
<b>fogav5</b>	0.41496	0.08664	4.79	<.0001

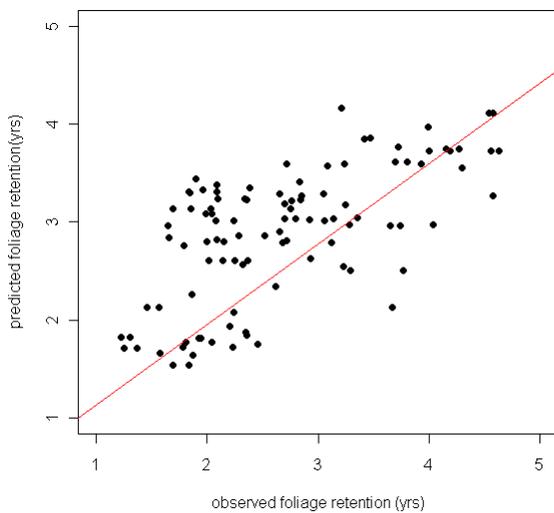


Figure 3. The relationship between predicted and observed foliage retention.

Subsequent research has supported the conclusion that winter temperature and spring moisture are useful factors for predicting both annual and longer term trends in the spatial distribution of SNC in western Oregon (Stone and Coop 2006). As an index to reflect the severity of SNC, foliage retention can also be predicted by such climate variables. Stone and Coop (2007) developed a foliage retention model as a function of winter degree days, relative humidity in July, and aspect, while Latta (2009) developed foliage retention model by mean temperature in January and Climate Moisture Index in July. However, other climate and site variables can affect foliage retention (Xiao 2003). In this study all possible climate variables and site variables were tested to attempt to improve foliage retention predictions.

The foliage retention models developed using either climate variables, site variables, or both types of variables combined, have  $R^2$  ranging from 0.657-0.682, 0.564-0.569, and 0.670-0.720, respectively. From this, it can be inferred that climate variables are the most important factors affecting foliage retention. In the coastal area, climate and site variables are closely correlated; in other words, climate variables are highly reflective of site.

The best model has five predictors, including pre10, pre7, tmax1, tmin8, and fogav5. Precipitation in October (pre10), is presumably an indicator of fall root growth. Greater fall root growth probably gives the tree several advantages: greater uptake of water and nutrients in the spring and associated increases in early season tree vigor, greater use of soil water early in spring that can be recharged by early growing season precipitation, and increased fall photosynthesis. In addition, increased amounts of fall precipitation presumably lead to earlier rehydration of the tree, which may be important for retaining needles at precisely the time when older foliage tends to be dropped (Weiskittel and Maguire 2007). The negative association of July precipitation (pre7) with foliage retention is undoubtedly the same association that has linked moist conditions in the spring with successful fungal spore germination, dissemination and infection. Although July is on the periphery of the period that has been associated with infection, moist sites in July would certainly also be moist earlier in the spring. It may be that delineating sites by summer moisture is a surrogate for frequency of moisture during the peak infection period, earlier in the spring. In fact, numerous models contained a significant term for August precipitation (Table 2). The positive association of August minimum temperature (min8) with foliage retention is may be due to the negative effect of high vapor pressure deficits and the corresponding drying effects on fungal hyphae and their ability to grow on the needle surface, and may also reflect the gradient in foliage retention with distance from the coast. The anti-fog index (fogav5) consistently suggests that foliage retention is greater where there is a greater difference between average temperature and dewpoint temperature, another method of describing humidity. Finally, the negative effect of greater January temperature (tmax1) on foliage retention is consistent with the idea that warmer winter temperatures lead to enhanced fungal development within needles.

The best model developed in this study has a better precision ( $R^2=0.669$ ) compared with Stone and Coop ( $R^2=0.389$ ) and Latta et al.'s ( $R^2=0.363$ ) models using the same data set. Although the Latta et al. (2009) analysis produced a greater  $R^2$  (0.72) after adjusting for spatial autocorrelation, use of this tool still leaves the correlations between foliage retention and specific climate or site variables unknown. This is a liability in the long term if foliage retention predictions are to be used for specific climate change scenarios.

The precision of the validation is significantly lower ( $R^2=0.412$ ). This may be due to the fact that the RCT and PP stands were less frequently sampled than older stands and that visual estimation of foliage retention was more difficult on the taller trees. Overall, the best model has reasonable precision, and could be used for predicting foliage retention for Douglas-fir along the Oregon and SW Washington coasts.

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# Climate Models for Predicting Distribution and Severity of Swiss Needle Cast

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## Abstract

Spatial climate based models for predicting the distribution and severity of Swiss needle cast were developed using multiple data sets. Final models included winter temperature and either June-July dewpoint deficit or total June-July precipitation, with an adjusted  $R^2$  of 57%. The precipitation model contained a quadratic term, and was, therefore, less suitable for combination with global climate models (GCMs) for prediction of changes in SNC distribution under various climate change scenarios. By applying climate based disease models for current distribution with downscaled GCMs changes in SNC distribution under climate change were predicted for 2040 and 2090. Under the most extreme emission combination (MIROC A2 GCM), the area affected by severe SNC, with foliage retention less than 60% of normal, was predicted to increase from the current 3700 km<sup>2</sup> in western Oregon to about 5700 km<sup>2</sup> by 2040, and to double by 2090, with the majority of the affected area remaining in the Oregon Coast Range.

## Introduction

Several previous studies have reported a relationship between climate factors and the abundance of *Phaeocryptopus gaeumannii* (T. Rohde) Petr., the severity of Swiss needle cast (SNC) and the resultant growth reductions in Douglas-fir due to reduced foliage retention. The biological mechanisms linking abundance of *P. gaeumannii* with disease severity is now well established. Fruiting bodies (pseudothecia) of *P. gaeumannii* physically occlude the stomata of Douglas-fir needles, thereby impairing gas exchange and photosynthesis (Manter et al. 2003). The premature loss of foliage and resulting growth reduction in Douglas-fir are directly related to a decrease in CO<sub>2</sub> assimilation that, in turn, is directly linked to the abundance of the pathogen (Manter et al. 2003). This relationship has been convincingly demonstrated in both Oregon and New Zealand by using the proportion of occluded stomata as a measure of pathogen abundance, and using host needle retention to quantify foliage loss (Manter et al. 2005, Stone et al. 2007).

There is also strong evidence that the variation in abundance of *P. gaeumannii* across the landscape is regulated by climate. Hood (1982) first noted an apparent relationship between *P. gaeumannii* abundance and regional differences in spring precipitation in the Pacific Northwest. Later research identified a relationship between variation in *P. gaeumannii* abundance and winter temperature and spring precipitation (Manter et al. 2005, Stone et al. 2007, 2008). The relationship between *P. gaeumannii* abundance, SNC severity and climate factors, therefore, should be suitable for developing spatial surfaces that describe variation in SNC severity across wide environmental ranges. Such predictions of the disease would be of considerable use to forest managers, since foliage retention has been found to be the key determinant of volume loss in Douglas-fir (Maguire et al. 2002). The use of climate based models for disease distribution under current climate, in combination with global predictions of climatic change, could provide

forest managers with a useful tool for forecasting potential future disease severity to help evaluate and manage the risk of growth losses in Douglas-fir plantings due to SNC.

Here we examine variation in SNC distribution and severity in relation to specific climate variables by using a direct measure of disease severity (abundance of *P. gaeumannii* pseudothecia, % stomatal occlusion), rather than indirect measures of symptom severity (such as foliage retention, discoloration, etc.) that have been used in prior modeling studies to quantify disease severity. In addition, we compare *P. gaeumannii* abundance to the corresponding individual year climate data, rather than average climate over a series of years. This approach reflects current knowledge regarding epidemiology of SNC and should provide a more accurate reflection of the relationship between climate factors, abundance of *P. gaeumannii* and severity of SNC, because variables, such as foliage retention and discoloration, may be affected by various environmental factors, in addition to *P. gaeumannii* abundance. The goal of this research is to develop spatially and temporally robust disease models that can be used to predict past, current and future distribution and severity of SNC in the Pacific Northwest. Such models will be useful as management decision support tools, and, more generally, to investigate the interaction between climate change, pathogens and forest health.

## Materials and Methods

Several studies of SNC severity in western Oregon during the past ten years have used proportion of stomata occluded by *P. gaeumannii* fruiting bodies (“pseudothecia density”) to quantify disease levels. Of these, the Manter (2001-2005), SNCC-GIS (2005, 2008), Cascades (2002, 2006), and Stone-SNC (2002-2007) data were available for model development and validation. Because of the range of sources, methodologies and intensity of sampling effort from these available data, the Manter dataset (N=29) was selected for use as the primary model building dataset, because it was considered the best documented, most intensively sampled and best quality multi-year data available that represented a range of SNC severity across western Oregon.

### *P. gaeumannii* abundance

In the Manter (2001 – 2005) dataset used for model building, abundance of *P. gaeumannii* was estimated from 50-needle samples of one- and two-year-old needles collected from 20 trees at each study site. Each set of 50 needles was examined under a binocular dissecting microscope at 40x to determine the proportion of needles bearing pseudothecia (infection incidence). The first ten needles on each card with pseudothecia present were then used to determine the proportion of stomata occluded by pseudothecia (pseudothecial density). The needles were examined under a dissecting microscope fitted with a counting grid, and the proportion of stomata occluded by pseudothecia in three, 2.6 x 0.26 mm segments (base, middle, tip) of each of the ten needles was determined and averaged. A colonisation index (*CI*), was calculated as the product of infection incidence ( $n = 50$ ) and pseudothecial density ( $n = 10$ ). *CI* was averaged for each needle age class and sample year for each study site; site averages were then rescaled by setting the maximum value for each sample year in the dataset to 1 and expressing all values within the corresponding sample year as a fraction of this maximum. Rescaling was undertaken for all combinations of sample year and foliage age class, and then averaged to determine an average for each site. These site mean normalised values, referred to

hereafter as  $CI_{norm}$ , were used in all analyses transformed to a more normal distribution by using  $\sqrt{CI_{norm} \times 100}$  (Fig. 1).

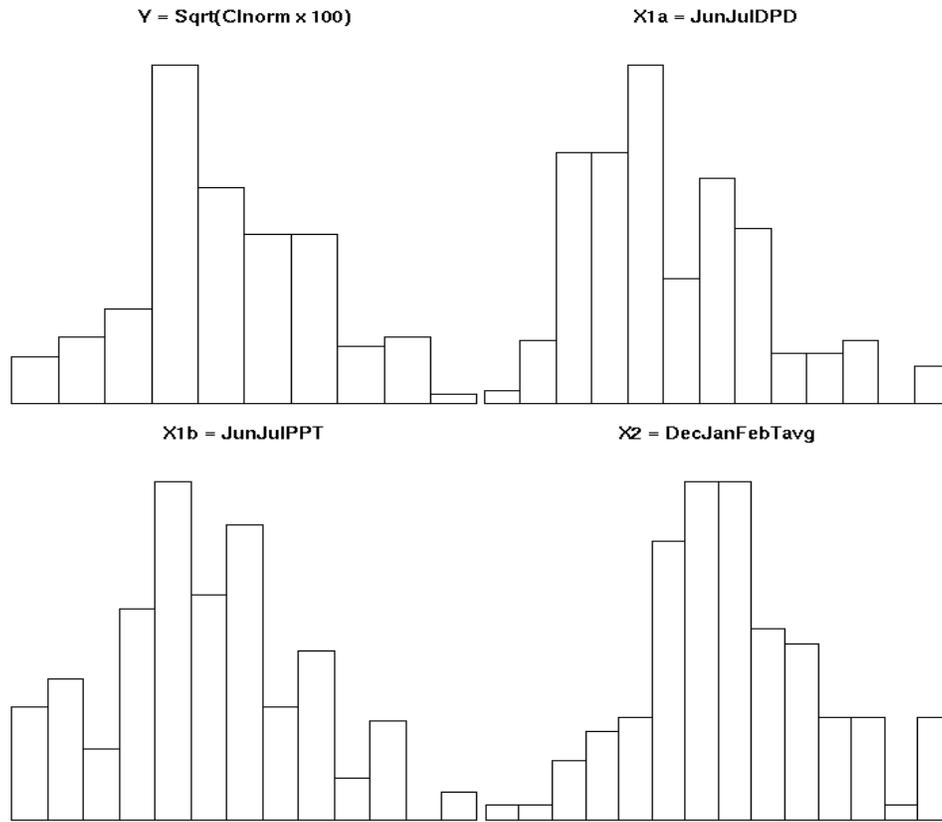


Figure 1. Frequency histograms of data used to model SNC. Upper left, SNC Colonization index (square root transformation), upper right, June and July (averaged) Dew point deficit, lower left, June and July (averaged) precipitation; lower right, Dec., Jan. and Feb. (averaged) Temperature.

### Climate data

Gridded climate data (ca. 800M spatial and monthly time resolution) were obtained from The PRISM Group (<http://www.prism.oregonstate.edu>) for average daily maximum and minimum temperatures, average dew point, and precipitation amount. PRISM climate data covered all Douglas-fir forested zones from 121 Longitude west, for Oregon and Washington. These data were downscaled to 180m by using geographically weighted regression (GWR), which uses a 5x5 moving window linear regression model with elevation as the independent variable (Fotheringham et al. 2002). Each sample location (latitude, longitude) and year were used to sample historical spatial climate datasets produced by the PRISM climate modeling system (Daly et al. 1994, 1997). Dew point deficit (DPD) was calculated as the difference between monthly average temperature and dew point.

The months and climate parameters sampled were determined from the earlier studies that indicated these to be of highest potential importance in the current model. These include the parameters listed in Table 1. Previous studies have demonstrated that ascospores of *P. gaeumannii* are dispersed in wet periods during spring and require surface moisture to germinate and infect needles. Consequently, moisture in late spring/early summer is an important epidemiological factor. However, direct estimates of leaf wetness are not generally available in past or future spatial climate models. Therefore, total or mean monthly precipitation and DPD are available or readily converted from other available parameters (e.g. Tavg = Tmax+Tmin/2; dew point can be converted from vapor pressure).

Table 1. Summary of variables used in correlation and regression analyses.

Variable	Mean ±stdev	Min.	Max.
Latitude	45.03 ± 0.45	43.28	46.09
Longitude	-123.6 ± 0.28	-124.3	-122.5
Elevation (m)	266.2 ± 181	4.0	1090.0
CI yr 1 needles	4.544 ± 6.11	0.00	24.51
CI yr 2 needles	15.70 ± 12.48	0.00	55.31
normalized CI	0.250 ± 0.22	0.00	0.98
JunJulPPT (mm)	10.88 ± 5.27	0.35	25.03
JunJulDPD (°C)	4.64 ± 1.22	2.15	8.423
JulDPD (°C)	5.10 ± 1.52	2.47	9.543
DecJanFebTavg (°C)	5.20 ± 1.22	1.91	8.20
JanFebTavg (°C)	5.31 ± 1.22	1.92	8.36

### Terrain data

Several variables related to potential terrain effects on sampled *P. gaeumannii* density were tested for inclusion in models. Of these, aspect (coded to maximum = 2 at southwest orientation and minimum = 0 at northwest orientation) was seen to correlate most strongly in previous studies (Rosso and Hansen 2003, Coop and Stone 2007). At elevations above 800 m, SNC has seldom been severe, and, therefore, aspect is unlikely to be significant at higher elevations. Likewise, at elevations below 200m, including valley floors and areas where fog forms, the effect of aspect would be negligible in limiting *P. gaeumannii*. Aspect was therefore allotted additional elevation-based conditions according to the following rule: "r.mapcalc "asp2e=if(dem90m.nw>550,0.1,if(dem90m.nw<200,1.6,aspect))".

### Climate Change Data

Global Circulation Model (GCM) climate change forecasts for monthly average data were provided by the Ron Nielsen Research group (USDA Forest Service PNW), based on nine different combinations of three GCM models (CSIRO, MIROC, and HADLEY) and three emission scenarios (B1, A1b, A2). The GCMs and emission scenarios are described in detail in Solomon et al. (2007). These were downscaled from 2.5° (ca 320 km) to 30 second (ca 800 m)

resolution by using climatologically aided interpolation (CAI; Hunter and Meentemeyer 2005) using PRISM 30-year normals (1971-2000) climate data as the downscaling grid. Downscaled GCMs were available for 2006 to 2100. Modeled parameters included monthly average temperatures, vapor pressure, and precipitation. Dew point and DPD were calculated from vapor pressure and temperature. Predictions of SNC severity for the years 2040 and 2090, were based on the GCM projections for the relevant months for the respective years.

### ***Model Analysis***

Models were constructed with these objectives as guidelines: 1) Build the best models available that both reflect our current understanding of SNC epidemiology, and can be readily applied to available current and future climate change data, 2) Build a version of the model employing the same variables used by Watt et al. (2010) to allow for comparisons of model predictions of SNC distribution in New Zealand and Oregon, and 3) Reflect single-year comparisons of disease severity to more closely match the approach taken by Manter et al. (2005), whereby epidemiological processes were mechanistically modeled. This approach is potentially more robust, both spatially and temporally, than average climate models built to predict disease impacts in which foliage retention, rather than *P. gaeumannii* abundance (pseudothecial density), is used as the dependent variable. The conversion of pseudothecial density to percent foliage retention is done as a secondary step to obtain foliage retention values normally used to measure disease effects on growth reduction in numerous studies. This final conversion equation was based on the best available data from Manter et al. (2005).

For model building, climate variables (Table 1) were sampled for each location and year of the available data sets (described above). Models were constructed using the statistical computing program R (Venables and Ripley 2002) procedures lm (linear models), rlm (robust linear models); and using 1) correlation, histogram, and scatterplot analysis, 2) manual variable selection, 3) stepwise regression, and 4) the Shapiro–Wilk test to evaluate whether residuals were normally distributed. The resulting models were applied to PRISM climate data (2000-2008), then averaged, for assessment and comparison to GCM based predictions.

### **Results and Discussion**

Climate variables resulting from correlation and regression analyses, along with correlation coefficient values ( $r$ ), are displayed in Table 2. Two variables were available to represent late spring/early summer moisture in relation to *P. gaeumannii* abundance (expressed as square-root transformed normalized colonization index, or  $\text{Sqrt}(CI_{\text{norm}})$ ): DPD and precipitation (PPT). From the correlation analysis, the former showed much greater potential for prediction of *P. gaeumannii* abundance. For example, for June-July average DPD, the correlation coefficient ( $r$ ) was 0.484, versus  $r = 0.045$  for average PPT (same months) when all three study data sets were combined (Table 1). However, June-July average precipitation was well correlated with the Manter data set ( $r = 0.417$ ). Both winter (average Dec-Jan-Feb;  $r = 0.471$ ) and average Jan-Feb ( $r = 0.514$ ) mean temperatures were highly correlated with  $\text{Sqrt}(CI_{\text{norm}})$  for all data sets. A site-factor variable, aspect, recoded to 2 = SW and 0 = NW, with additional elevation constraints, was also well correlated with  $\text{Sqrt}(CI_{\text{norm}})$  for all data sets ( $r = 0.330$  to  $r = 0.770$ ). Correlation coefficients were generally highest for the Manter data set, suggesting it may be best used for model building.

Table 2. Correlation coefficients ( $r$ ) for monthly average climate and terrain-based variables used to construct models to predict *P. gaeumannii* infection index (1 and 2 year old needles, % stomatal occlusion, transformed to  $\text{Sqrt}(CI_{\text{norm}})$ ), for three independently collected data sets.

Months/Parameter	Average correlation coeff. ( $r$ ) vs. $\text{Sqrt}(CI_{\text{norm}})^a$				
	Var. Name	Manter	Stone	SNCC-GIS	All
June, July precipitation	JunJulPPT	0.417*	0.100ns	-0.134ns	0.045ns
July dewpoint deficit	JulDPD	-0.648***	-0.478**	-0.413**	-0.523***
June-July dewpoint deficit	JunJulDPD	-0.630***	-0.403**	-0.382*	-0.484***
Dec, Jan, Feb average temp	DecJanFebTavg	0.615***	0.486**	0.623***	0.491***
Jan, Feb average temp	JanFebTavg	0.592***	0.493**	0.563***	0.471***
Aspect	Asp2e	0.770***	0.539**	0.330ns	0.514***

<sup>a</sup>Significance codes: < 0.001, \*\*\*; < 0.01, \*\*, < 0.05, \*, <0.1, . > 0.1 ns

Models for each of the three data sources (Manter, Stone, and SNCC-GIS) are presented in Table 3 (using DPD as the early summer moisture variable), and in Table 4 (using the quadratic form of PPT as the early summer moisture variable). Both models were highly significant when fitted with data from all study data sets ( $F = 31.85$  and  $25.01$  for DPD and PPT based models, respectively), and all parameters in both models were individually significant to  $p < 0.01$ . However, models built with data from all three studies had much lower  $R^2$  values than did Manter study-only built models (0.442 vs. 0.725 for DPD-based models, and 0.451 vs. 0.718 for PPT-based models). These Manter study based-models had smaller error, average residual values, and steeper slopes, than did models based on the other two available data sets.

Table 3. Dew point deficit (DPD) model-based parameters, values and significance values using monthly average climate, and terrain-based variables to predict *P. gaeumannii* infection index (1 and 2 year old needles, % stomatal occlusion, transformed to  $\text{Sqrt}(CI_{\text{norm}})$ ), for three independently collected data sets.

Parameter	Study (parameter value and significance)				
	Var. Name	Manter	Stone	SNCC-GIS	All 3
F-statistic	F	25.64	8.13	10.53	31.85
Degrees of freedom	df	25	37	44	114
Adj. $R^2$	$R^2$	0.725 ***	0.348 ***	0.378 ***	0.442 ***
Intercept	–	0.1023 ns	3.392 *	-1.123 ns	3.342 ***
Winter average temperature	DecJanFebTavg	0.643 *	0.257 ns	1.133 ***	0.414 ***
June, July dewpoint deficit	JunJulDPD	-4.963	-2.936	-0.080 ns	-4.734 ***
Aspect w/elev.	Asp2e	2.529 ***	0.871 *	0.544 ns	1.071 ***

Significance codes: < 0.001, \*\*\*; < 0.01, \*\*, < 0.05, \*, <0.1, . > 0.1 ns

Table 4. Precipitation model-based parameters, values and significance values using monthly average climate, and terrain-based variables to predict *P. gaeumannii* infection index (1 and 2 year old needles, % stomatal occlusion, transformed to  $\text{Sqrt}(CI_{norm})$ , for three independently collected data sets.

Parameter	Study (parameter value and significance)				
	Var. Name	Manter	Stone	SNCC-GIS	All 3
F-statistic	F	18.83	6.51	8.11	25.01
Degrees of freedom	DF	24	36	43	113
Adj. R <sup>2</sup>	R2	0.718 ***	0.355 ***	0.377 ***	0.451 ***
Intercept	–	-4.699 *	0.322 ns	-1.264 ns	-2.460 **
Winter Average Temperature	DecJanFebTavg	0.707 ns	0.423	1.294 ***	0.722 ***
June, July Precipitation	JunJulPPT	0.510 ns	0.0357 ns	-0.117 ns	0.307 ***
(June, July Precipitation) <sup>2</sup>	JunJulPPT <sup>2</sup>	-0.023 ns	0.0020 ns	0.0053 ns	-0.010 **
Aspect	Asp2e	2.584 ***	0.931 *	0.462 ns	1.147 ***

Significance codes: < 0.001, \*\*\*; < 0,01, \*\*; < 0.05, \*; <0.1, .; > 0.1 ns

The subset of data points used for final parameter value estimation emphasized a) the Manter data set by subsampling the GIS and Stone study data sets to equivalent sample sizes and b) removing outliers from the essential regression lines displayed in Figures 2 & 3 (points vs. Manter regression line). This reduced combined data set provided a better balance of site characteristics, climate variability, and larger sample size than the Manter study data set alone, while avoiding the apparent greater sampling error of the other studies, which were designed for objectives other than to model climate effects on *P. gaeumannii* infection and growth. Details for the two final models, based on June-July DPD or precipitation, respectively, are shown in Table 5.

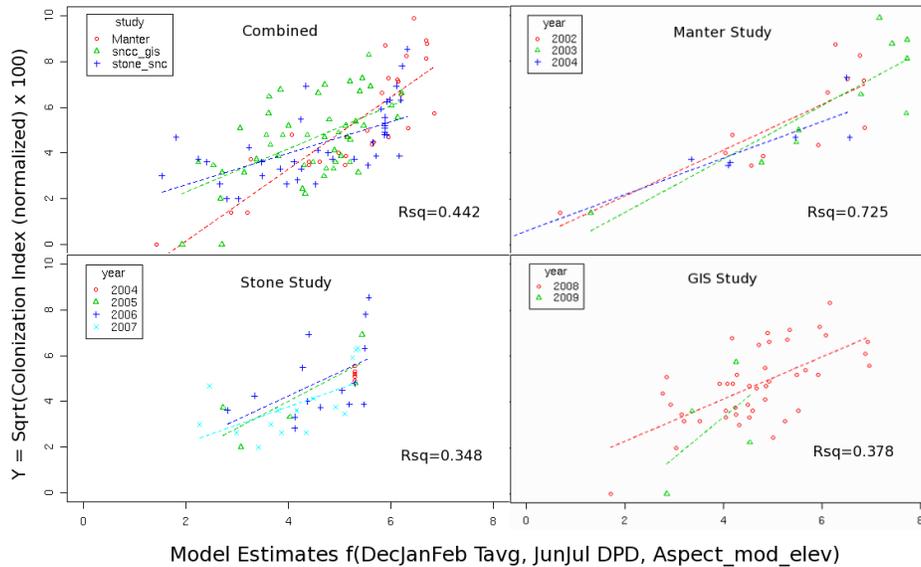


Figure 2. Fitted versus observed SNC Colonization index (normalized for age 1 and 2 year old needles, square root transformed) data, using June-July average dew point deficit as the spring moisture component, for a combined model utilizing all three studies (upper left), Manter only (upper right), Stone only (lower left), and SNCC-GIS only (lower right). Individual studies with symbols denoting year of study. Other independent variables include Winter (Dec. Jan. Feb.) average temperatures, and aspect constrained by elevation.

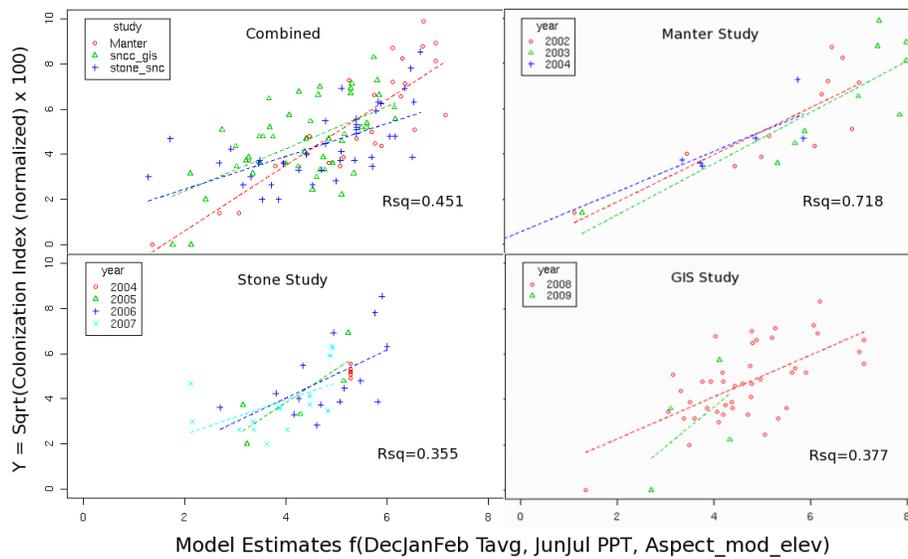


Figure 3. Fitted versus observed SNC Colonization index (normalized for age 1 and 2 year old needles, square root transformed) data, using June-July average precipitation (quadratic,  $x + x^2$  form) as the spring moisture component, for a combined model utilizing all three studies (upper left), Manter only (upper right), Stone only (lower left), and GIS only (lower right). Individual studies with symbols denoting year of study. Other independent variables include Winter (Dec. Jan. Feb.) average temperatures, and aspect constrained by elevation.

Table 5. Final models used for parameter estimation.

Dewpoint deficit-based model				
Coefficients	Estimate	Std. Error	t value	Pr(> t )
Intercept	2.7656	1.1005	2.513	0.014060 *
Winter Tavg	0.5405	0.1441	3.751	0.000339 ***
JunJulDPD	-6.1788	1.3475	-4.585	1.72e-05 ***
asp2e	1.4951	0.3024	4.943	4.38e-06 ***
Degrees of Freedom	77			
F	36.61			8.254e-15***
R <sup>2</sup>	0.5718			
Precipitation-based model				
Intercept	-4.475325	1.035102	-4.324	4.60e-05 ***
Winter Tavg	0.899264	0.154693	5.813	1.36e-07 ***
JunJulPPT	0.078794	0.019397	4.062	0.000117 ***
(JunJulPPT) <sup>2</sup>	-0.0004901	0.0001670	-2.934	0.004417 **
asp2e	1.537967	0.301092	5.108	2.35e-06 ***
Degrees of Freedom	76			
F	28.35			2.028e-14***
R <sup>2</sup>	0.5776			

Significance codes: < 0.001, \*\*\*; < 0.01, \*\*; < 0.05, \*; < 0.1, .; > 0.1 ns

The parameter estimates for the two final models, as expected, are intermediate between values obtained from the Manter study alone and from all three studies combined (Tables 2, 3 and 4). All variables are highly significant at 0.001 or less, except the precip<sup>2</sup> term (p = 0.004). Both models have normally distributed residuals, as determined using the Shapiro-Wilk normality test (p < 0.01). Model fitted curves are compared for least squares (linear) and lowess (locally weighted smoothing) methods (Fig. 4) as a simple test of response non-linearities. This comparison reveals a possible minor non-linearity at high sqrt(CI<sub>norm</sub>) values, where lowess lines dip slightly below linear between 4.5 and 6.5, then above linear from 6.5 to 8.0. While slight, this may be either an artifact of sampling error, or may represent a threshold at which *P. gaeumannii* densities and disease effects are rapidly compounded. This would be an expected effect of severe disease if it followed a typical logistic disease progress curve (Gilligan 1990). Some of this nonlinearity was already removed by using the square root transformation of CI<sub>norm</sub>.

Comparison of separately fitted regression lines for each study (Manter, Stone, and SNCC-GIS) are displayed in Figure 4. Among these, slopes are generally very similar, whereas the GIS study appears to have a slightly higher intercept than the other studies. This may warrant further remedial measures to correct for sampling bias, but, currently, no basis for development is available. Use of robust regression for the Manter data set and all three combined study data sets produced no apparent differences in parameter values or scatterplots, suggesting that outliers had no appreciable effect on the models.

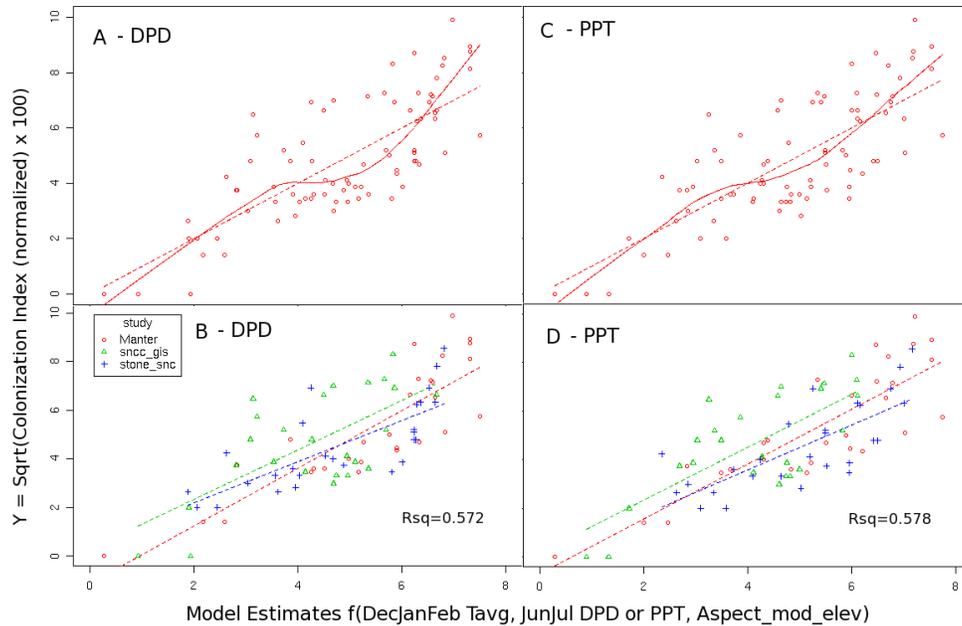


Figure 4. Final models used to estimate model parameter values for (A & B) – dew point deficit spring moisture based model and (C & D) – precipitation spring moisture based model. (A & C) - Full model with least squares and loess (locally weighted scatterplot smoothing) fitted lines. (B & D) – Separate least squares fitted lines for each study showing relative differences. R-squared values are for full models (all data displayed).

### Conversion of $CI_{norm}$ to Foliage Retention

The model developed by Watt et al. (2010) was compared to data and models based solely on Manter (Oregon) data (Fig. 5), showing the relationship between  $CI_{norm}$  and percentage foliage retention. The Watt et al. (2010) model had a similar slope, but had a higher Y intercept (at 100% foliage retention, as would be expected). Using the square root transformation, the Oregon derived model performed much better ( $R^2 = 0.83$  vs. 0.74), and also resulted in the Y intercept reaching 100%. The following model was then used to convert all model predictions for  $CI_{norm}$  to percent foliage retention for comparisons:

$$\text{Est. Foliage Retention (\%)} = -6.84 \times \text{sqrt}(\text{norm. } CI) + 101.04$$

$$R^2 = 0.83$$

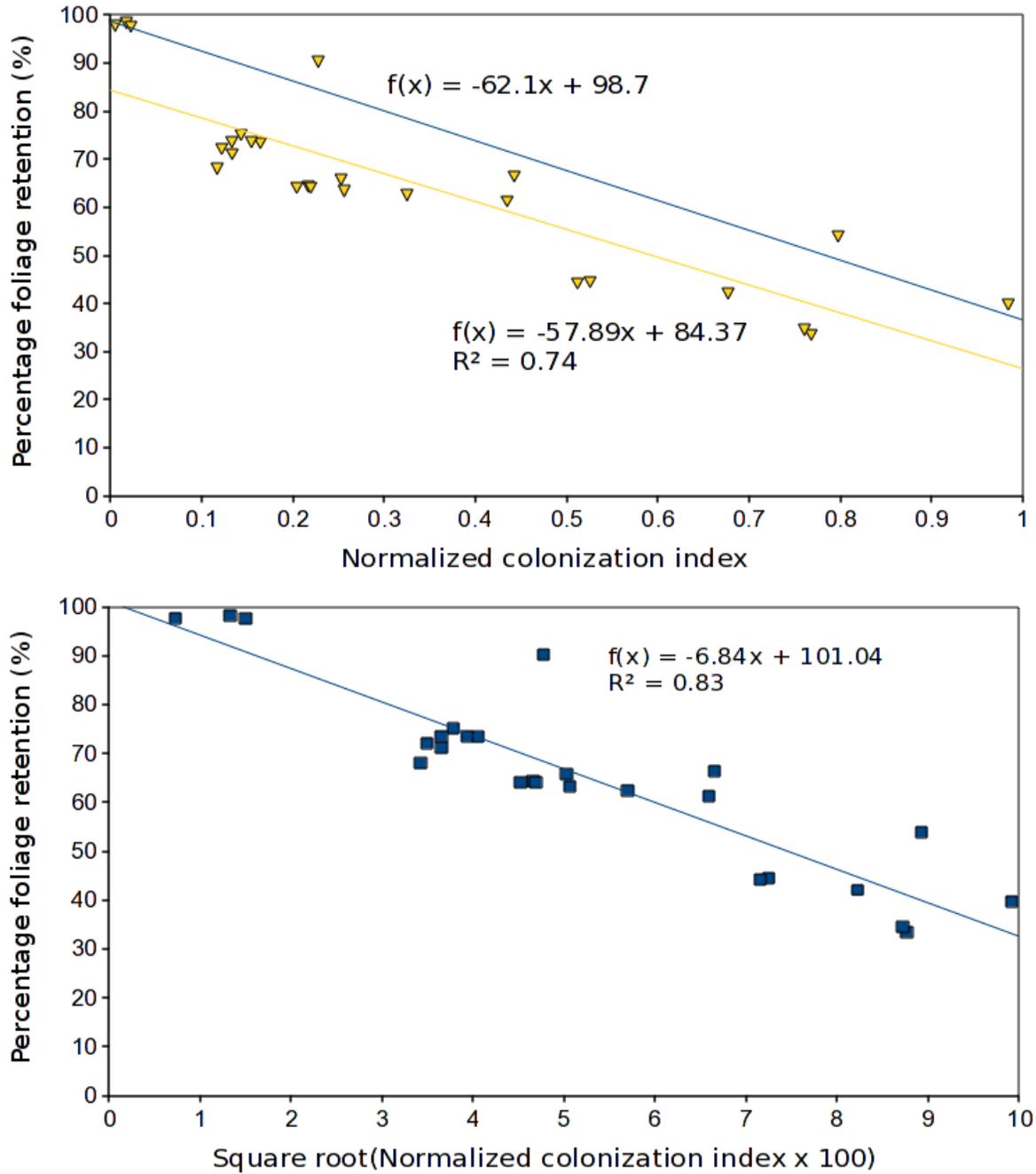


Figure 5. Conversion models for pseudotheical counts (normalized colonization index from 1 and 2 year old needles) to percent foliage retention. Top- Manter Oregon data (not sqrt transformed) compared to model fit (lower line) and to conversion model of Watt et al. (2011), Bottom – Square root transformed Manter Oregon data and final model used for conversion.

### *Application of Models to GCM Climate Change Data*

All GCM scenarios and models available were fitted to the two final model parameters sets; based on both June-July DPD and on June-July PPT (with quadratic term). First, the models were fitted to a standard reference, using PRISM data averaged over 2001 through 2007 as a representation of distribution of SNC under “current” climate. Winter (Dec-Feb) average temperatures, the climate factor having the greatest effect on SNC distribution, are predicted to change from 3.65 C (baseline 2001-7) to 1.67 C (2040) and 6.27 (2090), under the Hadley A1b GCM. However, temperatures used in the baseline calculation included five of the warmest years on record, and so the baseline was actually warmer than the prediction for Hadley A1b, a fairly conservative scenario and model, for 2040.

All areas of Oregon and Washington west of -121:30 longitude (approx. crest of Cascade range) had a 2001-7 DPD model-based baseline mean for foliage retention (FolRet) of 87.4%. Predicted changes in regional average FolRet for the three GCMs varied from 83.8 to 92.4% by 2040 under scenario A2, from 81.6 to 97.8% FolRet for 2040 under scenario A1b, and to 86.8% for 2040 MIROC B1. The MIROC GCM, with scenario A2, predicted modest decreases in average foliage retention to 83.8% by 2040 and to 81.6% by 2090. From all GCM scenarios, most SNC impact from climate change to 2090 remains in the Coast Range; disease predicted for the Cascade Range remains relatively insignificant.

For the region of Coastal Oregon for which annual SNC aerial surveys have been conducted (west of -124.10 and north of Gold Beach, OR), i.e. the current ‘epidemic area’, the average baseline foliage retention was 78.2%. This is predicted to decrease to 73.2% (2040) and 70.3% (2090) under MIROC GCM with emissions scenario A2. Using a high severity category threshold of 60% or less foliage retention, the land area potentially affected by severe SNC is predicted to increase from the current baseline of 3,682 km<sup>2</sup> (coastal Oregon) and 4,604 km<sup>2</sup> (all western Oregon and Washington), to 5,767 km<sup>2</sup> (coastal Oregon) and 8,730 km<sup>2</sup> (all western Oregon and Washington) under MIROC A2 by 2040, and to 7,185 km<sup>2</sup> (coastal Oregon) and 13,476 km<sup>2</sup> (all western Oregon and Washington) by 2090 (Fig. 6). This model scenario (MIROC A2), therefore, predicts that the potential area affected by severe SNC would approximately double in the Oregon coastal zone, and expand an additional ca. 8,900 km<sup>2</sup> in other areas by 2090.

The results presented here are intended to illustrate potential applications of disease prediction models in combination with climate change predictions, and should not be used as the basis for specific management decisions. The preliminary results should be accepted only with great caution; the technique is new and appears to have multiple uses. For example, application of GCMs to current data-derived models may help identify the most robust climate parameters for use in predicting future disease. Dewpoint may be superior to precipitation for such models, as evidenced both by low correlation scores and by non-intuitive out of range GCM model results. Because PPT was fit as a quadratic function (both in the Watt et al. (2010) New Zealand model and for Oregon), this was not robust with respect to future climate change, which may also indicate that it is a poor choice of parameters to represent early summer moisture. In contrast, dewpoint based models appeared to perform as expected, producing plausible future changes in SNC distribution for most climate change scenarios.

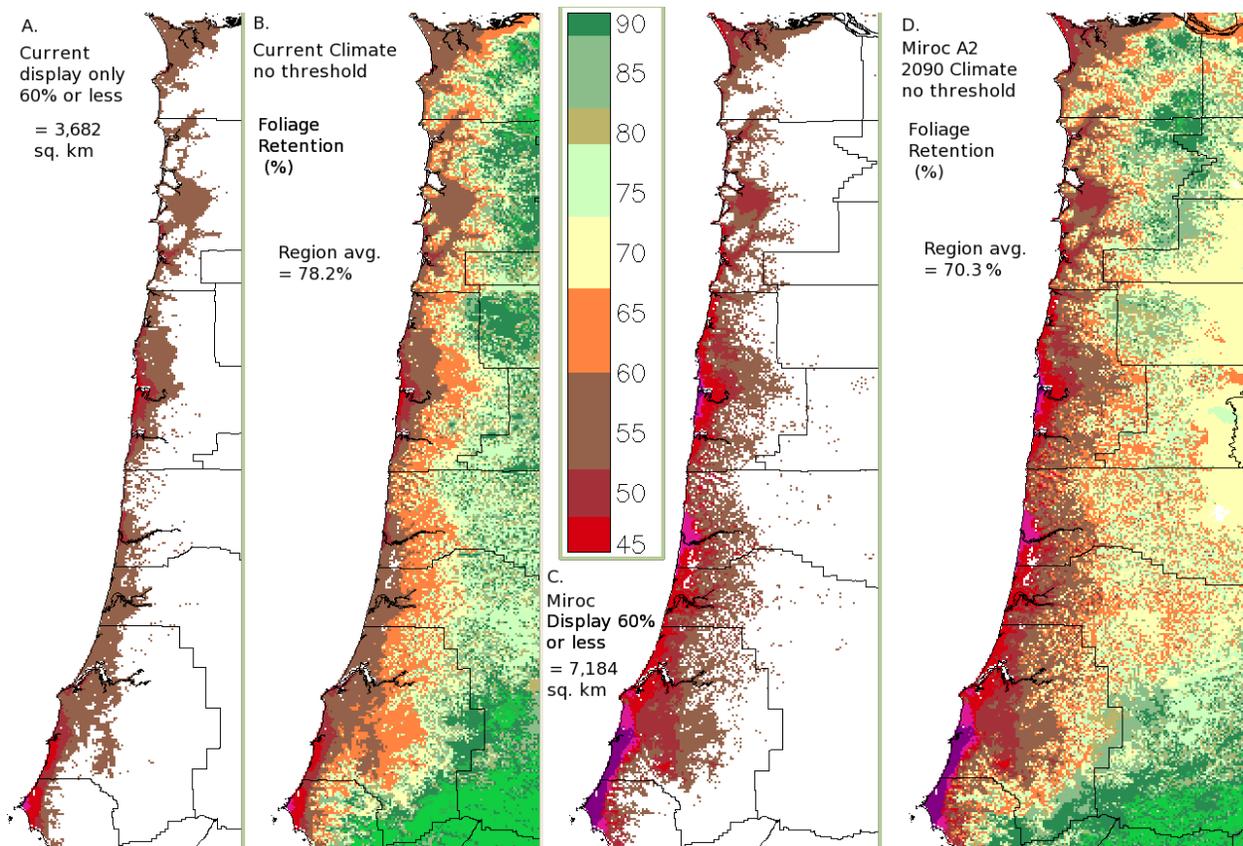


Figure 6. Modeled extent of current and future example SNC-affected foliage retention of Douglas fir needles. A. Current (2001-2007 model estimate showing only areas predicted with 60% or less foliage retention), B. Current model estimate for region, C. Miroc A2 2090 scenario showing only areas with 60% or less foliage retention, D. Miroc A2 2090 model estimate for region.

Further work is needed to refine and verify current disease models and investigate their application under climate change. The GCMs used in this application initially varied with respect to magnitude of air temperature changes by 2040 and 2090. However, some GCM scenarios showed the potential for SNC severity shifting southward to the Coos bay region, which needs further verification/investigation as to possible causal factors.

A specific limitation of the results presented here is that disease models based on current disease distribution were applied directly to GCM predictions for climate variables in 2040 and 2090. A better approach would be iterative, applying annual or decadal averages to changes in air temperature and DPD predicted under climate change scenarios to better display trends. Furthermore, some critical aspects of the disease cycle, such as timing of ascospore release, host bud break etc, and interactions between *P. gaeumannii* abundance and foliage retention, may be climate-mediated and could result in differences between predicted and observed disease severity.

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## **Diameter Measurement of Nehalem First-Generation Douglas-Fir Progeny Test Sites**

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The Nehalem test series, planted in 1986, has been a very important source of data on inheritance of tolerance to Swiss needle cast (SNC) disease and selections for the North Oregon Coast. A large number of families (over 400) were tested at ten sites from near Knappa to east of Dolph; the tests were successfully established and have provided high quality data. Data were obtained for all trees on all sites in 1989 and 1995, and diameters on a subset of five sites in 2001-2. Foliage traits (needle retention, crown density and color) were assessed between 1993 and 1996. Data from the third measurement strongly indicated the ability of some families to continue diameter growth even after years of substantial SNC impact.

Following eight to nine more years with severe to moderate SNC in the Oregon Coast Range, members of the Swiss Needle Cast Cooperative and members of the Trask Second-Cycle Tree Improvement Cooperative approved another study of the growth progress of families in this series, by means of a fourth measurement (the third for DBH) on five sites in 2010. The five sites (Slick Rock, Acey Creek, Coal Creek, Cole Mountain and Davis Creek) were all owned by ODF and had (1) DBH data from 2001-2 and (2) estimated needle retentions of 1 to 1.5 years based on the Adams / Latta model. All sites, with the exception of Davis Creek, had been pruned to 7' above ground line. Cole Mountain, Davis Creek and Set 10 had been pre-commercially thinned about five years ago, and the remaining nine sets on three sites in early-2010. All sites were thinned by removing alternate diagonals.

The original plan was to measure all ten sets, but the recent pre-commercial thinning of three sites had left a deep accumulation of logging slash, hindering the work of the field crew. In order to stay within budget, we therefore opted to measure five sets (including set 10) containing over 200 families and 5,962 surviving trees. The incidence of ramicorn branches and forks was recorded, since it added very little to measurement time. The work was done between July 22 and August 18, 2010 (age 25.5 from seed). The number of families, sites and trees should still be adequate to draw conclusions on the following questions: (1) have there been notable changes of ranks for dbh over the years? (2) how much diameter growth is occurring in the top families? (3) what is the predicted gain for total dbh and dbh increment of the top families? (4) what is the correlated gain for dbh at age 25.5 from selection for height/ dbh/ volume index/ crown traits at age-11? These questions will be addressed during the next year.

# Third-year Response of Ectomycorrhizae to Soil Nitrogen Amendments and SNC Disease

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## Abstract

Three years after treatment, across seven blocks, the nitrogen treatment decreased feeder-root density by 43% ( $p = 0.06$ ), but no effects were detected on ectomycorrhiza type richness ( $p = 0.44$ ). The effect of block was not significant for either variable ( $p = 0.16$  and  $0.11$ , respectively).

For control plots, ectomycorrhizal fungus species richness was significantly correlated with root density;  $R^2 = 0.74$ ,  $p = 0.01$ .

For urea plots, ectomycorrhizal species richness was not correlated with root density;  $R^2 = 0.02$ ,  $p = 0.76$ .

For control plots, ectomycorrhizal species richness was significantly correlated with Douglas-fir needle retention;  $R^2 = 0.63$ ,  $p = 0.03$ .

For urea plots, ectomycorrhizal species richness was not correlated with Douglas-fir needle retention;  $R^2 = 0.15$ ,  $p = 0.40$ .

For control plots, ectomycorrhizal root density was not significantly correlated with Douglas-fir needle retention;  $R^2 = 0.35$ ,  $p = 0.16$ .

For urea plots, ectomycorrhizal root density was not correlated with Douglas-fir needle retention;  $R^2 = 0.000002$ ,  $p = 0.998$ .

This study focused on sites with moderate to strong Swiss needle cast disease, where ectomycorrhizal root density and species richness was lower than on less impacted sites. Mean root density varied by 2.5x among sites while mean ectomycorrhizal species richness varied by about 2x. We speculate that our observations demonstrate a threshold of root density below which mean richness stabilizes at about two ectomycorrhizal types per 350 cc soil core volume. Ongoing work will examine this hypothesis.

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

## Introduction

### *Ectomycorrhizae and Silvicultural Manipulations*

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

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

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

### *Previous Results*

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

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

tolerant” EM fungi are important for sustaining Douglas-fir in the face of SNC disease (Luoma and Eberhart 2008)

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

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

In 2009, across six blocks of the Kinsey treatment, no effects were detected, two years after treatment, on either feeder-root density ( $p = 0.84$ ) or ectomycorrhiza type richness ( $p = 0.96$ ). The effect of block was significant for both variables ( $p = 0.02$  and  $0.009$ , respectively). Mean root density varied by nearly 8x among sites while mean EM species richness varied by about 3x.

Ectomycorrhiza species richness was significantly correlated with root density;  $R^2 = 0.75$ ,  $p = 0.01$ .

Ectomycorrhizal root density was not significantly correlated with Douglas-fir needle retention;  $R^2 = 0.41$ ,  $p = 0.12$ .

Ectomycorrhiza species richness was significantly correlated with Douglas-fir needle retention;  $R^2 = 0.70$ ,  $p = 0.02$ .

Three years post-treatment, we present results as part of the “Beyond Nitrogen” fertilization study. This study focused on sites with moderate to severe SNC disease, where EM root density and species richness was lower than on less impacted sites (Luoma and Eberhart 2009). Our findings provide an essential component to assess functional fertilizer effects on SNC disease. Ectomycorrhizae are the organs through which any nutritional benefits of fertilization are conferred to Douglas-fir trees.

## Methods

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

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

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

Landowner	Location	Block code	Retention (yrs.)
Stimson (Green Diamond <sup>1</sup> )	Hemlock	GDH	1.65
Hampton	Grand Ronde	HAGR	2.00
Cambell (Menasha <sup>1</sup> )	Menasha - north	MNN	1.66
Cambell (Menasha <sup>1</sup> )	Menasha - south	MNS	1.92
Oregon Dept. Forestry	Elk City	ODF	2.18
Oregon State University	McDonald Forest	OSU	3.04
Starker	Burnt Woods	STR	2.47

<sup>1</sup> Landowner at start of study

For the nitrogen treatment, one 350 cc soil core was taken from beneath the canopy of five randomly chosen treatment trees in each block. In the two previously unsampled blocks, five randomly selected control trees were also sampled. Five of the trees in five blocks were sampled from the control treatment in 2009. A total of 70 soil cores were used (10 trees/block x 7 blocks) for this analysis. When possible, soil cores were obtained about 15 cm from the marked 2007 soil core location. In a few instances, the location of the previous core could not be determined, in which case the new core was located the same distance from the base of the tree (1m) and on the side of the tree from which the nearest adjacent trees were at the greatest distance, following the same procedures used in previous samples (Luoma and Eberhart 2009).

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

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

Linear regression was used to examine gradient responses in feeder root density and EM species richness to among-block variation in SNC disease (average tree-level foliage retention rounded to the hundredth of a year). 2009 needle retention data were provided by D. Mainwaring and were obtained following the methodology described in Mainwaring and Maguire (2008). Mean years needle retention did not require transformation. Linear regression was also used to measure the association between feeder root density and species richness. When necessary, to better meet the assumptions of normality and constant variance, we

transformed the dependent variables (Sabin and Stafford 1990). To test for fertilizer treatment effects, feeder root density and EM richness were square-root transformed, as was the case when testing for among-block variation in the response variables and for the linear regression analysis.

## Results and Discussion

Across seven blocks, the nitrogen treatment decreased feeder-root density by 43%; Control mean = 228 EM root tips/soil core, N mean = 129 EM root tips/soil core ( $p = 0.06$ , SE = 39.7 and 18.2, respectively). No effects were detected on EM type (species) richness; Control mean = 3.0 species/soil core, N mean = 2.5 species/soil core ( $p = 0.44$ , SE = 0.3 and 0.2, respectively). The effect of block was not significant for either variable ( $p = 0.16$  and 0.11, respectively). Nitrogen treatment response by block for feeder-root density is presented in Fig. 1.

For control plots, ectomycorrhizal root density was not significantly correlated with Douglas-fir needle retention;  $R^2 = 0.35$ ,  $p = 0.16$ . For urea plots, ectomycorrhizal root density was not correlated with Douglas-fir needle retention;  $R^2 = 0.000002$ ,  $p = 0.998$ .

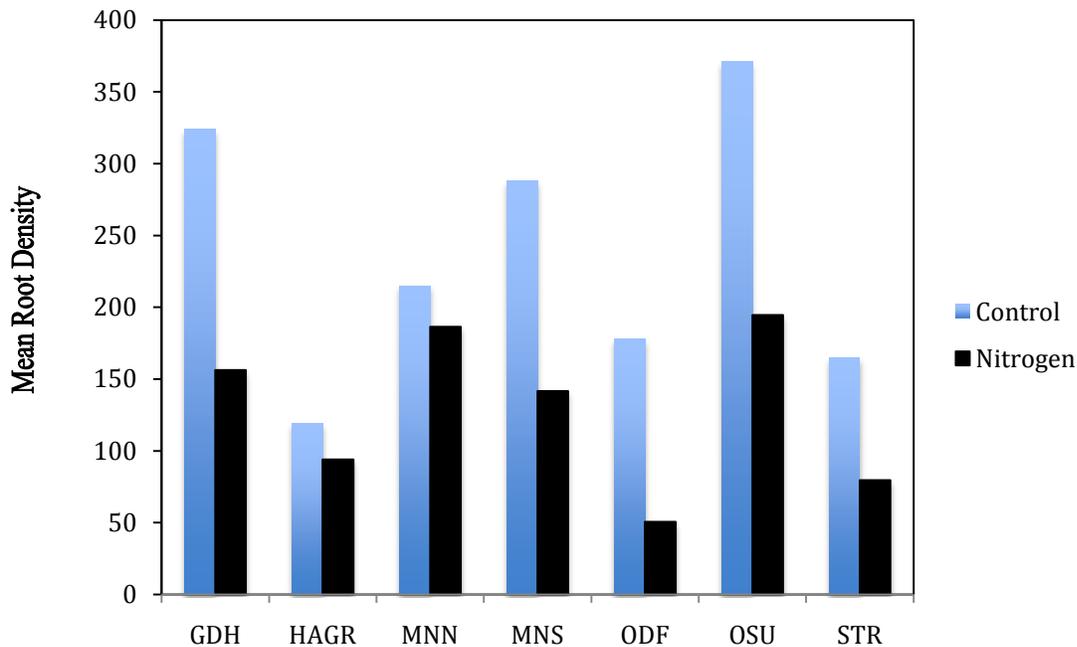


Figure 1. Variation in feeder root density (mean # of ectomycorrhizal root tips/soil core) by treatment across study sites (blocks). The treatment means were different across blocks ( $p = 0.06$ ,  $n = 5$ ). Mean root density was not different among blocks ( $p = 0.16$ ). Site codes are provided in Table 1.

The one-time application of N (as urea) in our study, at a rate of 230 kg/ha, is at the high end of application rates for which EM responses have been reported. The reduction in ectomycorrhizae found here closely mirrors the results of Nilsson and Wallander (2003) who found that EM fungi produced about 50% less mycelium in the soil after N fertilization of 100 kg/ha/yr (as ammonium sulfate) for ten years. Kårén and Nylund (1997) found a 49% reduction

in EM root biomass associated with N fertilization of 100 kg/ha/yr (as ammonium sulfate) for six years prior to sampling. Conversely, Jonnson et al. (2000) found that moderate nitrogen (as ammonium nitrate) additions of 35 Kg/ha/yr for four years had little effect on EM root tip density.

For the control treatment, ectomycorrhizal fungus species richness was significantly correlated with root density;  $R^2 = 0.74$ ,  $p = 0.01$  (Fig. 2). For the nitrogen treatment, ectomycorrhizal species richness was not correlated with root density;  $R^2 = 0.02$ ,  $p = 0.76$ .

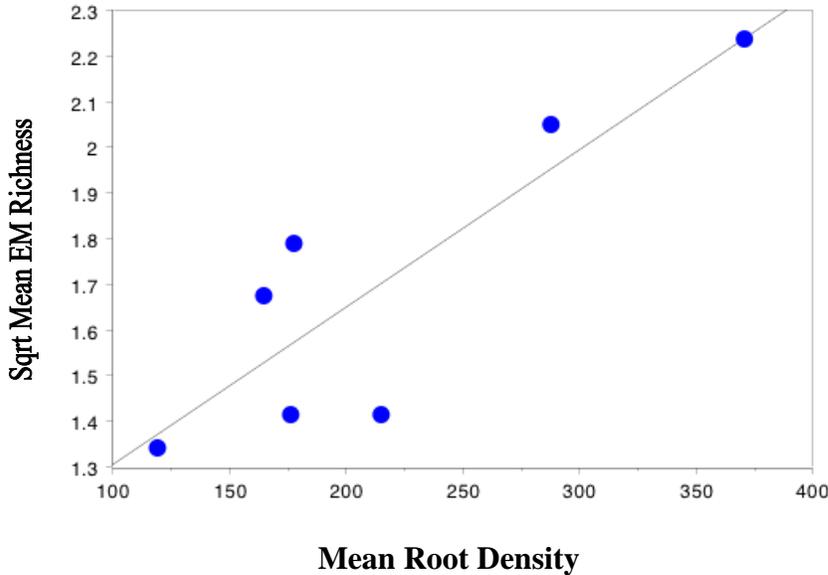


Figure 2. Control treatment regression of mean ectomycorrhiza species richness (square-root transformed) against mean root-tip density (# of EM tips/soil core),  $Y = .958 + .003 * X$ ;  $R^2 = 0.74$  ( $p = 0.01$ ,  $n = 5$  in each block).

For control plots, the regression relationship between EM richness and root density remained similar to past values, even though two highly impacted SNC sites were added to the analysis and two low-impact sites were excluded (2007:  $R^2 = 0.65$ , 2009:  $R^2 = 0.75$ , 2010:  $R^2 = 0.74$ ). The nitrogen treatment eliminated that correlation. Mean root densities under the nitrogen treatment trees ranged from 40 to 200 EM tips/soil core and species richness ranged from two to three EM types/soil core. Though there is a strong correlation between root tip density and EM species richness over a range of densities, including mean values as high as 1200/soil core (Luoma et al. 2006, Luoma and Eberhart 2009), at the low root densities imposed by the nitrogen treatment, mean EM species richness fell to a low value (2.5/soil core), with no correlation over the limited range of root densities. We speculate that the data show a threshold effect at about 250 EM tips/soil core ( $< 1$  tip/cc soil volume), below which EM species richness stabilizes. The apparent stability may simply reflect the physical limit of EM richness to drop below 1, as long as live EM roots are present.

For control plots, ectomycorrhizal species richness was significantly correlated with Douglas-fir needle retention;  $R^2 = 0.63$ ,  $p = 0.03$  (Fig. 3). For urea plots, ectomycorrhizal species richness was not correlated with Douglas-fir needle retention;  $R^2 = 0.15$ ,  $p = 0.40$ .

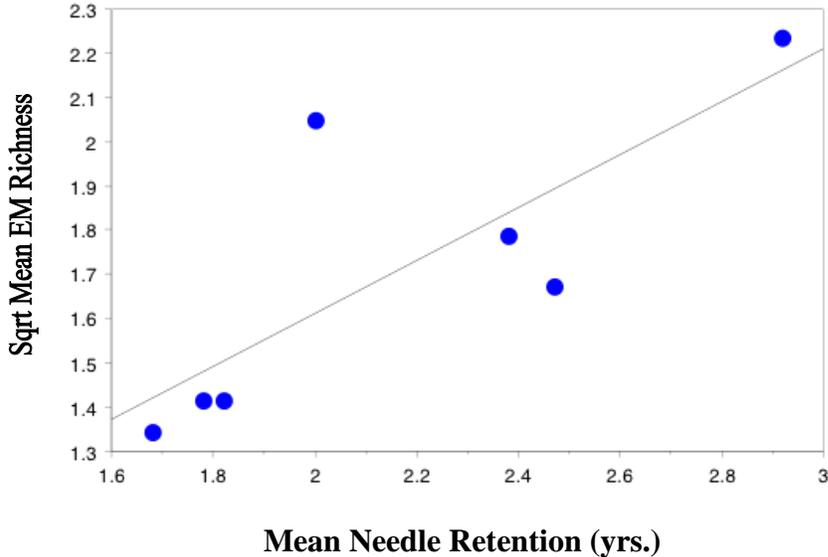


Figure 3. Control treatment regression plot of mean ectomycorrhiza root density (square-root transformed) against mean years needle retention,  $Y = 0.415 + 0.599 * X$ ;  $R^2 = 0.63$  ( $p = 0.03$ ,  $n = 5$  in each block).

Although EM type (species) richness was significantly related to needle retention in the control treatment samples (Fig. 3), the strength of the relationship was far less than we found in 2007 ( $R^2 = 0.90$ ) or 2008 ( $R^2 = 0.93$ ). Again, this is likely related to the blocks that were sample in 2010 being weighted more towards higher levels of SNC disease than in the past sampling efforts. In addition, the MNS site was something of an outlier with higher than expected EM species richness, given the level of SNC disease on the site. The correlation between root density (EM habitat availability) and species richness helps explain the lack of a significant regression between EM richness and needle retention in the nitrogen treatment plots. Low root densities associated with nitrogen fertilization across the range of retention limited the opportunities for EM fungus species to colonize roots.

Although EM root-tip density did not have a statistically significant regression relationship with needle retention, there was a striking difference in the correlation between the control and N treatments. For the control treatment, the correlation coefficient was 0.59 while the N treatment had a correlation of 0.001. This suggests stronger absolute changes in response to nitrogen at higher root densities.

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

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

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

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



Figure 4. An ectomycorrhiza of *Lactarius* on Douglas-fir that was growing in buried class IV coarse woody debris.

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# Interaction between Fertilization Treatment and Swiss Needle Cast Disease Severity in Douglas-fir Seedlings

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## Abstract

There is continued interest in the relationship between host nutrient status and Swiss needle cast disease severity. The aim of this study is to investigate the interaction between nitrogen concentration in Douglas-fir foliage and subsequent infection and colonization by *Phaeocryptopus gaeumannii*. Containerized Douglas-fir seedlings were fertilized and exposed to natural inoculum at a site with moderate disease-intensity in the Oregon Coast Range (Norton Hill near Summit, OR) from mid-May to late-July 2010. Foliar nitrogen concentration will be assessed early-November 2010 from a subset of seedlings from each treatment to verify that the concentration of nitrogen in host needles is reliably correlated with the four fertilization treatment levels. Fertilization will continue in spring after dormancy, and seedlings will again be exposed to natural inoculum during the 2011 growing season. Pseudothecia incidence and density on one and two year old needles will be assessed in 2012 as a measure of *P. gaeumannii* colonization.

## Introduction

*Phaeocryptopus gaeumannii* (Rohde) Petrak, the causal agent of Swiss needle cast (SNC) disease, is a foliar pathogen that results in chlorosis, premature needle abscission and growth loss of Douglas-fir trees. *P. gaeumannii* is endemic to western North America, and is ubiquitous throughout the native range of Douglas-fir (Boyce 1940). Although *P. gaeumannii* was once believed to be a minor pathogen in the Pacific Northwest, reports of severe SNC disease symptoms in Douglas-fir plantations covering large areas of coastal Oregon and Washington in the mid-1980s and 1990s led to the establishment of the Swiss Needle Cast Cooperative (SNCC) in 1997 (Hansen et al. 2000).

A reoccurring research theme throughout the life of the SNCC, related to mitigating disease impacts and understanding host-pathogen interactions, has been investigating the relationship between soil and foliar nutrition and SNC disease severity through field observational studies and silvicultural and growth chamber experiments (Appendix I, this report). Although there are theories as to how host nutrition might impact fungal colonization, no studies to date have established a clear mechanistic linkage between foliar nutrient status and the ability of *P. gaeumannii* to colonize host needles. The relative biomass of the *P. gaeumannii* within host needles is directly correlated to the proportion of needle stomata occluded by fungal fruiting bodies (Winton et al. 2003), the means by which the fungus causes disease (Manter et al. 2000). It has been postulated that high levels of nitrogen relative to other essential micronutrients compromise host cell membrane integrity. This is suggested to cause increased nutritional leakage into the apoplast, where it can be accessed by the pathogen and contribute to

its proliferation (Rose et al. 2000, Rose et al. 2001, Rose and Manter 2002, Kavanagh et al. 2003, El-Haaj et al. 2004). The results of SNC-nutrient studies have not allowed for consistent conclusions to be drawn, and, in many cases, multiple interpretations of the results have been possible.

The current study aims to: 1. establish consistent levels of foliar nitrogen concentration in Douglas-fir seedlings using different levels of fertilization ( $H_0$ : [N] and total N is equal among needles of the same age class across treatments), 2. assess whether seedlings with higher percent or total nitrogen (and fertilized with larger quantities of nitrogen) experience greater fungal colonization following exposure to the same level of inoculum ( $H_0$ : infection index (needle infection incidence \* pseudothecia density) is the same across treatments), 3. assess if and how infection alters foliar nitrogen levels ( $H_0$ : [N] and total N is the same across treatments), and 4. assess the impact of fertilization treatment on height and diameter growth ( $H_0$ : there is no difference in seedling height or diameter across treatments). The results of this study are expected to complement the ongoing *Beyond-N* study, which has been designed to assess the impacts of different fertilization treatments on tree growth and disease-severity in forest plantations across a range of SNC disease severity.

## Materials and Methods

One-hundred and eighty 1+1 Douglas-fir seedlings (donated by Starker Forest Inc.) were potted in 4 x 4" pots with Sun Gro potting soil (Sun Gro Horticulture Canada Ltd., Seba Beach, AB), in February 2010 and stored outdoors at the Forest Research Laboratory (Oak Creek Facility, Corvallis, OR). Seedlings were transplanted to 6 x 6" pots on April 1, 2010, because it was determined that 4 x 4" pots were too small and that soil levels were too close to the brim of the pots to allow for proper watering and fertilization. Seedlings were randomly assigned to four fertilizer treatments (N= 45), which were applied to seedlings for the first time from April 1- 15, 2010, and for the second time from May 26- June 9, 2010. Fertilization spanned several weeks because each nitrogen application was limited to 50 ppm (0.25g fertilizer (0.05g N) in 1L of water per plant) to prevent salt toxicity, and treatments were applied seven days apart.

Fertilizer was a high-end, balanced container blend (Jack's Classic All Purpose 20-20-20, J.R. Peters Inc., Allentown, PA), composed of 20% total nitrogen, 20%  $PO_2O_5$ , 20%  $K_2O$ , and micronutrients in chelated form (Table 1). For both of the fertilization periods, the four fertilizer treatments were: 1) Control (unfertilized, water-only), 2) Low N (0.05g N in one application), 3) Med N (0.10g N in two applications), and 4) High N (0.15g N in three applications). Fertilizer solution was prepared in large batches at a ratio of 0.25g fertilizer: 1L clean tap water. Plants were watered with 2L of water pre-treatment, followed by 1 L of fertilizer solution, and were not watered for at least four days post-treatment.

Table 1. Composition of Jack's Classic All Purpose 20-20-20 Fertilizer used to treat Douglas-fir seedlings (J.R. Peters Inc., Allentown, PA).

Total Nitrogen (N)	20%
2.1% Nitrate Nitrogen	
17.9% Urea Nitrogen	
Available Phosphate (P <sub>2</sub> O <sub>5</sub> )	20%
Soluble Potash (K <sub>2</sub> O)	20%
Boron (B)	0.02%
Copper (Cu)	0.05%
0.05% Chelated Copper (Cu)	
Iron (Fe)	0.10%
0.10% Chelated Iron (Fe)	
Manganese (Mn)	0.05%
0.05% Chelated Manganese (Mn)	
Molybdenum (Mo)	0.00%
Zinc (Zn)	0.05%
0.05% Chelated Zinc (Zn)	

Seedling height and diameter at base (DAB) were measured early-April, concurrent with the first fertilization treatment, and no significant differences in initial height or DAB were detected between treatments (ANOVA p-values 0.13 and 0.38, respectively, Tables 2 and 3). Seedlings were transported to a moderate disease-intensity site in the Coast Range near Norton Hill and Summit, Oregon, on April 16, 2010. *Phaeocryptopus gaeumannii* ascospore dispersal coincides with natural Douglas-fir budbreak and shoot elongation from May to late-July (Chastagner and Byther 1983, Michaels and Chastagner 1984), and seedlings remained at the site for natural inoculum exposure for the duration of the sporulation period. Seedlings were arranged in boxes (4 per box) that contained multiple treatments, and boxes were positioned in a line behind a deer fence in full-sun. Seedlings were watered 1-2 times per week ( $\geq 2L$  per plant), as needed, until they were returned to the Forest Research Laboratory in Corvallis, OR on July 30, 2010. Watering continued approximately once per week through mid-September, after which seedlings received only rainwater. Natural photoperiod and temperature cues will trigger winter dormancy.

Table 2. Summary and test for initial height differences between treatments.

Anova: height (cm)						
SUMMARY						
Groups	N	Sum	Average	Variance		
Control	45	2444	54.31111	166.7192		
Low N	45	2659	59.08889	142.5374		
Med N	45	2700	60	188.0909		
High N	45	2592	57.6	99.38182		
ANOVA						
Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	841.6611	3	280.5537	1.88061	0.13457	2.655939
Within Groups	26256.09	176	149.1823			
Total	27097.75	179				

Table 3. Summary and test for initial diameter at base differences between treatments.

Anova: diameter at base (mm)						
SUMMARY						
Groups	N	Sum	Average	Variance		
Control	45	380.98	8.466222	3.394074		
Low N	45	404.79	8.995333	2.376403		
Med N	45	404.92	8.998222	3.113379		
High N	45	398.15	8.847778	1.956263		
ANOVA						
Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	8.471044	3	2.823681	1.041937	0.375398	2.655939
Within Groups	476.9652	176	2.71003			
Total	485.4363	179				

## Future Work

Foliage samples were collected November 8, 2010. At this time, growth measurements were recorded for all seedlings (DAB and height), and five random seedlings from each fertilization treatment were destructively sampled for foliar nutrient analysis. One- and two-year old needles from each sample seedling will be analyzed separately. The primary objective of this analysis is to determine whether or not foliar nitrogen concentration is correlated with the quantity of nitrogen applied across the four fertilization treatments.

If fertilization has not resulted in a gradient of foliar nutrient levels, the study design will be re-examined. Provided that the desired spread in foliar nitrogen levels has been achieved, seedlings will be fertilized in early-Spring 2011 using the same fertilization protocol. Seedlings will then be transported to the Norton Hill site for exposure to natural inoculum from late-April to late-July, and foliage samples will be collected for nutrient analysis in mid-October. In April 2012, one- and two-year old foliage samples will be collected for the assessment of SNC disease severity. ANOVA will be used to test treatment differences in infection index (the product of infection incidence and pseudothecia density).

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## Summary Table of SNC-Nutrient Studies (Appendix I)

Abbreviations: DF= Douglas-fir; PG= <i>P. gaumanni</i> ; Tx= treatment; FAA= free amino acids; [ ]= concentration; QPCR= quantitative polymerase chain reaction; PCT= pre-commercially thinned; fol. ret.= foliage retention.							
Study	Authors/Report(s)	Objectives	Study Design Summary	Timeline	Fertilization Treatments	Relevant Findings	Comments
Effects of soil nutrients on infection levels	Stone, Winton, Capitano, Manter, Rosso, Reeser, Sutton, Hansen  Annual Report: 1998 (p27).	To determine if there is a relationship b/t soil nutrients and infection levels.	Fertilized potted DF seedlings exposed for different periods of time to natural inoculum at Juno Hill & Soil analysis at 9 test sites near Tillamook.	Limited information provided on fertilization timing and methods.	Macronutrient blend fertilizer; three soil Tx: 1. Juno Hill soil 2. Juno Hill soil plus fertilizer 3. Soil from plantation with minimal disease	No difference in infection levels detected for three Tx; no evidence of a relationship between foliar nutrients and infection level in field plots.	Foliar nutrient levels not assessed in seedling study to ensure that Tx effectively increased foliar [N].
Effects of fertilization and vegetation control on SNC infection and growth of coastal DF saplings	Crane, Robin Rose, Ketchum, Haase, Rosner (participants vary over time)  Annual Reports: 1999 (p39), 2000 (p59), 2001 (p69), 2002 (p74), 2004 (p59).  (2001 & 2002 reports relevant to nutrients & SNC)	To determine how fertilization and vegetation control influence SNC infection and subsequent growth of coastal DF seedlings.	3 sites on E-W gradient; 7-9 yr old DF plantations; 70 x 70ft plots; randomized block design; 5 reps/site; fertilizer Tx applied to each of the 15 trees in plots designated for fertilization; 6 Tx total (2 veg control x 3 fertilization); assessed tree growth, foliar nutrients & SNC.	-Plots established May 1999 -Pre-Tx foliar nutrient analysis Oct 1998 -Fertilizer applied Sept 1999, April and Oct 2000, and April 2001 -Growth & SNC characteristics monitored and foliage collected Dec 2000	Simplot controlled release fertilizer with minor elements; surface-applied around tree base; applications made Sept 1999; 3 Tx: 1. unfertilized control 2. 200g 17-17-17 3. 200g 9-17-17 Due to inconsistent foliar response to Tx (other than Boron), changed to soluble form in April 2001.	2001: fertilizer Tx showed no increase in relative [nutrient] or content, while B, Zn and Cu increased 20-25% compared to controls; needle wts greatest in plots with complete veg removal; at Charlie Olson site, veg control resulted in a 15-25% increase in foliar N. 2002: foliar [N] have increased with veg control and fertilization in yr 2, [P] decreased in fertilizer Tx. 2003: fertilization	2001: QPCR showed that Bushy Peterson site was more heavily infected than S Drake, but had higher fol. ret. and is farther from the coast (this challenges the paradigm that fol. ret. and PG biomass are well-correlated); at one site, foliar [N] increased with veg control-only Tx (does this suggest that N is limiting and not "in excess"?). 2002: lack of growth response to foliar N suggests that increased nutrient availability did not occur in yr 1; soluble fertilizer and increased rate allowed for fertilizer response in yr 2.
Effect of elemental S on SNC infection and growth of coastal DF saplings	Crane, Robin Rose, Ketchum, Haase  Annual Report: 2000 (p66).  (also summarized in other reports, but 2000 is relevant to nutrients & SNC)	To determine how applications of S influence SNC infection and subsequent growth of coastal DF seedlings.	Toledo/S Drake site; 6 yr old plantation; 10 reps of 5 Tx: 1. control, 2. Bravo, 3. Thiolux ground 4. Thiolux foliage 5. Thiolux foliage w/ sticker	-Tx applied June 1999 -1-yr fol. ret. assessed July 1999 -Needles collected for SNC quantification April and Feb 2000 -Current yr foliar and soil nutrient samples collected Dec 1999 -Foliar nutrient samples collected Nov 2000	Fertilizer not applied. Fungicide Tx at 2-wk intervals around budbreak and shoot elongation.	Trees that received Bravo Tx had significantly > foliar [N]; this might suggest that PG consumes N in infected needles or that tree redirects N away from infected needles (2000 Report); higher foliar [S] in trees treated with S Tx (but needles not washed pre-analysis); no significant differences in soil nutrients among Tx other than SO <sub>4</sub> (2x > in Thiolux ground vs. control).	2000 Annual Report the only report relevant to nutrients & SNC; important to consider multiple interpretations of higher N content in sprayed foliage (fungal consumption vs. whole-tree resource allocation).
Nutritional imbalance as predisposing factor in SNC disease (Part I)	Cathy Rose, Kavanagh, Waring  Annual Reports: 2000 (p70), 2001 (p55).  See related summary below.	To determine if higher levels of FAA are associated with higher levels of SNC; to determine how [FAA] changes with needle age.  Suggests that high levels of disease linked to high N:S ratio, which causes FAA to leak into apoplast and provide PG with increased nutrient.	Four 12-20 yr old DF plantations with varied SNC (Juno Hill, S Drake, Beaver Ck & Coal Ck); 3 trees per Tx or disease level; Tx varied by site; 30-50 needles collected on 3 "well-illuminated branches" per tree at 4 times around bud break; FAA levels quantified.	Juno Hill: Tx applied at bud break in 1995-1998. S Drake: Tx applied June 8, June 25 and July 10th 1999. Beaver Ck.: Tx applied 1998, 1999 and 2000 at budbreak & 1 mo. later. Coal Ck.: Compared adjacent trees (obs. study; diseased vs. healthy).	Juno Hill: 1) 3 unsprayed control branches from 3 trees; 2) 3 branches from the same 3 trees treated w/ Bravo (rate unknown). South Drake: 1) 3 unsprayed control trees; 2) 3 trees with surface application of Thiolux (2 oz /tree). Beaver Ck: 1) 3 unsprayed control trees; 2) 3 trees with surface Bravo Coal Ck: 1) 3 trees with low SNC (> 3 yrs foliage); 2) 3 trees w/ high SNC (< 1.2 yrs foliage).	All current year foliage contained higher [FAA] than expected based on "baseline"; % N high (≥ 1.5%), esp. post-budbreak, and higher in trees with low disease severity; FAA did not vary with SNC; S was not limiting at any sites; seasonal patterns [FAA] consistent across sites; in all cases, unsprayed trees had reduced [FAA] and sprayed saplings had [FAA]>controls; "our finding that FAA levels decline with high levels of infection is consistent with the hypothesis that the fungus is metabolizing FAA".	Possible that higher [FAA] in sprayed branches is b/c the whole tree allocates FAA to needles that assimilate sufficient C for growth & maintenance (esp. Juno Hill); FAA w/in, b/t cells and w/in the fungus not differentiated (relevant b/c pathogen can only access nutrient in apoplast); DF on Vancouver Is. used to provide "baseline" levels of foliar N; small n & different Tx used at different sites; at Juno Hill, control & Tx trees the same; "information from both pristine and N-enriched sites suggest that needle N values above a threshold of 1.4- 1.5% reflects surplus N uptake in conifers"; but this compares N levels in different DF ecosystems; differences b/t control & Tx in current foliage post-budbreak not significant.

Abbreviations: DF= Douglas-fir; PG= <i>P. gaeumannii</i> ; Tx= treatment; FAA= free amino acids; [ ]= concentration; QPCR= quantitative polymerase chain reaction; PCT= pre-commercially thinned; fol. ret.= foliage retention.							
Study	Authors/Report(s)	Objectives	Study Design Summary	Timeline	Fertilization Treatments	Relevant Findings	Comments
Nutritional imbalance as predisposing factor in SNC disease (Part II)  (2002 Title: "The role of N in SNC disease: modifying foliar N to improve needle retention")	Cathy Rose, Kavanagh, Waring  Annual Reports: 2001 (p55), 2002 (p33).  See related summary above.	To determine if there is an association between disease severity and foliar [N] and [FAA] (Part I, above); to test whether fungal growth in needles respond to [N] and [FAA] in potted 1-0 seedlings grown under a wide range of N (Part II).	Part I: See above Part II: 4 blocks of 5 fertilizer Tx; 6 seedlings per block; seedlings exposed to natural inoculum at Salal (moderate SNC intensity site).  Second set of seedlings not inoculated in 2001, ½ inoculated in 2002 (current and 1-yr needles analyzed).	-Fertilizer Tx applied wkly Jan to May 2001, then bi-wkly -Pre-inoculation samples collected late-May 2001 (N, FAA and PG biomass) -Exposed to inoculum in June -Data collected Oct 2001 and during winter dormancy -PCR analysis Dec 2001 and April 2002	Fertilizer (liquid solutions) formulated to create a wide range of N availability (target values based on Walker and Gessel 1991); fertilized wkly w/ different levels of N and complete balanced macronutrients, then bi-wkly after June 1; nutrient levels assessed pre-inoculation.	Lack of disease response to nutrient levels in Dec 2001 and April 2002; at the start of growing season, only a 25% range in %N (1.4-1.75%), so Tx effect not expected (or detected), but better spread in N levels by Dec; April 2002 foliar analysis showed significant drawdown in foliar N from older needles (seasonal change); in June 2002, significant drawdown of total N (20-30%) in low N Tx, but not in optimal and high N Tx; notable increase in [FAA] in current yr needles of seedlings that had been inoculated in 2001; results indicate that nearly 1 yr is required to drawdown N reserves in fertilized seedlings.	Postulates that reduced C intake may compromise ability to rebalance foliar N:S:C ratio and that imbalance causes FAA to leak into apoplast; 2002 Report makes very broad claims regarding what relationships have been established b/t nutrients and SNC in past coop studies; states that prior studies were compromised b/c trees influenced by disease for several yrs prior to sampling, but PG is a ubiquitous, endemic fungus, so exposure is difficult to avoid; despite lack of infection response, they state that "the peak in [FAA] in current yr needles of inoculated seedlings during June 2002 indicates that there may be a feed-forward mechanism associated with fungal colonization. Such a mechanism would be expected based on known responses of conifers to stomatal induced inhibition of photosynthesis. If this is true, then high foliar N may be an important factor in the intensification of this disease over several years".
The effect of nutritional status of DF on PG: Evidence from foliar chemistry and stable isotopes	Kavanagh, El-Hajj, Cathy Rose  Annual Report: 2003 (p75).  Published (2004): <i>New Phytologist</i> 163: 139-147  "N and C dynamics of a foliar biotrophic fungal parasite in fertilized DF"	To examine the relationship b/t foliar [N] and [FAA] and disease severity in DF foliage; To determine if the N and C isotopic signals can provide insight into host-pathogen nutrient dynamics.	Priest River, ID at USDA Exp. For.; 2001-02; 10 yr old naturally PG-infected DF; 5 trees fertilized with isotopic-N fertilizer and 5 with traceable foliar N spray; random branches collected at 1.2m; foliage surface washed to remove residual fertilizer; pseudothecia density estimated; N fertilization served as the plot, while trees, blocks and needles as observational units.	-Fertilizer applied June 2001, post-bud break -Isotopic-N-enriched fertilizer applied April 2002 -FAA, isotopes N15 and C13 quantified in foliage and quantity of pseudothecia assessed in Oct 2002	Initial fertilization Tx applied at 2 levels post bud break: high urea (HU) and low urea (LU); lag in N-uptake observed; granular formula; isotopic fertilizer applied to soil and traceable foliar N amendments sprayed on branch foliage on 5 additional trees.	Increase in foliar [N] associated with increased pseudothecia in 2- and 3- yr needles (2.2 and 2.6x higher than controls), although [FAA] increased in current yr foliage only; C isotopes unaffected by soil N Tx; LU foliage lacked N signal; pseudothecia on sprayed foliage had high isotopic N, so PG acquired N from foliar application; % N and C in pseudothecia positively correlated; uptake of isotopic C indicated that PG derived C from ground, not spray fertilizer (sucrose or other form of C in apoplast).	Study examines the impacts of fertilization on fungal colonization; still limited understanding of mechanism by which fertilization impacts PG access to nutrient; very small sample size (study should be replicated, cautious interpretation advised); odd 0-4 scale used to assess SNC severity; unsprayed branches on treated trees as controls (consider whole-tree resource allocation of various forms of N); methods described in minimal detail, not possible to replicate experiment; higher N and pseudothecia in fertilized needles contradicts findings in prior studies of lower N and FAA in heavily infected needles.
Trends in soil and foliar nutrients across a range of SNC severity  Continued below in GIS (2001) summary.	Maguire, Waring, Cromack and Boyle  Annual Report: 2000 (p79).	To identify apparent imbalances of nutrients in both soil and foliage samples; to test the hypothesis that SNC severity is correlated with the degree of one or more nutrient imbalances.	25 plots (15 GIS, 10 PCT) to represent extremes of SNC disease severity; composite soil samples near subset of trees with foliage collected; soil & foliage analyzed; nutrients as % of dry wt; multivariate regression analysis w/ nutrient departures from optimum as predictors of disease severity.	-No Tx applied -Samples collected winter/spring 2000 -PCT & GIS permanent plots initially established 1998	Fertilizer not applied; observational study.	Foliar [N] had the strongest correlation w/ mean fol. ret., followed by Ca and S; soil results more limited; when foliage and soil variables included, one model explained 92% variation in retention (foliar Ca, soil N, soil ammonium, and variance from optimum); variation much higher for 13 plots representing extreme SNC conditions.	Caution advised in using fol. ret. as the response variable and as a surrogate for disease severity considering the established relationship b/t foliar [N] and fol. ret. (lower fol. ret. at relatively higher levels of foliar N); however, when the QPCR assay is used as response variable, the results are generally consistent; if nutrient imbalance is an underlying cause of SNC, would high variation be expected in plots representing extreme SNC, as was found in this study?

Abbreviations: DF= Douglas-fir; PG= <i>P. gaeumannii</i> ; Tx= treatment; FAA= free amino acids; [ ]= concentration; QPCR= quantitative polymerase chain reaction; PCT= pre-commercially thinned; fol. ret.= foliage retention.							
Study	Authors/Report(s)	Objectives	Study Design Summary	Timeline	Fertilization Treatments	Relevant Findings	Comments
Growth impact study  Continuation of above summary (2000).	Maguire and Kanaskie  Annual Report: 2001 (p14).  (also in other reports, but 2000 & 2001 relevant to nutrients & SNC)	To identify apparent imbalances of nutrients in both soil and foliage samples; to test the hypothesis that SNC severity is correlated with the degree of one or more nutrient imbalances.	25 plots (15 GIS, 10 PCT) to represent extremes of SNC disease severity; composite soil samples near subset of trees with foliage collected; soil & foliage analyzed; nutrients as % of dry wt; multivariate regression analysis w/ nutrient departures from optimum as predictors of disease severity.	-No Tx applied -Samples collected winter/spring 2000 -PCT & GIS permanent plots initially established 1998	Fertilizer not applied; observational study.	Highest levels of N associated with poorest fol. ret. and growth; curvilinear relationship with peak growth at 1.1% foliar N, then growth declines.	Important to compare these results with those of above studies, many of which show higher foliar N in healthier trees, presumably b/c fungus is not consuming excess foliar N; consider both proposed mechanisms: 1. PG benefits from increased N, 2. N translocated from prematurely abscised needles to remaining needles, and accelerated mineralization on forest floor due to changed light and litter environment.
Electrolyte leakage and nutrient status in SNC-infected DF	Manter and Stone  Annual Report: 2001 (p31).	To assess the impact of PG infection on host membrane permeability by the electrolyte leakage (EL) technique (i.e. to investigate the extent to which plant metabolites diffuse into the intercellular space, which depends on host membrane integrity).	Seedlings exposed to natural inoculum for 2, 4 or 8 wks (high correlation between exposure time and disease severity); 1-yr needles from each tree pooled in test tube and EL measured, then autoclaved and EL re-measured to calculate relative conductivity; formula used to distinguish the relative contribution of leakage from host and pathogen cells based on their relative biomass.	-Seedlings exposed to inoculum in June 2000 -Branches harvested and 1-yr needles pooled in Dec 2000, then EL assessed	Fertilizer not applied; this study investigated the impact of disease on membrane integrity.  This is highly relevant to nutrient-SNC studies because nutrient imbalance is proposed to compromise membrane integrity, allowing PG increase access to nutrient.	No evidence of significant impact of PG infection on membrane integrity and permeability (compared to >25% increase in EL shown with other fungal diseases).	This study did not aim to examine the effects of nutrients on membrane permeability, but instead examined whether PG directly alters the host membrane to increase access to nutrient in the apoplast (mechanism of pathogenicity); this technique should be applied to examine whether nutrient imbalances in needles impact membrane integrity/permeability; Calkins and Swanson (1990) showed that relative conductivity, as measured by EL, is a surrogate for host membrane damage and permeability.
Tree responses to experimental alteration of nutrient availability across a gradient in SNC severity  (Growth of young forest stands after balanced fertilization)	Maguire, Mainwaring, Gourley, Fletcher, Trobaugh, Johnson, Dew, Sevitts, Christensen, Waring, Higgins, Cromack and Boyle  (participants vary over time)  Annual Reports: 2001 (p62), 2003 (p71), 2004 (p71), 2005 (p51).	To identify mechanisms linking SNC severity to nutritional status, and to develop operational prescriptions to mitigate nutrient imbalances that may predispose DF to SNC.  To test the response of young DF stands to balanced fertilizer additions and to test the response of fol. ret. to fertilization with alternative formulations.	8-12 yr and 20-30 yr PCT DF plantations; 16 sites (blocks) total, each containing 32 or 40 miniplots (.025 or .065 ac); plots centered on a pair of DF measure trees; 6 fertilization Tx (including control); 8-10 reps/Tx/stand; 2 sample trees per miniplot assessed pre-Tx and at 2-yr intervals; 1-yr needles collected from 5 (of 20) trees/Tx from all 16 sites 4-5 yrs post-Tx; soil collected and analyzed pre-Tx; foliage from trees of same Tx and site pooled for analysis.	-Balanced nutrient study initiated 1996 (data also collected from other studies initiated by coop contributors) -Tx applied Nov 1997 to Feb 1998 -Pre-Tx measurement 1998, and pre-growing season 2000 & 2003 of tree growth measurements and SNC symptoms -Foliage samples collected winter 2001 for nutrient analysis and PG biomass	1. NPK (high K) 2. NPK (low K) 3. NPK (low K + nutrients) 4. NPK (high K + nutrients) 5. N only 6. control  Fertilization rates given as lbs/ac, probably applied in granular form on soil surface; N applied at 200 lbs/ac, P applied at 60 lbs/ac, K applied at high or low rate (100 or 250 lbs/ac, higher rate in more diseased stands); added micronutrients included Mg, S, B, Cu, Fe, Zn and Ca.	ANOVA indicated no Tx effect on fungal biomass (QPCR); regression analysis shows a marginal positive effect of N and negative effect of Ca on PG biomass and little effect on soil or foliar chemistry; fertilizer Tx had a significant effect on basal area and volume growth, but did not affect fol. ret./SNC severity (i.e. fertilizer impacts on growth were independent of SNC); Tx response depended on initial fol. ret. (growth positively correlated with higher fol. ret.); foliar nutrients showed little separation among Tx; some single elements were significantly influenced (B, Mn, SO <sub>4</sub> ); for soil, only K was significantly higher in high K vs. low K & control Tx.	Interesting that the rank of fertilization Tx (best to worst) were: NPK-plus, N-only, then NPK (volume growth 14%, 10.6% and 6.9% higher than control, respectively); would have expected that NPK would have outperformed N-only based on nutrient imbalance hypotheses; interpretation must account for years since Tx (as stated in report); needles collected for PG biomass and foliar N in winter, but foliage usually sampled for disease in early-spring; unclear as to whether or not collected needles (exposed to inoculum in 2000) were still affected by Tx at time of exposure.

Abbreviations: DF= Douglas-fir; PG= <i>P. gaeumannii</i> ; Tx= treatment; FAA= free amino acids; [ ]= concentration; QPCR= quantitative polymerase chain reaction; PCT= pre-commercially thinned; fol. ret.= foliage retention.							
Study	Authors/Report(s)	Objectives	Study Design Summary	Timeline	Fertilization Treatments	Relevant Findings	Comments
Mineral nutrition and SNC	Stone and Reeser  Annual Report: 2001 (p65).	To determine whether deficiency or sufficiency of specific macronutrients affect PG colonization of DF	Potted DF seedlings fertilized with balanced complete mineral nutrients with 1 nutrient/Tx added back; 3 Tx blocks, 5 seedlings/Tx; seedlings stored at the OSU Botany Farm under 50% shade; exposed to natural inoculum at Salal (a moderate disease site).	-Seedlings planted in coarse sand Feb 2000 -Fertilizer applied w/ly May-Aug 2000, and monthly until sampling April 2001 -Exposed to inoculum May-June 2000	Seedlings in coarse sand with balanced complete mineral nutrient solution at half strength (Murashige and Skoog modified basal salts mixture with NHNO <sub>3</sub> and KNO <sub>3</sub> ); nutrients applied in liquid solution at w/ly intervals; add-back nutrients included N, P, K, Ca, S & control; fertilization based on Walker & Gessel 1991.	Composition of nutrient medium had no effect on SNC incidence or severity as assessed by pseudothecia counts, frequency of infected needles or QPCR.	[Foliar nutrients] not measured pre- or post- inoculation, so impact of fertilization Tx on foliar nutrient levels unknown; fertilizer Tx not conducted in advance of inoculation, so impacts would have most-likely been limited to the post-inoculation period; short-duration study (results obtained over single year).
Control of SNC in forest plantations by aerially applied elemental S fungicide	Stone, Chastagner, Kanaskie  Annual Reports: 2003 (p40), 2004 (p49).  Another nutrient/Sulfur fungicide study (2000) listed in Table on p1.	To evaluate the efficacy of aerially applied S fungicide for SNC control in forest plantations (to mimic realistic application).	Paired 5-ac plots (control and Tx) at 6 sites in the Coast Range in 15-20 yr and 20-25 yr PCT DF plantations; trees assessed for color, retention and pseudothecia density; additional trial in WA; aerial application of elemental S (60 lbs/ac).	-Tx applied 2x early and mid June 2002 & 2003 -fol. ret. & color rated in fall 2002 & 2003 (10 random trees climbed for needle collection for infection & nutrient analyses) -Foliage for pseudothecia counts late May 2003 & 2004	Fertilizer not applied (fungicide only).	S Tx associated with increased foliar % S and SO <sub>4</sub> (needles not washed pre-analysis), decreased % Fe, and unchanged % N, K, C and Cu. Infection significantly lower for treated 2002 & 2003 foliage, but not for untreated 2001 foliage.	Results of this study contrast with others that have examined foliar nutrients after fungicide Tx; this study reported no Tx effect on %N, whereas others have documented increased N in treated foliage.
“Beyond N”  Three-year growth response of young Douglas-fir to nitrogen, calcium, phosphorus, and blended fertilization treatments in OR and WA  Nutrient limitations to growth of western OR DF forests	Mainwaring, Maguire, Perakis, Harrison and Fletcher  (participants and titles vary over time)  Annual Reports: 2006 (p37), 2007 (p41), 2008 (p37, 57), 2009 (p52), 2010 (p27).	To test whether specific nutritional amendments might diminish or offset the effects of SNC; to test the growth response of individual trees to fertilizations across a range of SNC disease severity; to evaluate foliar nutrient dynamics of SNC infected DF following fertilization.	16 study sites across a gradient of SNC from Coos Bay, OR to Mineral, WA; study established winter 2006/2007; target stands were 20+/- 5 yrs old with 300 +/- 100 TPA and no past fertilization; 5, 7 or 8 Tx/site (some excluded site-specific Tx); Tx randomly assigned to .025-ac plots centered on “undamaged” plot tree; measurements on plot center trees included dbh, ht, ht to crown, sapwood width, diameter at 18ft, fol. ret., and foliar nutrients; 2 soil cores/plot, pooled for each Tx/site	-Tree measurements, foliage samples and soil analysis conducted prior to fertilization in Fall 2006 and fall 2009 -Foliar and chemical analysis conducted in winter of 2007/2008 -Fertilized Feb-April 2007  For the most up-to-date presentation of the study timeline and results, see the write-up on p27 (this report).	1. Control 2. N urea (200 lbs N/ac) 3. Lime (calcium carbonate; 1000 lbs Ca/ac) 4. Calcium (calcium chloride; 100 lbs Ca/ac) 5. Phosphorus (monosodium; 500 lbs P/ac) 6. Kinsey (site-specific; fertilized over 2 yrs to avoid over-application) 7. Fenn (site-specific)	Analyses accounted for stand variables and looked for the effect of fertilization on various response variables, including: 1. change in fol. ret. 2. change in volume growth 3. change in form quotient 4. change in sapwood area at crown base  For the most up-to-date presentation of the study timeline and results, see the write-up on p27 (this report).	Foliage samples were collected in May 2009 and are currently being processed for disease severity (pseudothecia incidence and density) in the Shaw lab. More than 660 of 1200 samples have been fully processed, while the remaining samples have been partially processed.
Interaction between fertilization Tx and SNC in DF seedlings	Mulvey, Mainwaring, Shaw and Robin Rose  Annual Report: 2010 (p93).	To assess whether seedlings with higher % or total N experience greater fungal colonization following exposure to the same level of inoculum.	180 1-1 seedlings in 6 inch pots; 4 fertilization Tx (inc. control; N=45; randomly assigned to Tx and exposed to inoculum at moderate disease severity site near Summit, OR (Norton Hill).	-Seedlings potted in Feb 2010 and repotted April 2010 -Seedlings fertilized April 1-15 2010 and May 26-June 9 2010 -Exposed to inoculum April to July 2010	1. Control 2. Low N (0.05g N) 3. Med N (0.10g N) 4. High N (0.15g N) Fertilizer solution (20-20-20) prepared at 0.25g: 1L water; Tx 2 and 3 fertilized 2-3 times (1 wk apart).	Preliminary results only. Seedlings were measured (ht and basal diameter) pre-fertilization and no significant differences b/t Tx detected; 5 seedlings/Tx destructively sampled Nov 2010 to assess foliar [N].	Foliar [N] analysis will show whether the desired spread in foliar N has been achieved through fertilization. If so, seedlings will be re-exposed to natural inoculum April-July 2011. If not, fertilization methods and the overall study design will be reevaluated. See write-up on p93 (this report)

## List of Refereed Publications (Appendix II)

### Disease Distribution, Severity and Epidemiology

- Hansen, E. M., Stone, J. K., Capitano, B. R., Rosso, P., Sutton, W., Winton, L., Kanaskie, A. and M. G. McWilliams. 2000. Incidence and impact of Swiss needle cast in forest plantations of Douglas-fir in coastal Oregon. *Plant Disease*. 84: 773-779.
- Manter, D. K., Reeser, P. W., and J. K. Stone. 2005. A climate-based model for predicting geographic variation in Swiss needle cast severity in the Oregon coast range. *Phytopathology*. 95: 1256-1265.
- Rosso, P. H. and E. M. Hansen. 2003. Predicting Swiss needle cast disease distribution and severity in young Douglas-fir plantations in coastal Oregon. *Phytopathology*. 93: 790-798.
- Stone, J. K., Hood, I. A., Watt, M. S. and J. L. Kerrigan. 2007. Distribution of Swiss needle cast in New Zealand in relation to winter temperature. *Australasian Plant Pathology*. 36: 445-454.
- Stone, J. K., Capitano, B. R. and J. L. Kerrigan. 2008. The histopathology of *Phaeocryptopus gaeumannii* on Douglas-fir needles. *Mycologia*. 100: 431-444.
- Stone, J. K., Coop, L. B. and D. K. Manter. 2008. Predicting the effects of climate change on Swiss needle cast disease severity in Pacific Northwest forests. *Canadian Journal of Plant Pathology*. 30: 169-176.
- Watt, M. S., Stone, J. K., Hood, I. A. and D. J. Palmer. 2010. Predicting the severity of Swiss needle cast on Douglas-fir under current and future climate in New Zealand. *Forest Ecology and Management* (*in press*).

### Forest Protection Issues

- Kelsey, R. G. and D. K. Manter. 2004. Effect of Swiss needle cast on Douglas-fir stem ethanol and monoterpene concentrations, oleoresin flow, and host selection by the Douglas-fir beetle. *Forest Ecology and Management*. 190: 241-253.
- Shaw, D. C., Filip, G. M., Kanaskie, A., Maguire, D. A. and W. Littke. 2011. Managing an epidemic of Swiss needle cast in the Douglas-fir region of Oregon: The Swiss Needle Cast Cooperative. *Journal of Forestry* (*in press*).

## **Genetic Resistance/Tolerance in Douglas-fir**

- Kastner, W., Dutton, S. and D. Roche. 2001. Effects of Swiss needle cast on three Douglas-fir seed sources on a low-elevation site in the northern Oregon Coast Range: Results after five growing seasons. *Western Journal of Applied Forestry*. 16 (1): 31-34.
- Johnson, G. R. 2002. Genetic variation in tolerance of Douglas-fir to Swiss needle cast as assessed by symptom expression. *Silvae Genetica*. 51: 80-86.
- Temel, F., Johnson, G. R. and J. K. Stone. 2004. The relationship between Swiss needle cast symptom severity and level of *Phaeocryptopus gaeumannii* colonization in coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*). *Forest Pathology*. 34: 383-394.
- Temel, F., Johnson, G. R. and W. T. Adams. 2005. Early genetic testing of coastal Douglas-fir for Swiss needle cast tolerance. *Canadian Journal of Forest Research*. 35: 521-529.

## **Genetics of *Phaeocryptopus gaeumannii***

- Winton, L. M., Hansen, E. M. and J. K. Stone. 2006. Population structure suggests reproductively isolated lineages of *Phaeocryptopus gaeumannii*. *Mycologia*. 98 (5): 781-791.
- Winton, L. M., Stone, J. K. and E. M. Hansen. 2007. The systematic position of *Phaeocryptopus gaeumannii*. *Mycologia*. 99: 240-252.

## **Mensuration and growth effects**

- Maguire D. A., Kanaskie, A., Voelker, W., Johnson, R. and G. Johnson. 2002. Growth of young Douglas-fir plantations across a gradient in Swiss needle cast severity. *Western Journal of Applied Forestry*. 17: 86-95.
- Maguire, D. A. and A. Kanaskie. 2002. The ratio of live crown length to sapwood area as a measure of crown sparseness. *Forest Science*. 48: 93-100.
- Weiskittel, A. R., Garber, S. M., Johnson, G. P., Maguire, D. A. and R.A. Monserud. 2007. Annualized diameter and height growth equations for Pacific Northwest plantation-grown Douglas-fir, western hemlock, and red alder. *Forest Ecology and Management*. 250: 266-278.
- Weiskittel, A. R., Maguire, D. A., Garber, S. M. and A. Kanaskie. 2006. Influence of Swiss needle cast on foliage age class structure and vertical distribution in Douglas-fir plantations of north coastal Oregon. *Canadian Journal of Forest Research*. 36: 1497-1508.
- Weiskittel, A. R., Maguire, D. A. and R. A. Monserud. 2007. Modeling crown structural responses to competing vegetation control, thinning, fertilization, and Swiss needle cast in coastal Douglas-fir of the Pacific Northwest, USA. *Forest Ecology and Management*. 245: 96-109.

- Weiskittel, A. R., Maguire, D. A. and R. A. Monserud. 2007. Response of branch growth and mortality to silvicultural treatments in coastal Douglas-fir plantations: Implications for predicting tree growth. *Forest Ecology and Management*. 251: 182-194.
- Weiskittel, A. R. and D. A. Maguire. 2007. Response of Douglas-fir leaf area index and litterfall dynamics to Swiss needle cast in north coastal Oregon, USA. *Annals of Forest Science*. 64: 121-132.
- Weiskittel, A. R. and D. A. Maguire. 2006. Branch surface area and its vertical distribution in coastal Douglas-fir. *Trees*. 20: 657-667.
- Weiskittel, A. R., Temesgen, H., Wilson, D. S. and D. A. Maguire. 2008. Sources of within and between-stand variability in specific leaf area of three ecologically distinct conifer species. *Annals of Forest Science*. 65: 103-112.

### **Nitrogen and soil interactions**

- Waring, R. H., Boyle, J., Cromack, K. Jr., Maguire, D. and A. Kanaskie. 2000. Researchers offer new insights into Swiss needle cast. *Western Forester*. 45 (6): 10-11.
- El-Hajj, Z., Kavanagh, K., Rose, C., and Z. Kanaan-Atallah. 2004. Nitrogen and carbon dynamics of a foliar biotrophic fungal parasite in fertilized Douglas-fir. *New Phytologist*. 163: 139-147.
- Perakis, S. S., Maguire, D. A., Bullen, T. D., Cromack, K., Waring, R. H. and J. R. Boyle. 2005. Coupled nitrogen and calcium cycles in forests of the Oregon Coast Range. *Ecosystems*. 8: 1-12.

### **Pathology and physiological host effects**

- Black, B. A., Shaw, D. C. and J. K. Stone. 2010. Impacts of Swiss needle cast on overstory Douglas-fir forests of western Oregon Coast Range. *Forest Ecology and Management*. 259: 1673-1680.
- Manter, D. K., Bond, B. J., Kavanagh, K. L., Rosso, P. H. and G. M. Filip. 2000. Pseudothecia of Swiss needle cast fungus, *Phaeocryptopus gaeumannii*, physically block stomata of Douglas-fir, reducing CO<sub>2</sub> assimilation. *New Phytologist*. 148 (3): 481-491.
- Manter, D. K. 2002. Energy dissipation and photoinhibition in Douglas-fir needles with a fungal-mediated reduction in photosynthetic rates. *Phytopathology*. 150: 674-679.
- Manter, D. K., Bond, B. J., Kavanagh, K. L., Stone, J. K. and G. M. Filip. 2003. Modeling the impacts of the foliar pathogen, *Phaeocryptopus gaeumannii*, on Douglas-fir physiology: net canopy carbon assimilation, needle abscission and growth. *Ecological Modeling*. 164: 211-226.
- Manter, D. K. and Kavanagh, K. L. 2003. Stomatal regulation in Douglas-fir following a fungal-mediated chronic reduction in leaf area. *Trees*. 17: 485-491.

- Manter, D. K., Kelsey, R. G., and J. K. Stone. 2001. Quantification of *Phaeocryptopus gaeumannii* colonization in Douglas-fir needles by ergosterol analysis. *Forest Pathology*. 31: 229-240.
- Manter, D. K., Winton, L. M., Filip, G. M. and J. K. Stone. 2003. Assessment of Swiss needle cast disease: temporal and spatial investigations of fungal colonization and symptom severity. *Phytopathology*. 151: 344-351.
- Winton, L. M., Manter, D. K., Stone, J. K. and E. M. Hansen. 2003. Comparison of biochemical, molecular and visual methods to quantify *Phaeocryptopus gaeumannii* in Douglas-fir foliage. *Phytopathology*. 93: 121-126.
- Winton, L. M., Stone, J. K., Watrud, L. S. and E. M. Hansen. 2002. Simultaneous one-tube quantification of host and pathogen DNA with real-time polymerase chain reaction. *Phytopathology*. 92: 112-116.
- Winton, L. M., Stone, J. K. and E. M. Hansen. 2007. Polymorphic microsatellite markers for the Douglas-fir pathogen *Phaeocryptopus gaeumannii*, causal agent of Swiss needle cast disease. *Molecular Ecology*. 7: 1125-1128.

### **Silviculture and Control**

- Filip, G., Kanaskie, A., Kavanagh, K., Johnson, G., Johnson, R. and D. Maguire. 2000. Research Contribution 30, Forest Research Laboratory, College of Forestry, Oregon State University, Corvallis, Oregon.
- Mainwaring, D. B., Maguire, D. A., Kanaskie, A. and J. Brandt. 2005. Growth responses to commercial thinning in Douglas-fir stands with varying intensity of Swiss needle cast. *Canadian Journal of Forest Research*. 35: 2394-2402.
- Stone, J. K., Reeser, P. W. and A. Kanaskie. 2007. Fungicidal suppression of Swiss needle cast and pathogen reinvasion in a 20-year-old Douglas-fir stand. *Western Journal of Applied Forestry*. 22: 248-252.

### **Wood Quality**

- Johnson, G. R., Gartner, B. L., Maguire, D. and A. Kanaskie. 2003. Influence of Bravo fungicide applications on wood density and moisture content of Swiss needle cast affected Douglas-fir trees. *Forest Ecology and Management*. 186: 339-348.
- Grotta, A. T., Leichti, R. J., Gartner, B. L. and G. R. Johnson. 2004. Effect of growth ring orientation and placement of earlywood and latewood on MOE and MOR of very-small clear Douglas-fir beams. *Wood and Fiber Science*. 37: 207-212.
- Johnson, G. R., Grotta, A. T., Gartner, B. L. and G. Downes. 2005. Impact of the foliar pathogen Swiss needle cast on wood quality of Douglas-fir. *Canadian Journal of Forest Research*. 35: 331-339.

Access publications, annual reports and information on the  
Swiss Needle Cast Cooperative Website:

<http://www.cof.orst.edu/coops/sncc/>

