Oregon State University | College of Forestry

Swiss Needle Cast Cooperative

Annual Report 2017

Members of the Swiss Needle Cast Cooperative

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Cascade Timber Consulting

Greenwood Resources, Inc. Lewis & Clark Tree Farms, LLC

Oregon Department of Forestry

Starker Forests

Stimson Lumber

USDA Forest Service

Weyerhaeuser Corporation

Swiss Needle Cast Cooperative Staff

Dave Shaw – Director and Associate Professor of Forest Health

Gabriela Ritóková – Assistant Director

Edited by Gabriela Ritóková and David Shaw Cover Photo by Gabriela Ritóková

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SNCC Income Sources and Expenditures: 2017

Income

Membership dues	80,000
Oregon State Legislature	95,000
Carry-over	-15,897
Total 2017 Income	**$159,103**

Expenditures

Salaries and wages	120,470
Travel	2,923
Operating expenses	5,427
Materials and Supplies	118
Indirect Costs	16,762
Total 2017 Expenditures	**$145,700**

Balance	**$13,403**

SNCC Background and Organization

A major challenge to intensive management of Douglas fir in Oregon and Washington is the current Swiss needle cast (SNC) epidemic. Efforts to understand the epidemiology, symptoms, and growth losses from SNC have highlighted gaps in our knowledge of basic Douglas-fir physiology, growth, and silviculture. The original mission of the Swiss Needle Cast Cooperative (SNCC), formed in 1997, was broadened in 2004 to include research aiming to ensure that Douglas-fir remains a productive component of the Coast Range forests. 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. Our objective is to carry out projects in cooperation with members on their land holdings.

SNCC 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.

SNCC 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.

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February 19, 2018

To: Swiss Needle Cast Cooperative Members

From: David Shaw, Director, and Gabriela Ritóková, Assistant Director
Swiss Needle Cast Cooperative, College of Forestry, Oregon State University

Dear Members,

Thank you all for you continued support of the Swiss Needle Cast Cooperative in 2017. We are making significant progress in furthering our fundamental understanding of this Douglas-fir foliage disease, while also making progress on monitoring and management solutions. However, there is no silver bullet and SNC management is very site and stand dependent. For example, our collaborations with regional scientists, especially Henry Lee from the EPA, have shown us that the exact climatic factors that control epidemiology of *Phaeocryptopus gaeumannii* vary with geographical location (elevation, distance from coast) so that a one-size-fits-all epidemiological model does not necessarily explain all responses on the landscape. This is fundamental to understanding why most models built so far don't use the same exact climatic factors. (My own comment which won't be in the letter is that this last comment isn't really correct).

After finishing the 2016 annual survey, the SNCC membership and collaborators agreed to conduct aerial surveys biannually. This saves the SNCC about $23,000 every other year. With this approach both Oregon AND Washington will be surveyed concurrently. In addition, the aerial survey teams will also continue to survey portions of the western Cascades foothills.

Field and laboratory components of the Research and Monitoring Plot Network study have been completed, all the data collected for the first round of sampling and measurements have been archived, with analysis on-going. Disease severity, needle retention, and foliage and soil nutrients for all the sites have been collected. Gabriela Ritóková, Sky Lan, Jeff Hatten, and Dave Shaw have been working on the plan for the initial analysis. Sky has been investigating the link between SNC disease severity, needle retention and nitrogen for chapters of her Ph.D. dissertation, while Jeff is undertaking broader studies of which factors, among soil/foliar nutrients, climate, or geographical setting, appear to control disease.. Plot climate data has been determined with PRISM and included in these analyses.

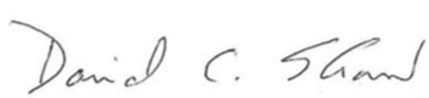
In 2017, Gabriela led a Cascade foothills disease assessment of 47 sites owned by SNCC members during the late spring and early summer months. Data show that at elevation above 1,700 ft, only limited needle loss was observed. We plan to continue visiting these plots each year we do the aerial survey.

We continue collaboration with Jared LeBoldus, OSU Forest Pathology Professor. In 2017 Gabriela assisted a PhD candidate, Mireia Gomez Gallegos, who worked with Jared LeBoldus on the interaction of *Phytophthora pluvialis* and *Nothophaeocryptopus gaeumannii* in New Zealand and the United States. Gabriela assisted Jared and Mireia in locating research plots and doing field work, and the SNCC contributed $5,000 to assist with laboratory supplies for isolations and molecular work. In other international news, the Ministry of Forestry in British Columbia, Canada is also beginning to take SNC seriously and we have been actively collaborating. See the update on BC issues in the annual report.

Gabriela Ritóková is leading efforts to produce the SNC Silviculture Guide. We will produce two versions: one with significant textual and quantitative detail and a simplified version for field practitioners. A first draft has been completed. You will find a wide breadth of reports and studies in the Annual Report, with recent papers published, and updates from scientists on their recent findings. Finally, we want to thank BLM for the longstanding support and encouragement they have provided since the inception of the SNCC, and we hope they can return to membership at some point in the near future.

Again, thank you all for continuing to support the important work of the SNCC, dedicated to Douglas-fir forest health.

Sincerely,



David C. Shaw

Gabriela Ritóková

Swiss Needle Cast Cooperative Research and Monitoring Plot Network in Coastal Oregon, Southwestern Washington and Oregon Cascade Foothills

Gabriela Ritóková[1], Dave Shaw[1], Doug Maguire[1], Doug Mainwaring[1], John Browning[2], Mark Gourley[3], Greg Filip[4], Alan Kanaskie[5], Bill Marshall[6]

[1]Forest Engineering, Resource, and Management, Oregon State University, 2Weyerhaeuser Corporation, [3]Starker Forests, [4]US Forest Service, [5]Oregon Department of Forestry, [6]Cascade Timber Consulting.

Among the long-term objectives of the Swiss Needle Cast Cooperative (SNCC) is a constant monitoring of disease conditions and the development of tools to combat the disease. This has been accomplished by aerial surveys and complemented by on-the-ground experiments and periodic measurements of trees to determine growth loss resulting from Swiss Needle Cast (SNC.)

The Oregon Department of Forestry and U.S. Forest Service had been conducting aerial surveys in Oregon annually since 1996. Starting in 2016, rather than flying the Oregon coast only, the SNCC membership decided to do a thorough monitoring of disease in coastal Oregon and Washington, the Oregon Cascades foothills and Northern California every other year. Researchers in British Columbia have decided to complement this effort and conduct an aerial survey in 2018.

The flights generally take place in the spring when the disease signature, yellowing foliage, is strongest. Surveyors map the symptomatic areas on a computer. Most infected areas are detected within 25 miles from the coast. Easternmost areas that were flown in 2016 were approximately 70 miles from the coast, in the Cascade foothills.

Along with the aerial surveys, a plot network was installed in 1998. However, it was limited to north coastal Oregon and was retired due to advancing age and the resulting difficulty of assessing crown conditions. The plots were used to monitor disease severity and growth loss. In 2013, the SNCC initiated an effort to install a new, more extensive plot network, which covers the entire coast of Oregon and southwestern Washington. These plots have been installed in 10 – 25 year stands, which will allow monitoring of disease conditions and growth loss for minimum of 10 years. In 2017, our Canadian colleagues established 13 plots in BC based on our methodology with objective of expanding the SNCC reach.

The key features of this network include growth impact assessment, continuous disease monitoring of distribution and severity, and the validation of the aerial surveys. These plots will provide data that will improve models that predict growth impacts and geographic distribution of disease severity.

In addition to the new permanent plot network, the coop began a long-term monitoring of disease conditions in the Cascade Foothills on the properties of SNCC members. In 2018 we plan to revisit these transects to complement the highly anticipated aerial survey.

Methods

Sampling matrix and Plots

The methodology for the coastal plot network establishment was described in the 2016 annual report.

In the three-year installation period effort, we established 106 research plots, of which 98 are located in Oregon and eight are in SW Washington (Figure 1.) In 2016, the OSU College of Forestry Research Forests thinned the buffer zone of one research plot in the Blodgett tract, reducing its size. However, we are still able to collect data from it.

The transect study of the Cascades foothills was conducted on lands owned by Weyerhaeuser, Cascade Timber Consulting, Oregon Department of Forestry, and a private landowner, Melcher Logging and Timber Harvesting Inc. The elevation of the transect stands was below 2,500 ft, and ages were limited to between 10 and 25 years. At every 20 m of the 100 meter transect we selected two dominant or codominant Douglas-fir trees. Four-year-old mid-crown lateral branches were collected from the south side of each sample tree to determine foliage retention (in years) and SNC disease severity. We measured and sampled 470 trees in 47 plots in June 2017. Figure 2 shows a distribution of transects within the areas flown in 2016 in Oregon Cascades. The white polygon represents flight lines periphery. Colored pins represent plots on cooperative members' properties; Blue – ODF, Yellow – CTC, pink – Weyerhaeuser.

Foliage retention estimate

The foliage retention estimate protocol was adopted from the field methods described by Kanaskie and Maguire, 2002.

Figure 1. Coastal Research Plot Network matrix and research plots distributed throughout the matrix.

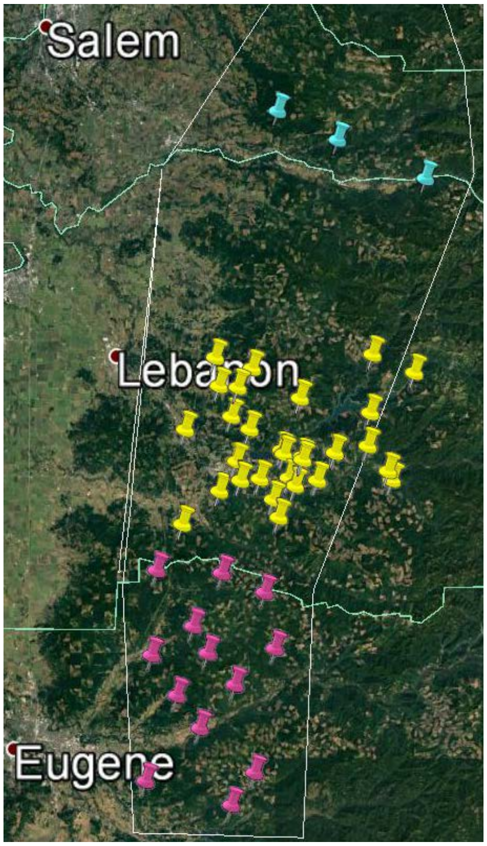


Figure 2. Transect plots in Oregon Cascades.

Four-year old secondary lateral branches from each crown third were used to estimate the average number of annual needle compliments present. This was done by estimating the proportion of attached needles present within each cohort of the lateral's primary axis.

Incidence and Pseudothecial occlusion

SNC disease severity was observed in field and based on a scale from 0 to 3, where 0 was no pseudothecia present on second year needles, 1 was light pseudothecial occlusion, 2 was moderate occlusion and 3 represented severe occlusion of more than 50% occluded stomates.

The laboratory component of the coastal project has been completed; we processed all foliage samples, assessed incidence on one- and two- year old needles, and pseudothecial occlusion on two-year old needles. We are currently analyzing the collected data and we will present the completed results at the SNCC annual meeting in fall 2018.

Results

Coastal Study Results

A summary of the field data collected during the initial measurements on the plots of the new network are summarized in Table 1.

Table 1. Summary of the dataset.

	QMD(cm)		TPA		BA(ft2/ac)	
Mean	DF	non-DF	DF	non-DF	DF	non-DF
0-5 miles	9.29	4.29	353.04	197.61	31.56	4.52
5-15 miles	9.03	3.3	391.38	146.38	31.35	2.45
15-25 miles	8.43	3.28	398.08	62.88	28.34	1.32
25-35 miles	8.03	2.73	404.64	63.93	26.9	0.65
Max	**DF**	**non-DF**	**DF**	**non-DF**	**DF**	**non-DF**
0-5 miles	14.17	9.85	690	865	47.61	14.65
5-15 miles	13.78	9.46	1210	890	90.48	18.55
15-25 miles	13.06	7.34	860	305	43.84	7.35
25-35 miles	14.42	8.81	815	370	44.71	3.39
Min	DF	non-DF	DF	non-DF	DF	non-DF
0-5 miles	7.13	NA	170	NA	19.94	NA
5-15 miles	4.14	NA	165	NA	9.80	NA
15-25 miles	3.97	NA	155	NA	10.16	NA
25-35 miles	2.67	NA	145	NA	3.97	NA

One of the objectives of the coastal study was to observe dependency of foliage retention on the distance from the coast. As expected, there was a positive association between foliage retention and distance from the coast, regardless of crown position (fig. 3). This association is typical with the current SNC epidemic, though other needle-retention-influencing factors are present in these stands. Foliage retention in the lower crowns of highly infected stands is often relatively improved by the greater light penetration (due to upper crown defoliation) relative to uninfected stands. Conversely, lower crown foliage retention can be negatively impacted by Rhizoctonia, another needle disease.

The upper crown foliage retention shown in figure 3 doesn't represent a good measure of foliage retention across different levels of infection because the sampling methods often resulted in fewer cohorts being assessed. Because the sampling included young stands, the upper crown third of young trees often did not contain any four-year old laterals. In many cases, only two or three years of lateral cohorts were assessed, depending on the age of stands. Because mid-crown foliage retention does include all cohorts, and is essentially equal to the average of all three crown positions, for future analysis only mid-crown foliage retention will be used as a measure of whole tree foliage retention.

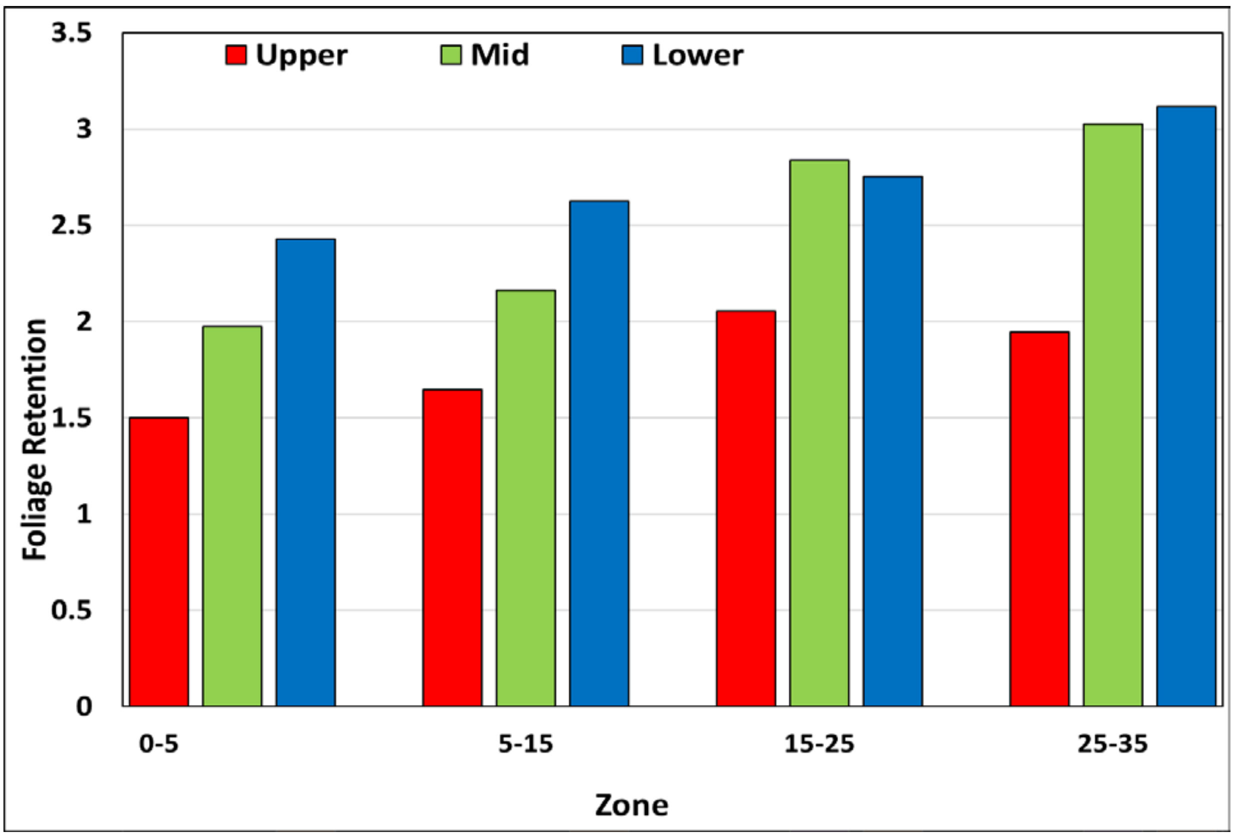


Figure 3. Foliage retention by crown position relationship in marked with a red circle.

The broad dataset allowed examination of other relationships. For instance, the relationship between pseudothecial occlusion and crown position was assessed to determine whether disease severity changes with distance from the coast. The only apparent differences observed were in the 25 – 35 mile zone, where less than 5% stomates were occluded in the upper crown compared to 22-26% in the upper crowns of the zones nearer the ocean (fig. 4). In contrast, occlusion was greater in needles of the middle and lower crowns of the 25-35 mile zone than in the 15-25 mile zone.

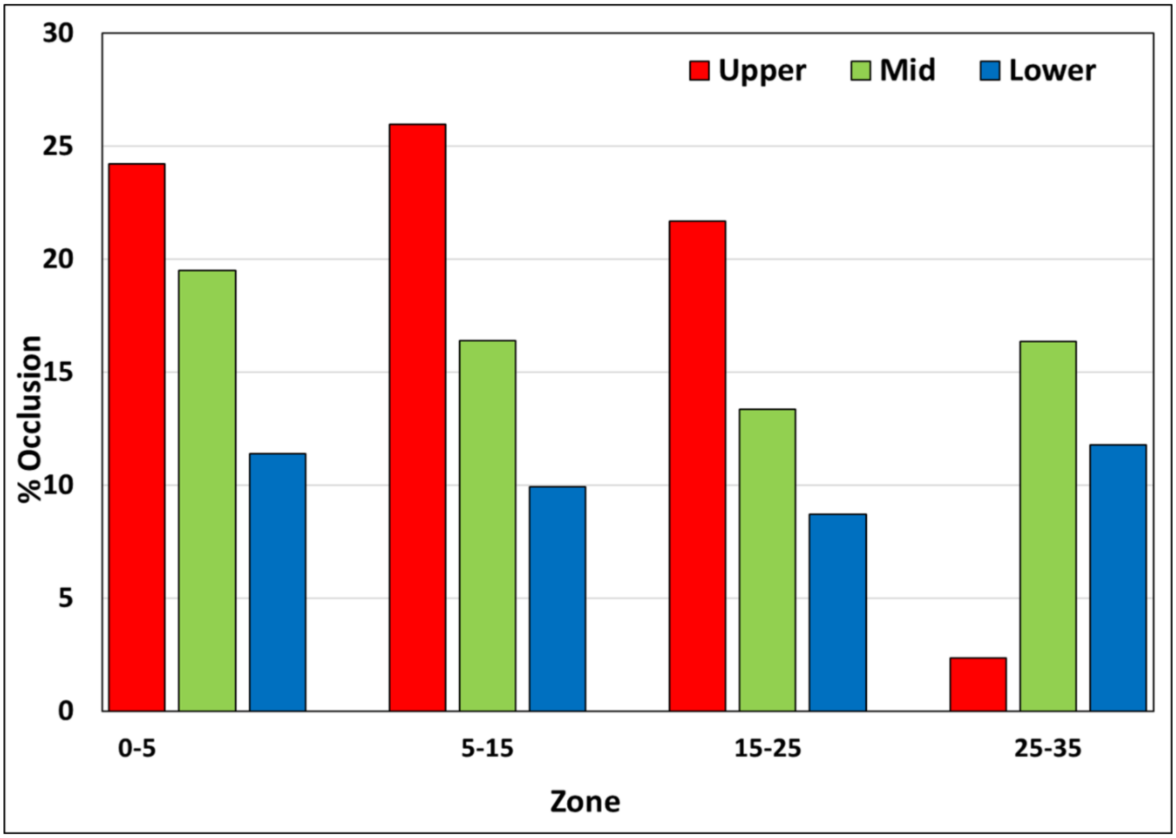


Figure 4. Occlusion by crown position. Red bars represent occlusion in the upper crown, green bars characterize mid-crown position, and lower crown branches are marked with blue color.

Below, Figure 5 shows the relationship between mid-crown foliage retention, site and zone. When differentiated by site, variation by zone tended to decrease with distance from the coast. The greater foliage retention in the southernmost coastal zones is consistent with what has been recorded by the aerial survey (SNCC Annual Report 2016) despite the associations made between these areas and predictive climate factors (Zhao et al. 2012).

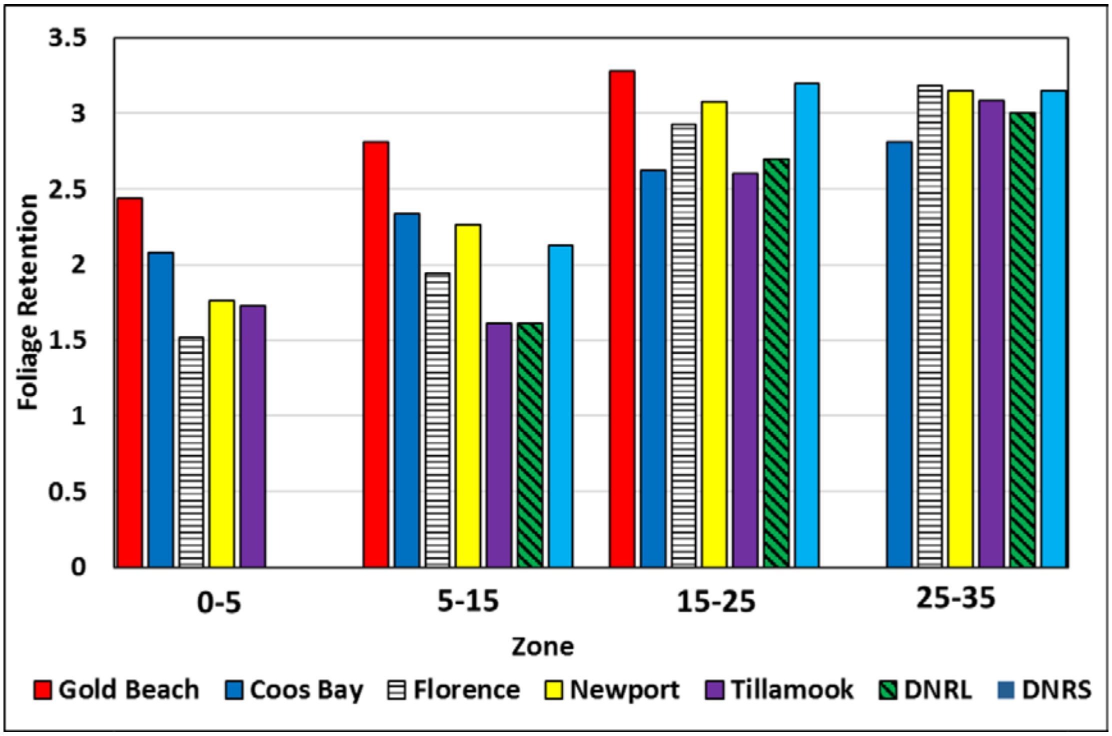


Figure 5. Mid-crown foliage retention, site and zone.

Oregon Cascades Study Results

Of the stands sampled as part of the Cascades sampling, foliage retention varied between 2.1 and 3.3 years. Stands sampled above 1700 feet did not exhibit foliage retentions below 2.8 years (Figure 6.)

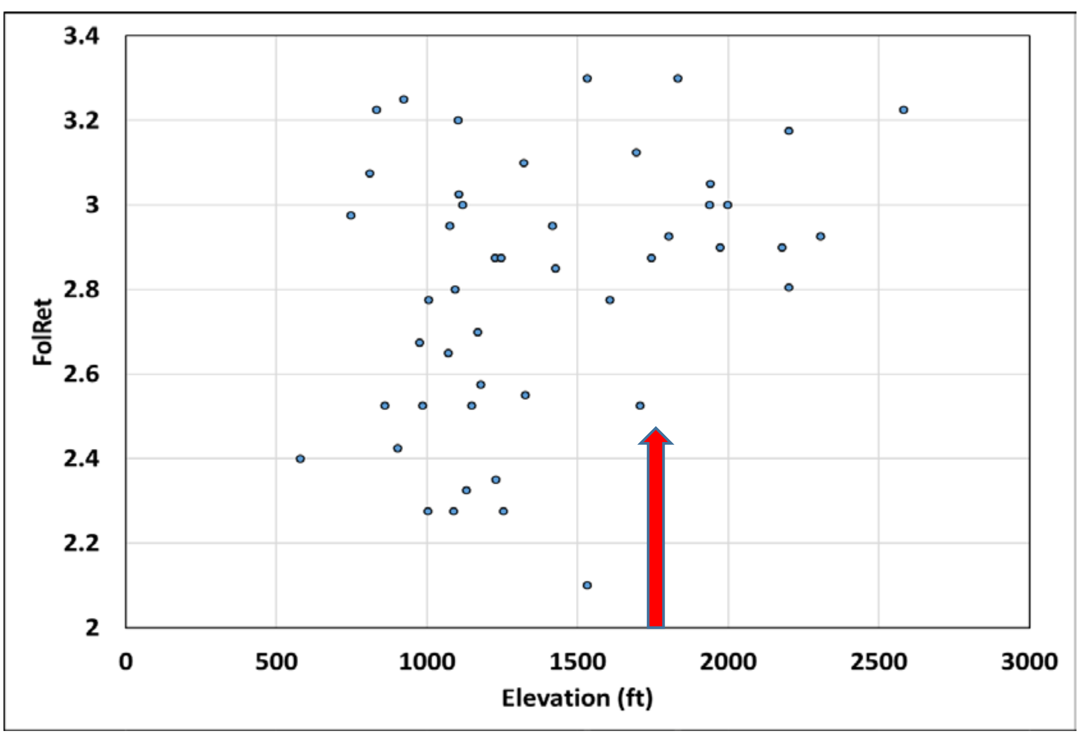


Figure 6. Mid-crown foliage retention and elevation relationship.

Trees on these plots exhibited a negative relationship between pseudothecial occlusion and foliage retention, suggesting that some of the explanation for differences in foliage retention can be explained by SNC (Figure 7.) These plots will be revisited in April and May 2018 to complete a reassessment of foliage retention and pseudothecial occlusion.

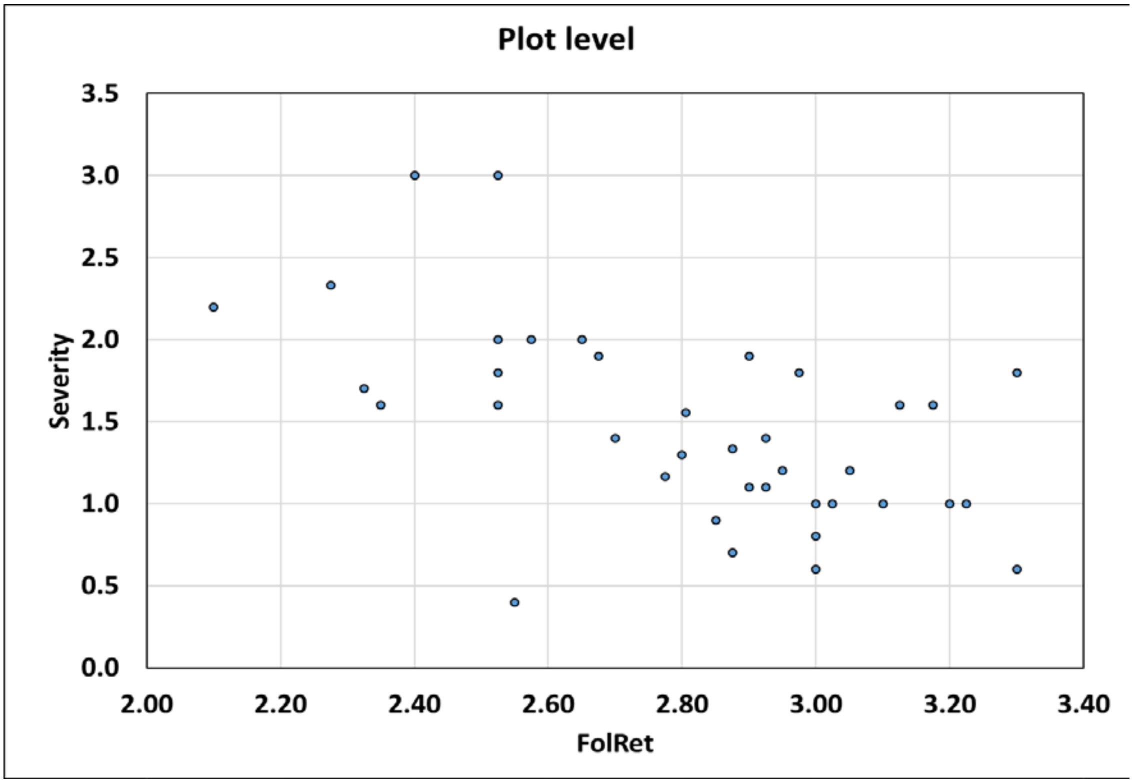


Figure 7. Severity by foliage retention on the plot level.

References

Kanaskie, A, Maguire, DA. March 30, 2002. Field Specifications and Manual for Rating Swiss Needle Cast in Douglas-Fir.

Zhao, J, Maguire, DA, Mainwaring, DB, Kanaskie, A. 2012. Climatic Influences on Needle Cohort Survival Mediated by Swiss Needle Cast in Coastal Douglas-Fir. Trees. 26:1361-1371.

Acknowledgements

We would like to express our appreciation for collaborative efforts from numerous landowners, who gave us permission to establish research plots on their lands and at times provided assistance in the field. Besides the SNCC members (Bureau of Land Management, Cascade Timber Consulting, Greenwood Resources (Lewis & Clark Tree Farms), Oregon Department of Forestry, Starker Forests, Stimson Lumber, USDA Forest Service, Weyerhaeuser), we are grateful to Washington DNR, Hampton Affiliates, Hancock Forest Management, Roseburg Resources, South Coast Lumber.

Swiss Needle Cast Monitoring in British Columbia

Stefan Zeglen[1] and Lucy Stad[2]
British Columbia Ministry of Forests, Lands and Natural Resource Operations and Rural Development, West Coast Region[1] and Chilliwack District[2]

Mounting evidence of the presence of Swiss Needle Cast (SNC; causal agent *Nothophaeocryptopus gaeumannii*) in plantations on the southwest coast of British Columbia (BC) is leading to concerns about the future of the disease on Douglas-fir. Looking south, the continued impact of the disease in stands in coastal Oregon and Washington does not paint an optimistic picture were we to experience disease incidence and severity of the same magnitude. Shifting weather patterns, especially those pertaining to seasonal precipitation, are likely driving an observed increase in the incidence of this otherwise previously benign endemic disease.

Unlike Rhabdocline needle cast, SNC was not even recognized as a notable forest pest in BC until 2012. Hence, there is a very poor record of where and when it may have occurred in the past. While aerial surveys have been conducted in Oregon for years, BC only tested the utility of an SNC-specific aerial survey in 2016 with a further test scheduled for spring 2018; both are in collaboration with the Oregon Department of Forestry. The area with the most reports of SNC affected plantations falls within the Chilliwack District located in the upper Fraser Valley east of Vancouver. Since 2013, monitoring lines installed in 39 7-15 year old stands across the district have been visited biennially to record foliar retention. Many of these stands have reported retention levels of less than two years foliage which is considered severe enough to affect tree growth (Figure 1).

A troubling aspect of these high levels of defoliation is that they are occurring in areas where Douglas-fir is a natural species for reforestation. Unlike Oregon, where the high severity areas west of the Cascades were often reforested to Douglas-fir in replacement of other non-susceptible native species, in BC most of our infected areas are ecologically suited to Douglas-fir. Also, most of these areas are further from the influence of the ocean than affected areas in Oregon and Washington. Many of the hardest hit stands in the Chilliwack district are more than 40 km from the nearest ocean influence suggesting that some of the mechanisms suspected of influencing infection in Oregon, like coastal fog, may not be relevant in BC.

In order to generate better tree and stand infection data that is compatible with that from the SNC Co-op, we have begun to install monitoring plots using the co-op protocol. The first 13 of these plots was installed in early 2017 across the Chilliwack District within one ecological subzone. We have completed collecting tree measurements and foliar and soils samples for these plots and are in the process of analyzing the data. At four plots, environmental monitoring stations were established to measure microsite variables such as air temperature and relative humidity, solar irradiance, leaf wetness and, for drought monitoring, soil wetness and temperature (Figure 2). In early 2018 we are planning to install a further 20 monitoring plots on

Vancouver Island and the Sunshine Coast, areas that have not attracted much attention regarding SNC but that are potentially just as suitable for infection as the Chilliwack area.

Figure 1. A SNC-infected tree along one of the monitoring lines.

Figure 2. An environmental monitoring station installed within a SNC monitoring plot.

Determining the Role of Soils in Swiss Needle Cast

Jeff Hatten and Dave Frey
OSU Forest Engineering, Resources & Management

Introduction

The severity of Swiss Needle Cast (SNC) has been shown to vary as a function of climate (Zhao et al., 2011; Zhao et al., 2012), and generally the disease is more severe with proximity to the coast and the climate and soil characteristics that brings. There has been some work showing that high foliar and soil nitrogen, low soil calcium, and low soil pH levels are correlated with SNC severity (Waring et al., 2000). This suggests that soils have some control over the disease. However, these studies have not covered the full latitudinal gradient of SNC and soil N (e.g. Perakis et al., 2006; Perakis et al., 2013). Most perplexing to this problem is the correlation between soil characteristics, climate, and SNC severity and occurrence. Therefore, it has been very difficult to separate the influence of soil from that of climate over the range of SNC in the coast ranges of Oregon and Washington. We hypothesize that there is an interaction of climate and soil along a latitudinal gradient that affects SNC occurrence and severity.

The results presented here are a preliminary modeling of SNC from climate, soil, and foliar characteristics.

Methods

Soil and Foliar Sampling

Soils and foliage were sampled from the SNC research and monitoring plots established by the Swiss Needle Cast Cooperative (SNCC). From each 0.08ha plot, soils were collected from O-horizons, 0-10, 10-20, and 20-30 cm depths. Soils were collected from 5 different locations within each plot, one near plot center and the other four samples were collected 4.5m from the corners toward plot center (this was approximately 2/3 the distance from the plot center towards the corners). O-horizons were sampled at the plot center by removing material from a known area using a cutting template 1m north of plot center. All material within the template was collected except live vascular plants and mineral soil. Depths of the O horizon were recorded along 4 sides of the template in order to calculate bulk density. Mineral soils were collected at 0-10, 10-20, and 20-30cm using a push probe form an area devoid of O-horizon. Mineral soils from each depth were composited across the 5 locations from each plot (i.e. one sample per plot per depth). One-year old needles were collected from three branch tips of one branch from 5th whorl of the south side of the tree. Since 5 or 10 midcrown samples were collected in each plot we collected 25-40 needles from each tree and composited this material prior to drying. Approximately 1 g of material was collected (200-250 needles). Foliage, O-horizon, and mineral soil samples were stored in a refrigerator (<4 °C) for less than 4 weeks prior to being oven dried at 40 °C until a constant weight achieved. Mineral soil samples were weighed, sieved to 2mm and the fine fraction weighed to determine coarse content.

Soil and Foliar Chemical Analyses

Mineral soil pH was determined in deionized water using the 2:1 method (Thomas, 1996). C and N were determined on dried and ground O-horizon, mineral soil (<2mm), and foliar material using dry combustion on a Thermo FlashEA 1112. Mineral soils were extracted using 50mL of 1M NH_4Cl to 5g of soil (<2m m) shaken for one hour and centrifuged prior to ICP analysis to extract the exchangeable pools of cations. O-horizons and foliar samples were digested using 30% H_2O_2 and a 1:10 nitric-hydrochloric (HNO_3-HCL) acid digestion of organic matter in conjunction with external heating (EPA method 3050; Benton and Wolf, 1997). Digests and extracts were analyzed for Ca, K, Na, Mg, B, Al, Cu, Fe, Mn, Mo, P, S, and Zn on an inductively coupled plasma atomic emission spectrometry (ICP-AES) using a Thermo Scientific ICP-OES 61E.

Ortho-phosphate was extracted for 3 minutes using a Bray 1 solution (0.03 M NH_4F and 0.025 N HCl) at a ratio of 7:1 (solution to soil) and filtered using a VWR 494 quantitative filter paper (Olsen and Sommers, 1982). The filtrate was analyzed for total extractable P using the previously described ICP-AES.

Climate Data

Climate data were retrieved from PRISM Data Explorer, using coordinates as location parameters. Monthly 30-year normals (1981-2010) for interpolated grid cells with a resolution of 800 m were downloaded for all climate variables. Additionally, monthly data for all climate variables for each individual year from January 1986 to December 2016 were downloaded. For annual data, resolutions of 4 km were used (freely available). Monthly data from the year prior to sample collection (lagged data) were used in model selection in addition to 30-year normal data, as climate in the year prior to sample collection may have exerted direct influences on SNC.

To reduce the number of variables used in model selection, 30-year normal and lagged climate data were either summed or averaged into seasonal categories (see Table 1). Seasonal summaries of lagged climate data were generated using the same calculations as in Table 1, using data from May of the year prior to sample collection to April of the year samples were collected. These values were then subtracted from the 30-year normal values, and consequently, differences from 30-year normal data in the year prior to sample collection were used for modeling.

Table 1: Summary of climate variables used for model selection. Seasonal precipitation data were derived from sums of monthly variables, and seasonal temperature and dew point data were derived from averages of monthly variables.

Scale		30-Year Normal Predictors		
Seasonal Data	Monthly Data	Precip (mm)	Temp (°C)	Dewpt(°C)
Spring	Mar Apr May	Σ(Mar-May)	$\bar{x}$(Mar-May)	
Summer	Jun Jul Aug	Σ(Jun-Aug)	$\bar{x}$(Jun-Aug)	
Fall	Sep Oct Nov	Σ(Sep-Nov)	$\bar{x}$(Sep-Nov)	
Winter	Dec Jan Feb	Σ(Dec-Feb)	$\bar{x}$(Dec-Feb)	

Foliar Data Reduction

Concentrations of foliar nutrients from samples collected from the middle canopy were included in model selection. Nutrients that may be important for mechanical or chemical defense from Swiss needle cast were used.

Soil Data Reduction

Mineral soil nutrient contents and pH averaged over soil samples of depths 0-10cm, 10-20cm, and 20-30cm were used in model selection. Contents were calculated using average bulk density values by depth, reported in Hynicka (2014). Additionally, the ratios of nutrient contents at 0-10cm to nutrient contents at 20-30cm were included in model selection, as this ratio may indicate how tightly a given nutrient is cycling in the system.

Swiss Needle Cast Data

Foliar retention, pseudothecial occlusion, and disease severity indices were modeled using only data collected from the middle canopy, as only middle canopy needles were measured for foliar nutrient concentrations.

Data Analysis

Data transformations

Three of the 106 sites were excluded prior to analyses, due to incomplete nutrient data. Additionally, the ratio of potassium in the 0-10 cm to 20-30 cm mineral soil layer was excluded, due to several extreme values that were likely to be highly influential during model selection. Logit transformations were performed on response variables (needle retention, pseudothecial occlusion, and severity indices) as the responses were all continuous proportions. Predictors were standardized prior to analyses, due to several large differences in scale.

Model Selection and Fitting

Models were selected for needle retention, pseudothecia proportions, and severity indices in four ways. Best subsets regression was performed in R, version 3.4.3, separately for the following groups, using the leaps package (Lumley, 2017): 1) Foliar nutrient concentrations and 30-year normal climate data; 2) Foliar nutrient concentrations and lagged climate data; 3) Soil nutrient contents, ratios, and 30-year climate data; and 4) Soil nutrient contents, ratios, and lagged climate data. These analyses were run individually to reduce issues with multicollinearity that arose when best subsets regression was initially performed with all possible predictors. One best additive model was selected using Mallow's Cp, where the maximum number of predictors was set to be ten (plus intercept). Larger models were not considered to avoid potential overfitting.

Models selected using best subsets regression were then analyzed for violations of the assumptions of multiple linear regression (normality and heteroskedasticity). Additionally, if multicollinearity was detected, one of the predictors in a given group of collinear predictors was removed from the dataset, and best subsets regression was performed again on the resulting data. This process was iterated until multicollinearity was sufficiently reduced (see Appendix for further explanation).

Model coefficients were calculated both on the standardized, logit scale and the odds ratio, original scale.

Model Validation

Model validation was performed using a bootstrapping procedure, where best subsets regression was iteratively executed on 1000 bootstrapped replicates (n=103 for each replicate) selected randomly with replacement. Data used for validation were generated from datasets from which final models were selected, and consequently, bootstrapping was performed on datasets from which several initial predictors may have been removed to account for multicollinearity (see Appendix for list of variables used in each procedure).

Due to uncertainty in the model selection procedure in both the size of the final model selected and the individual predictors selected, bootstrapping procedures were utilized to assess both of these sources of uncertainty. Hence, the proportion of times a best model of a particular size was selected and the proportion of times a given variable was selected, were each tabulated for the 1000 iterations.

Results/Discussion

Foliar retention (Table 2) was best predicted from climate and foliar characteristics with an R^2 of 0.565. Standardized coefficients indicate that climate variables (spring and summer temperature and spring Precipitation) had the strongest control on foliar retention; however as noted in previous studies, foliar N was also a strong predictor. Only 3 variables were needed to produce a model from soil characteristics with an R^2 of 0.518. The concentration of soil nitrogen was a significant predictor with spring and summer Temperatures.

Table 2. Model of foliar retention from 30-year climate normals and foliar chemical composition (left) and soil chemical composition (right). Estimates and confidence intervals are on the odds ratio scale. R squared values are for linear regression on standardized predictors used to predict logit transformed responses. Standardized coefficients are on the modeled scale, original scale variables are not standardized and are reported on the odds ratio scale

Foliar Retention * Foliar Nutrients						**Foliar Retention * Soil Nutrients**				
Standardized Coefficients						**Standardized Coefficients**				
Predictor	Estimate	CI.L	CI.U	p-value		Predictor	Estimate	CI.L	CI.U	p-value
(Intercept)	-1.152	-1.202	-1.103	5.41E-67		(Intercept)	-1.152	-1.204	-1.100	8.63E-67
N	-0.089	-0.149	-0.029	4.17E-03		Summer Temp	0.176	0.111	0.242	6.19E-07
Ca	0.048	-0.016	0.111	1.40E-01		Spring Temp	-0.153	-0.208	-0.097	3.39E-07
Mn	0.062	0.003	0.121	3.86E-02		N	-0.143	-0.206	-0.080	1.63E-05
P	0.056	-0.009	0.121	8.87E-02						
Summer Temp	0.147	0.083	0.212	1.81E-05						
Spring Temp	-0.109	-0.172	-0.046	8.38E-04						
Spring Precip	-0.045	-0.105	0.015	1.40E-01						
Original Scale						**Original Scale**				
Predictor	Estimate	CI.Lorig	CI.Uorig	p-value		Predictor	Estimate	CI.Lorig	CI.Uorig	p-value
Intercept	0.134	0.128	0.141	5.41E-67		Intercept	0.170	0.161	0.178	8.63E-67
N	0.713	0.568	0.896	4.17E-03		Summer Temp	1.186	1.113	1.264	6.19E-07
Ca	1.597	0.856	2.981	1.40E-01		Spring Temp	0.824	0.769	0.884	3.39E-07
Mn	23.423	1.184	463.460	3.86E-02		N	0.922	0.889	0.955	1.63E-05
P	7.491	0.733	76.538	8.87E-02						
Summer Temp	1.153	1.083	1.228	1.81E-05						
Spring Temp	0.871	0.804	0.943	8.38E-04						
Spring Precip	1.000	0.999	1.000	1.40E-01						
Adj Rsq	0.565					**Adj Rsq**	0.518			

Proportion of occluded pseudothecia (Table 3) was best predicted from climate and soil characteristics with an R^2 of 0.429. For both the foliar and soil models standardized coefficients indicate that climate variables (winter temperature and summer dew point) had the strongest control on Pseudothecia proportion. Both soil and foliar N had strong control on Pseudothecia proportion, but the cations K and Mg were also significant predictors. Interestingly soil Mn was a significant predictor of Pseudothecia proportion.

Table 3. Model of pseudothecia proportion from 30-year climate normals and foliar chemical composition (left) and soil chemical composition (right). Estimates and confidence intervals are on the odds ratio scale. R squared values are for linear regression on standardized predictors used to predict logit transformed responses. Standardized coefficients are on the modeled scale, original scale variables are not standardized and are reported on the odds ratio scale

Pseudothecia Proportion * Foliar Nutrients						**Pseudothecia Proportion * Soil Nutrients**				
Standardized Coefficients						**Standardized Coefficients**				
Predictor	Estimate	CI.L	CI.U	p-value		Predictor	Estimate	CI.L	CI.U	p-value
(Intercept)	-1.888	-2.028	-1.749	2.13E-46		(Intercept)	-1.888	-2.025	-1.752	3.81E-47
N	0.326	0.164	0.488	1.26E-04		Winter Temp	-0.242	-0.393	-0.091	1.94E-03
K	0.202	0.024	0.379	2.62E-02		Summer Dewpt	0.239	0.072	0.407	5.50E-03
Mg	-0.151	-0.319	0.016	7.61E-02		N	0.177	0.025	0.328	2.27E-02
P	-0.185	-0.345	-0.025	2.38E-02		Mg	0.197	0.044	0.350	1.20E-02
Winter Temp	-0.357	-0.547	-0.167	3.18E-04		Mn	-0.287	-0.449	-0.125	6.67E-04
Summer Dewpt	0.292	0.136	0.448	3.49E-04		Si	0.370	0.229	0.510	1.04E-06
Original Scale						**Original Scale**				
Predictor	Estimate	CI.Lorig	CI.Uorig	p-value		Predictor	Estimate	CI.Lorig	CI.Uorig	p-value
Intercept	0.000	0.000	0.000	2.13E-46		Intercept	0.001	0.001	0.001	3.81E-47
N	3.457	1.867	6.401	1.26E-04		Winter Temp	0.842	0.756	0.937	1.94E-03
K	16.372	1.402	191.204	2.62E-02		Summer Dewpt	1.599	1.152	2.219	5.50E-03
Mg	0.000	0.000	2.874	7.61E-02		N	1.106	1.015	1.206	2.27E-02
P	0.001	0.000	0.406	2.38E-02		Mg	1.001	1.000	1.001	1.20E-02
Winter Temp	0.776	0.678	0.888	3.18E-04		Mn	0.996	0.994	0.998	6.67E-04
Summer Dewpt	1.772	1.305	2.407	3.49E-04		Si	1.011	1.007	1.015	1.04E-06
Adj Rsq	0.406					**Adj Rsq**	0.429			

Severity index (Table 4) was best predicted from climate and foliar characteristics with an R^2 of 0.445. For both the foliar and soil models standardized coefficients indicate that climate variables (winter and summer temperature and summer dew point) had the strongest control on severity index. While soil and foliar N was a significant predictor for foliar retention and proportion of occluded pseudothecia only foliar N was a significant predictor of severity index. Again soil and foliar Mn was a significant predictor of severity index.

Table 4. Model of severity index from 30-year climate normals and foliar chemical composition (left) and soil chemical composition (right). Estimates and confidence intervals are on the odds ratio scale. R squared values are for linear regression on standardized predictors used to predict logit transformed responses. Standardized coefficients are on the modeled scale, original scale variables are not standardized and are reported on the odds ratio scale

Severity Index * Foliar Nutrients						**Severity Index * Soil Nutrients**				
Standardized Coefficients						**Standardized Coefficients**				
Predictor	Estimate	CI.L	CI.U	p-value		Predictor	Estimate	CI.L	CI.U	p-value
(Intercept)	-2.055	-2.244	-1.867	1.55E-38		(Intercept)	-2.055	-2.252	-1.859	1.99E-37
N	0.394	0.162	0.625	1.05E-03		Winter Temp	-0.442	-0.659	-0.224	1.11E-04
Ca	0.220	-0.007	0.447	5.69E-02		Summer Temp	-0.159	-0.372	0.053	1.39E-01
Mg	-0.437	-0.662	-0.211	2.17E-04		Summer Dewpt	0.485	0.255	0.714	6.11E-05
Mn	-0.253	-0.493	-0.013	3.91E-02		Mn	-0.366	-0.585	-0.146	1.32E-03
Winter Temp	-0.326	-0.583	-0.070	1.33E-02		Si	0.465	0.261	0.669	1.75E-05
Summer Temp	-0.252	-0.471	-0.033	2.43E-02						
Summer Dewpt	0.370	0.127	0.614	3.25E-03						
Original Scale						**Original Scale**				
Predictor	Estimate	CI.Lorig	CI.Uorig	p-value		Predictor	Estimate	CI.Lorig	CI.Uorig	p-value
Intercept	0.014	0.012	0.017	1.55E-38		Intercept	0.000	0.000	0.000	1.99E-37
N	4.469	1.855	10.764	1.05E-03		Winter Temp	0.730	0.626	0.853	1.11E-04
Ca	8.743	0.937	81.584	5.69E-02		Summer Temp	0.857	0.698	1.052	1.39E-01
Mg	0.000	0.000	0.000	2.17E-04		Summer Dewpt	2.583	1.648	4.048	6.11E-05
Mn	0.000	0.000	0.519	3.91E-02		Mn	0.995	0.992	0.998	1.32E-03
Winter Temp	0.793	0.661	0.952	1.33E-02		Si	1.014	1.008	1.020	1.75E-05
Summer Temp	0.784	0.634	0.968	2.43E-02						
Summer Dewpt	2.066	1.282	3.328	3.25E-03						
Adj Rsq	0.445					**Adj Rsq**	0.394			

Prediction of SNC behavior (i.e. foliar retention, pseudothecia proportion, and severity index) from soil and foliar chemical characteristics was moderately successful with this effort resulting in models that could predict around half of the variability (Adjusted R^2 ranged from 0.394 to 0.565; Tables 2-4). In all cases both climate and soil or foliar characteristics were needed to produce the best models. Winter temperatures and summer dewpoint were frequently found to be significant predictors of SNC behavior as has been found by other researchers. Foliar and soil N were also found to have significant controls on SNC behavior, as has been found in previous pilot-scale research. We also found that Mn and cations (Ca, Mg, and K) were frequently found to be significant predictors of SNC behavior.

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Relationships between Climate, Swiss Needle Cast Disease Severity, and the Genetic Structure of *Nothophaeocryptopus gaeumannii* Populations

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Introduction

Populations of the Swiss needle cast (SNC) fungus *Nothophaeocryptopus* (= *Phaeocryptopus*) *gaeumannii* (T. Rohde) Videira, C. Nakash., U. Braun & Crous in western Oregon and Washington comprise two reproductively isolated lineages. Lineage 1 occurs throughout the native range of Douglas-fir and in plantations around the world while Lineage 2 is more narrowly distributed. Lineage 2 is most abundant along the western Coast Ranges within a few kilometers of the coast, and its abundance decreases to the east where it is often supplanted entirely by Lineage 1 (Bennett and Stone, 2016; Winton et al., 2006). Because the distribution of Lineage 2 corresponds approximately with the region of greatest SNC severity, a causal relationship between Lineage 2 and the recent emergence and expansion of SNC in this region has been suggested. Compared with Lineage 1, recovery of Lineage 2 was twice as likely in severely diseased stands, and only half as likely in healthier stands (Winton et al., 2006). In Douglas-fir stands in the coastal SNC epidemic region, canopy density appeared to decrease with increasing Lineage 2:Lineage 1 ratios, suggesting that stands with higher proportions of Lineage 2 had greater defoliation (Winton et al., 2006). Visual estimates of foliage discoloration also appeared to increase with an increasing proportion of Lineage 2 isolates recovered from the stand (Winton et al., 2006). Isolates of *N. gaeumannii* collected from severely diseased sites also seemed to cause more severe SNC symptoms in inoculation trials, suggesting that selection for more virulent or aggressive genotypes may have occurred in the epidemic zone (Winton, 2001). These observations informed our hypotheses about the potential relationships between the spatial distribution of *N. gaeumannii* Lineage 2 and SNC severity.

It is also well documented that the distribution and severity of SNC is closely related to local climate (Coop and Stone, 2010; Hansen et al., 2000; Manter et al., 2005; Rosso and Hansen, 2003; Stone et al., 2008b, 2007; Watt et al., 2010; Zhao et al., 2012, 2011) Winter temperature is particularly influential as a determinant of *N. gaeumannii* abundance, and thus SNC severity, given that pseudothecia develop throughout winter following the spring/summer infection period (Capitano, 1999; Manter et al., 2005; Stone et al., 2008a). Leaf wetness and moisture availability (as precipitation, fog, or dew) during the spring and early summer are also highly influential in predictive models of SNC severity, presumably because moisture is required for spore dispersal, adherence, and germination on the needle surface (Manter et al. 2005; Capitano, 1999; Rosso and Hansen, 2003). Summer temperatures are negatively correlated with pseudothecia abundance and SNC symptoms, as these factors inhibit the development of *N. gaeumannii* (Capitano, 1999; Lee et al., 2017; Rosso and Hansen, 2003; Zhao et al., 2011). A combination of these factors explain a significant amount of the variation ($R^2 \approx 0.49$-0.78) in the current spatial distribution of SNC severity in western North America (Manter et al., 2005; Rosso and Hansen, 2003; Stone et al., 2008b; Watt et al., 2011). The climate in the western Coast Ranges in Oregon and Washington is becoming increasingly conducive to SNC intensification and expansion, given that winters are becoming warmer and spring moisture/rainfall is expected to increase in the coming decades (Lee et al., 2017; Stone et al., 2008b).

Our objectives for this study were to 1) map the spatial distributions of two lineages in relation to SNC severity in the OR and WA Coast Ranges, 2) determine whether any relationship exists between SNC severity (based on estimates of foliage retention) and the relative proportion of *N. gaeumannii* Lineage 2 isolates recovered from the tree, and 3) examine the relationships between the genetic structure of *N. gaeumannii* populations, SNC severity, climate, and geography with multivariate statistical analyses.

Methods

For this study, we analyzed 332 multilocus genotypes (MLGs) consisting of alleles for nine microsatellite (SSR) markers (Winton et al., 2007) from 549 *N. gaeumannii* individuals. Isolates of *N gaeumannii* were collected from the foliage of 5 randomly selected trees at each of 14 sites in the Swiss Needle Cast Cooperative plot network in northwestern Oregon and southwestern Washington in 2014 (Bennett and Stone, 2016; Ritóková et al., 2016), and from 9 sites in northwestern Washington in 2015 (Fig 1). Sampling, isolation, and molecular techniques were performed using the methods described in Bennett and Stone (2016). Genetic divergence among the MLGs was used to determine the relative abundances of the two *N. gaeumannii* lineages recovered from each site. Maps depicting the distributions of the two lineages in this region were superimposed on SNC aerial survey maps from surveys conducted by the Oregon Department of Forestry (ODF), the USDA Forest Service, and the Washington Department of Natural Resources (Ramsey et al., 2015; Ritóková et al., 2016). Foliage retention was estimated using the methods described in Ritóková et al. (2016), and the average foliage retention (AFR) was expressed as the percentage of foliage remaining across four needle age-classes from branches collected in the mid-canopy of each tree.

For the sites sampled in 2014 from the SNCC plot network, AFR was modeled as a function of the relative proportion of isolates of *N. gaeumannii* Lineage 2 recovered from each of the 64 Douglas-fir trees from which MLGs were available (Fig 2). Due to the fact that Douglas-fir foliage retention, SNC severity, and the relative proportion of *N. gaeumannii* Lineage 2 may vary independently along the west-east sampling gradient due to climate and other spatial geographic factors, a linear mixed-effects model was used to describe the influence of the proportion of Lineage 2 on foliage retention with the distance from the coast held at its mean value (32.6 km), and with site included as a random effect. We considered distance from the coast as a proxy for climate and other factors that might independently influence the explanatory and response variables. This model was designed to test the null hypothesis that the proportion of

Lineage 2 has no effect on average foliage retention after accounting for distance from the coast (H_0: $\beta_1 = 0$). All analyses were performed using R version 3.4.1 (R Core Team 2017).

$$Y_{ij} = \beta_0 + \beta_1 X_{ij} + \beta_2 X_{ij} + b_j + \varepsilon_{ij}$$

where:

Y_{ij} is the average foliage retention of the i^{th} tree at the j^{th} site,

β_0 is the mean average foliage retention when the proportion of Lineage 2 in the tree is 0 and the distance from the coast is 0,

β_1 is the coefficient for the effect of the proportion of Lineage 2 on mean average foliage retention,

X_{ij} is the proportion of Lineage 2 recovered from the i^{th} tree at the j^{th} site,

β_2 is the coefficient for the effect of the distance from the coast on mean average foliage retention,

X_{ij} is the distance from the coast of the i^{th} tree at the j^{th} site,

b_j is the random effect of the j^{th} site on mean average foliage retention, $b_j \sim N(0,\sigma^2_b)$,

ε_{ij} is the random error associated with the i^{th} tree at the j^{th} site, $\varepsilon_i \sim N(0,\sigma^2)$.

Non-metric multidimensional scaling (NMS) was used to compare the genetic differentiation between sample sites based on allele frequencies. NMS analyses were based on Euclidean distance measures, and were conducted in PC-ORD 7 (McCune and Mefford 2016).

Correlations between *N. gaeumannii* allele frequency variation and the climatic and geographic variables associated with each site were visualized with a joint-plot overlay, displayed as a series of radiating vectors with the direction of the vector corresponding to the statistical correlation with a given NMS axis and the length of the vector proportional to the strength of the statistical relationship. Included as vectors on the joint plot were the relative proportion of Lineage 2, geographic coordinates, elevation, and nine climate variables that have been used in predictive models of SNC severity and *N. gaeumannii* abundance (Manter et al., 2005; Stone et al., 2007, 2008; Watt et al., 2010) (Fig 3). Time-series values for the climate variables were obtained for each of the sample sites from the PRISM data explorer (http://www.prism.oregonstate.edu) (Table 1). For the second NMS analysis, a site-level average foliage retention estimate (AFR) was included as a vector (Fig 3B). Here, the percentage of foliage remaining among 4 needle age-classes was estimated as described in Ritóková et al. (2016) and averaged across 10 trees from each site.

Results

The spatial distributions of *N. gaeumannii* Lineages 1 and 2 in the western Oregon and Washington Coast Ranges in relation to SNC severity indicated a strong association between the geographic distribution of Lineage 2 and the visible SNC symptoms mapped during the aerial surveys. Sites nearest the coast generally had the highest proportions of Lineage 2 and the most severe SNC symptoms for both Oregon and Washington (Fig 1). Sites further inland, where Lineage 2 was generally rare or absent, had little or no SNC symptoms (Fig 1). To further explore this relationship, we devised a linear mixed-effects model depicting average tree-level foliage retention as a function of the proportion of *N. gaeumannii* Lineage 2 recovered from the tree, after accounting for the site's distance from the coast. There was no evidence to suggest a statistically significant association between AFR and the relative proportion of Lineage 2 isolates recovered (t_{49} = -0.301, p = 0.765) when the distance from the coast was held at its mean (Fig 2). On average, the AFR was estimated to decrease by approximately 2.1% ($\widehat{\beta}_1$ = -2.10, 95% CI: -16.13 to 11.93) with each incremental increase in the proportion of Lineage 2, but the 95% CI included 0 and thus we did not have sufficient evidence to reject the null hypothesis (H_0: $\beta_1 = 0$).

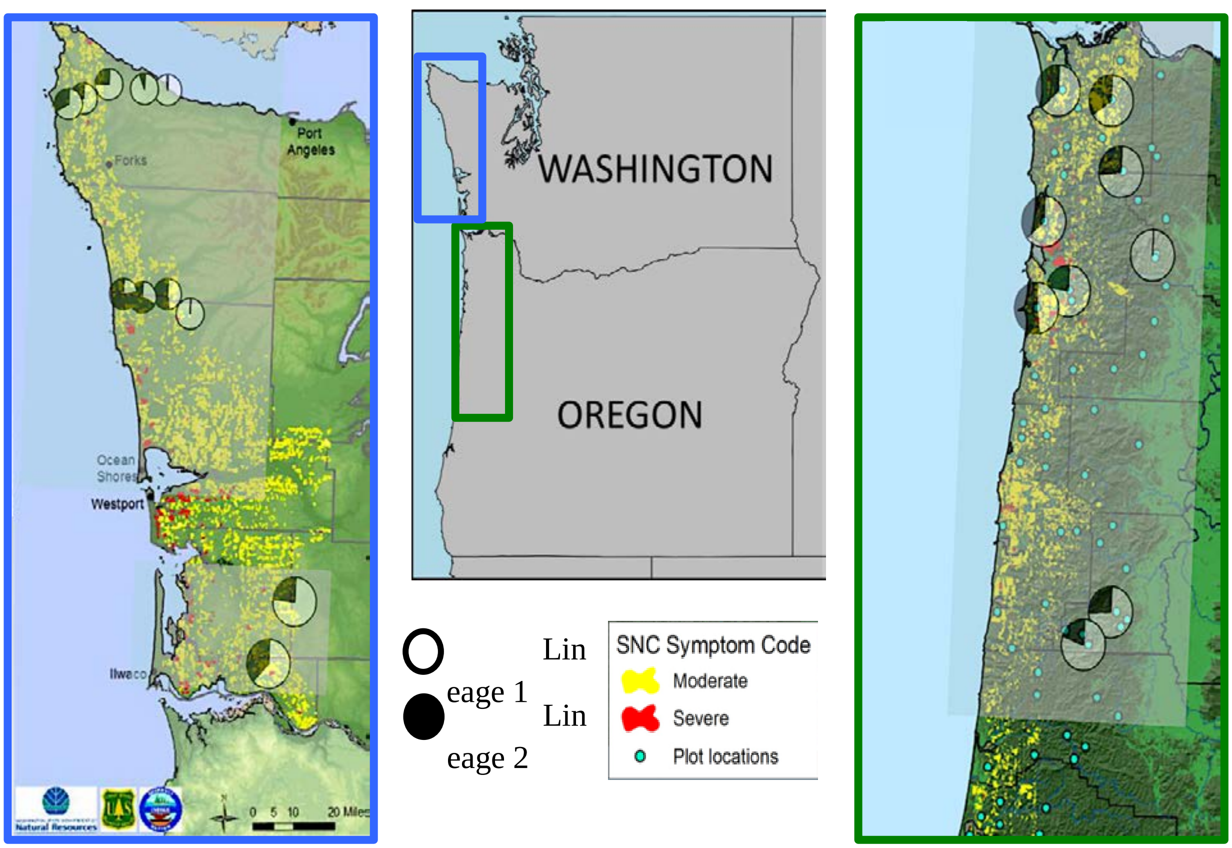

Fig 1. Aerial survey maps showing SNC disease severity with overlay showing the relative proportions of the two cryptic *Nothophaeocryptopus gaeumannii* lineages recovered from each site. Left: Washington SNC aerial survey 2015 map (Ramsey et al. 2015). Southern sites sampled in 2014, Olympic Peninsula sites sampled in 2015. Right: Oregon aerial survey map, sites sampled from SNCC plot network in 2014 (Ritóková et al. 2016). Some sites were combined into a single pie chart to prevent overlap.

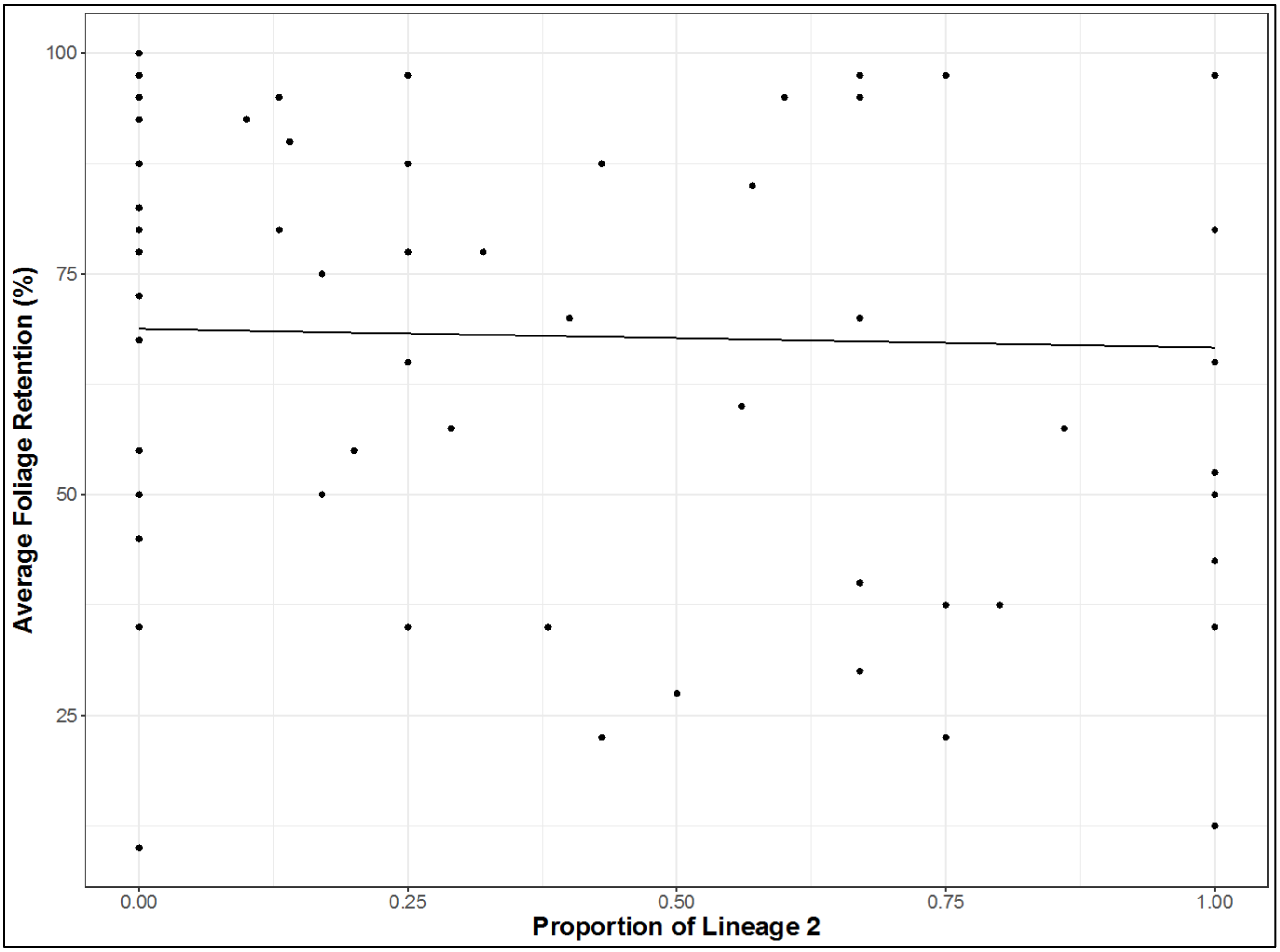

Fig 2. Scatterplot showing the estimated relationship between the average foliage retention (AFR) (%) and the proportion of *Nothophaeocryptopus gaeumannii* Lineage 2 recovered from each of the trees included in this analysis, after accounting for the distance from the coast. The line corresponds to predicted values from the model when the distance from the coast is fixed at its mean (32.6 kilometers), with the shaded region representing the 95% confidence intervals for the predicted values.

For the NMS ordinations, two axes accounted for most of the variation in allele frequencies (cumulative variance explained = 0.875 (Fig 3A), and 0.917 (Fig 3B)). The final stress values of 11.135 (Fig 3A) and 9.036 (Fig 3B) indicated that the distance between the points representing the sample sites in the ordination space were proportional to the genetic distances between the sample sites. The proportion of *N. gaeumannii* Lineage 2 (PL2) had the strongest relationship with NMS axis 1 in both plots (Fig 3, Table 2). Coastal sites and inland sites were aligned along this axis according to the geographic distributions of each lineage. Sites at the left side of the plot had higher proportions of Lineage 1, or Lineage 2 was absent, and sites at the right side of the plot had higher proportions of Lineage 2. Due to the fact that westernmost sites generally had greater proportions of Lineage 2 than inland sites (and thus higher frequencies of Lineage 2 alleles), longitude was strongly correlated with NMS axis 1 (Fig 3B, Table 2).

In the NMS that included all sites (Fig 3A), May-July dew point temperature had a positive relationship with both NMS axes (MADT, Axis 1: *r* = 0.426, Axis 2: *r* = 0.378), and covaried with mean winter temperature on both axes (Tmean Winter: Axis 1: *r* = 0.386, Axis 2: *r* = 0.313) (Fig 3A, Table 2). January 2014 minimum temperature had the strongest positive relationship with NMS Axis 2 (Jan Tmin, *r* = 0.447). August maximum temperature (Aug. Tmax, *r* = -0.549), summer mean temperature (Summ. Tmean, *r* = -0.383), summer average maximum temperature (Summ. Avg. Tmax, *r* = -0.409), and May-July maximum vapor pressure deficit (Max VPD, *r* = -0.402) were all negatively correlated with NMS Axis 2 (Fig 3A, Table 2)

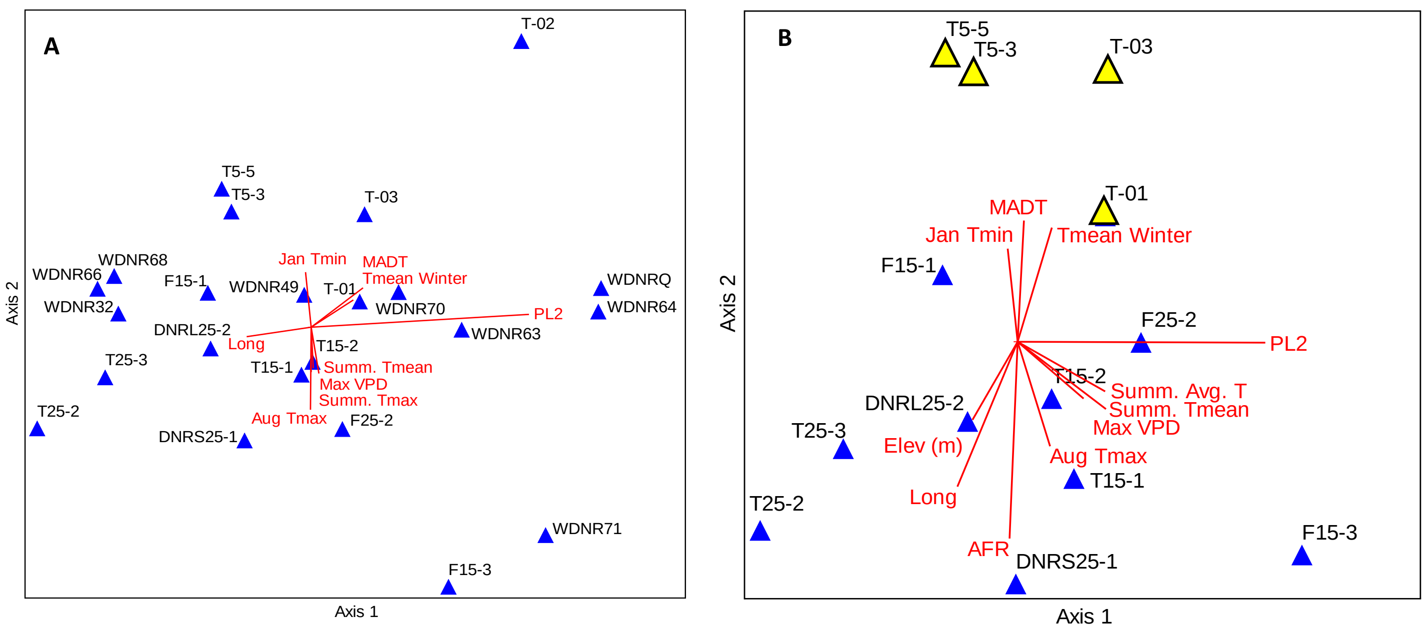

Fig 3. Joint plots from non-metric multidimensional scaling (NMS) ordination of sampling sites in multilocus SSR allele frequency space. The plots are overlaid with vectors representing environmental and geographic variables, and the relative proportion of Lineage 2 (PL2) recovered from the site (Table 1). Only variables with correlation coefficient (*r*) greater than 0.2 are shown. A) 14 sites sampled in northwestern Oregon and southwestern Washington in 2014, and 9 sites sampled in northwestern Washington in 2015 ($N_{isolates}$ = 853, cumulative variance explained = 0.875, final stress = 11.135). B) Sites sampled in 2014 only, with a vector representing an average foliage retention index (AFR) estimated for each site ($N_{isolates}$ = 549, cumulative variance explained = 0.917, final stress = 9.036). Site T-02 was removed from this analysis due to being a significant outlier. The yellow triangles in B represent sites in the original SNC epidemic zone near Tillamook, Oregon.

For the ordination that included only the 2014 sample sites (Fig 3B), summer maximum temperature and mean summer temperature were correlated with both axes (Summ. Avg. Tmax, Axis 1: *r* = 0.566, Axis 2: *r* = -0.430; Summ. Tmean, Axis 1: *r* = 0.569, Axis 2: *r* = -0.501). Elevation also had negative correlations with both axes (Elev (m), Axis 1: *r* = -0.404, Axis 2: *r* = -0.539). The average foliage retention had a very strong negative correlation with Axis 2 (AFR, *r* = -0.858). Variables corresponding to winter temperature and mean dew point temperature had strong positive correlations with Axis 2, while variables associated with summer temperature and vapor pressure deficit had strong negative correlations with this axis (Fig 3B, Table 2). A group of sites near the original Tillamook epidemic zone appeared to be highly genetically differentiated from other sites in the plot, and occupied a specific climatic zone with the highest winter temperatures and the highest May-July dew point temperatures. These sites also had the lowest foliage retention (Fig 3B). One site near Tillamook, OR (T-02) was removed because it was identified as a significant outlier that had a disproportionate influence on the ordination.

Table 1. Climatic, geographic, and disease variables used in NMS joint plot overlay in Figure 3.

Variable	**Abbreviation**
Latitude (decimal degrees)	Lat
Longitude (decimal degrees)	Long
Elevation (meters)	Elev (m)
January 2014 minimum temperature (˚C)	Jan Tmin
Winter 2014 mean average temperature (November 2013-March 2014) (˚C)	Tmean Winter
August 2014 maximum temperature (˚C)	Aug Tmax
Summer 2014 maximum temperature (May-September 2014) (˚C)	Summ. Avg. T
Summer 2014 mean temperature (May-September 2014) (˚C)	Summ. Tmean
May-July 2014 mean average dewpoint temperature (˚C)	MADT
May-July 2014 maximum vapor-pressure deficit (kPa)	Max VPD
Relative proportion of Lineage 2 isolates in sample site (Number of Lineage 2 Isolates/Total Number of Isolates)	PL2
Disease severity- Average foliage retention (%)	AFR

Table 2. Pearson coefficients (*r*) for correlations between the NMS axes and each of the variables used in the joint plot overlay in Fig 3 and described in Table 1. Shown in bold are correlation coefficients greater than 0.5 or less than -0.5.

	2014 + 2015 (Fig 3A)		**2014 only (Fig 3B)**	
Variable	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
Lat	0.121	0.106	-0.347	-0.047
Long	-0.477	-0.188	-0.470	**-0.736**
Elev (m)	NA	NA	-0.404	**-0.539**
Jan Tmin	-0.139	0.447	-0.191	**0.589**
Tmean Winter	0.386	0.313	0.356	**0.651**
Aug Tmax	-0.036	**-0.549**	0.343	**-0.625**
Summ. Avg. Tmax	0.166	-0.409	**0.566**	-0.430
Summ. Tmean	0.090	-0.383	**0.569**	**-0.501**
MADT	0.426	0.378	0.150	**0.672**
Max VPD	0.025	-0.402	0.490	-0.458
PL2	**0.878**	0.219	**0.955**	-0.049
AFR	NA	NA	-0.168	**-0.858**

Discussion

The spatial distributions of the two *N. gaeumannii* lineages in western Oregon and Washington appear to be correlated with SNC severity, as visible symptoms of the disease are most severe where the lineages coexist within ~ 30 km of the coast. Further inland, Lineage 2 is exceedingly rare and SNC symptoms are less severe or absent (Fig 1). Two sites at the southern end of our sampling distribution in Oregon did not fit this trend, as both lineages were present ~ 50 km inland, but the sites were outside of what is generally considered the SNC "epidemic" zone and did not exhibit visible symptoms in the aerial surveys. Overall, the observation that the region where the lineages overlap is where SNC is most severe seems to be in agreement with the findings of Winton et al. (2006), which suggested that stands with greater abundances of

Lineage 2 also had greater SNC severity. However, the results of our linear model suggested that, on average, after accounting for distance from the coast (as a proxy for climate and other variables that may influence foliage retention and SNC severity along the west-to-east sampling distribution) the proportion of *N. gaeumannii* Lineage 2 recovered from the foliage of a Douglas-fir tree was not significantly correlated with foliage retention. In the present study, sample sizes were much larger than those used for Winton's analyses, and foliage retention was measured systematically for each tree, as opposed to a stand-level visual estimation of canopy density. The fact that foliage retention and the proportion of Lineage 2 were assessed at the level of the tree, as opposed to the level of the site, lends to the statistical power of this analysis. The resulting model may better approximate the true relationship between Lineage 2 and disease severity.

The multivariate NMS ordination revealed strong spatial genetic differentiation between inland and coastal sample sites. This approach allowed for a visualization of the strength of the relationships between genetic variation and pertinent environmental, geographic, and disease variables. The geographic distribution of genetic variation was highly correlated with mean winter temperature, mean summer maximum temperature, maximum vapor pressure deficit, and mean average dew point temperatures in the year prior to sampling. Foliage retention varied most strongly with August maximum temperature and longitude, and was inversely related to May-July dew point temperature and winter temperature (Fig 3B). Foliage retention was lowest at sites where Lineage 1 and Lineage 2 coexisted near the coast in Tillamook County, Oregon. These sites had the warmest winter average temperatures and the highest January minimum temperatures, as well as the highest spring/summer dew point temperatures. These sites also had low summer temperatures and low vapor pressure deficits (Fig 3B). Foliage retention was much higher at the higher elevation inland sites where the winters were cold, summers were hotter and drier, and Lineage 2 was absent. These results corroborate previous models of SNC severity that included these variables (Lee et al., 2013, 2016; Manter et al., 2005; Stone et al., 2007, 2008; Watt et al., 2010, 2011), and provide further statistical support for their importance as predictors of disease severity. Not only does climate influence SNC severity, but it may also influence the distributions of the two *N. gaeumannii* lineages and the genetic structure of *N. gaeumannii* populations. It appears that the two *N. gaeumannii* lineages are adapted to different environments, and thus exhibit different habitat distributions that are determined, at least in part, by climate. The local environment has a potential to be a driver of genetic change in *N. gaeumannii* populations. The *N. gaeumannii* isolates collected from the most severely disease sites in the original SNC epidemic zone exhibited a unique allelic signature, suggesting that some adaptation to local climate or natural selection for advantageous genotypes has occurred in this region. Whether *N. gaeumannii* isolates in the coastal SNC epidemic zone are more aggressive or have increased fitness (and thus cause more severe SNC) is still unclear and should be the focus of future studies.

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