Oregon State University | College of Forestry

Swiss Needle Cast Cooperative

Annual Report 2021

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Oregon Department of Forestry

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Swiss Needle Cast Cooperative Staff

Dave Shaw – Director and Associate Professor of Forest Health

Gabriela Ritóková – Associate Director and Senior Faculty Research Assistant

Cover photo by Florian Deisenhofer

SNCC Income Sources and Expenditures: 2021

Income

Membership dues	*84,000*
Oregon State Legislature	*95,000*
Carry-over	*90,204*
Total 2021 Income	**$269,204**

Expenditures

Salaries and wages	*147,461*
Travel	*7,792*
Operating expenses	*6,512*
Materials and Supplies	*2,393*
Indirect Costs (@17.5%)	*28,728*
Total 2021 Expenditures	**$192,886**

Balance	**$76,318**

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2/13/2022

To: Swiss Needle Cast Cooperative Members

From: David Shaw, SNCC Director

Re: 2021 Annual Report

Dear Members,

Well, 2021 was quite a year for everyone, including the SNCC. But despite the craziness, Gabi managed to finish the 5-year remeasurement of the Research and Monitoring Plot Network, and we worked with CIPS and Doug Mainwaring to use the growth and yield data to improve predictive models.

Of course, the big SNCC news this year is that Gabi has joined ODF as the new State Forest Pathologist and is now representing ODF as a member of the coop! This is excellent news for ODF and Oregon!

2021 was a good year for new papers published on SNC in the PNW. These have been included in the Annual Report for your convenience. There are still some mysteries regarding SNC and *Nothophaeocryptopus gauemannii*, and the cooperative and various researchers in Oregon, Washington, and British Columbia continue to pursue these. Nevertheless, we feel that our Research and Monitoring Plot Network and the Cascades monitoring plots, as well as the weather stations, are making some substantial contributions to growth and yield models, as well as disease epidemiology.

There is increasing interest in SNC in SW British Columbia, where industry and government are apprehensive about what they are seeing in Douglas-fir plantations. We will continue collaborating with these players as we are seen as the go-to cooperative for information and ideas about SNC epidemiology and management.

Sincerely,

David C. Shaw

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, *Nothophaeocryptopus 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.

Five-year remeasurement of the SNCC research and monitoring plots

Gabriela Ritóková

Oregon Department of Forestry, Salem, Oregon.

The establishment of the new Swiss needle cast cooperative (SNCC) research and monitoring plot network (RPN) was initiated in 2013, and over a three-year period, 106 plots were installed in 10-25-year-old Douglas-fir plantations from the California-Oregon border to southwest Washington (fig. 1). We concluded the first five-year period of plot re-measurement, providing information about disease severity, growth loss, and its geographic distribution on 103 plots throughout the Coast Range. Three plots were not measured due to the Chetco Bar fire in 2017, accidental plot thinning of one of the research plots in the Tillamook block, and roadbuilding through another plot in the Newport block.

Figure 1. SNCC RPN.

Reports have been produced from the first remeasurement, including a peer-reviewed article on foliage dynamics (included within this annual report), the stand-level volume growth analysis (2020 annual report, page 24), and the development of ORGANON increment modifiers (2020 annual report, page 37).

The next round of remeasurement is due to resume in fall 2023, followed by foliage sampling in the spring. The ten-year re-measurement will conclude in the spring of 2026 with the final collection of foliage for disease severity assessment and foliage retention evaluation.

Results from simulating mixed stands with the updated ORGANON SNC modifier

Doug Mainwaring
Center for Intensive Planted-forest Silviculture, Forest Engineering, Resource, and Management, Oregon State University

Abstract

Swiss needle cast modification of diameter and height growth and volume within ORGANON was updated in 2021, based on newly fit diameter and height growth modifiers from the latest measurements of the SNCC's new research plot network, application of a newly fit SNC taper modification equation and an updated procedure for applying the modifiers within the model.

The updated model was used to simulate mixed stands of Douglas-fir and western hemlock to test the extent to which reductions in Douglas-fir growth results in improved western hemlock growth. Based on simulations, the standing volume of western hemlock in mixed stands did increase as Douglas-fir foliage retention decreased. However, this increase did not make up for the reductions of Douglas-fir volume resulting from greater SNC.

Introduction

Stands exhibiting the most severe Swiss needle cast symptoms are typically near the coast, where western hemlock is common. Although western hemlock log prices are lower than Douglas-fir, where SNC is severe, an improved likelihood of long-term viability makes it a natural replacement species for reforestation after harvest or possibly a better choice for retention in thinning operations (Zhao et al. 2014). Based on the implied growth rates from predictive equations and observations in severely infected coastal stands, poorly performing Douglas-fir can be overtopped and suppressed by neighboring western hemlock, despite typically being a faster-growing species in the absence of disease.

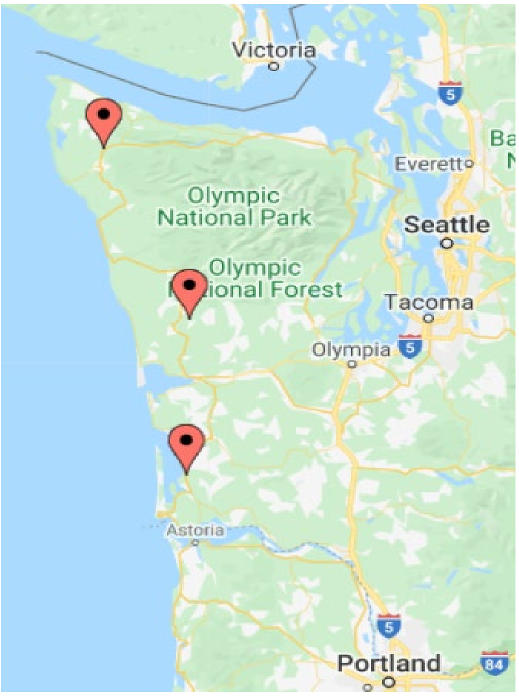

Figure 1. Locations of the DF-WH mixed species spacing trials, the source of data used for the ORGANON simulations.

Since SNC modification equations were introduced into ORGANON more than ten years ago, there remained an inconsistency between stand-level estimates of growth loss (Maguire et al., 2011) and those predicted from ORGANON simulations. Improvements to the SNC modification procedure within the regional growth model ORGANON were made in

2021, fixing this inconsistency. Accordingly, the model was used to project mixed stands of Douglas-fir and western hemlock to gauge the effects of reduced Douglas-fir foliage retention on the growth of both species.

Methods

Data

Measured plots from three SMC type 3 mixed species spacing trials were used for simulations. All located in coastal Washington (fig. 1), these sites were planted in the late 1980s with an approximate 50:50 mix of Douglas-fir and western hemlock to six different densities (100, 200, 300, 435 680, and 1210 trees per acre). Site indices at the three sites were estimated from the 300 TPA densities, with the reasoning that the inter-tree competition was less likely to impede the growth of dominant trees of either species at lower densities. These sites were productive, with 50-year site indices of both species ranging from 126 to 140 ft. At two sites, the estimated site indices of the two species were approximately equal, while at the third, the Douglas-fir site index was about 10% greater than that of western hemlock.

		Dbh (inches)		Ht (ft)		
Spacing	Species	Dominant	Mean	Dominant	Mean	TPA
21x21	DF	5.5	4.6	26.5	23.3	48
	WH	4.7	4.5	24.6	23.8	60
15x15	DF	5.5	4.3	29.0	24.4	116
	WH	5.2	4.2	28.4	25.1	128
12x12	DF	6.0	4.5	31.2	26.4	177
	WH	5.3	4.2	29.8	24.9	198
10x10	DF	6.0	4.6	31.4	27.2	225
	WH	5.4	4.1	30.7	25.6	207
8x8	DF	5.5	4.2	30.8	26.3	250
	WH	5.6	4.0	32.9	25.8	341
6x6	DF	5.8	4.2	36.2	28.9	541
	WH	5.9	3.9	36.4	28.2	546

Table 1. Average tree size and density data by spacing and species for the initial treelists used for the ORGANON simulations.

Simulations

Tree lists were projected from measurements made at plantation ages of 10-13 years, chosen to avoid the presence of small trees that had not yet reached 4.5 ft, the influence of competing vegetation in the plantations, and the age/size threshold necessary for projection with the SMC variant of ORGANON, version 9.1. The TPA and mean and dominant sizes of the trees in the initial tree lists can be found by species and spacing in table 1. Plots were projected to age 45 years, assuming no presence of SNC and at foliage retention of 2, 1.5, and 1.0 years. In addition, the same tree lists were projected with all trees assigned as 1) Douglas-fir; or 2) western hemlock. When projected as Douglas-fir, tree lists were projected at all four levels of SNC. Results are the average from all three sites.

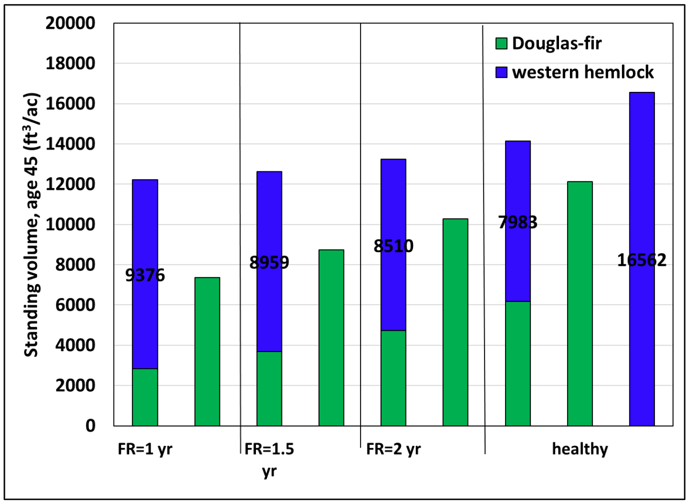

Figure 2. Stand-level cubic volume for the 435 TPA planting, projected as a mixed or pure stand at four levels of SNC. Labeled volumes are western hemlock only.

Results and Discussion

Simulated estimates of standing volume were high for age 45. Figure 2 shows the results for the 435 TPA planting, showing the expected reduction in Douglas-fir volume with reduced DF foliage retention and the subsequent increase in western hemlock volume due to diminished interspecies competition from "infected" Douglas-fir. Douglas-fir volume was estimated to be ~1500 ft3/ac lower than for a healthy stand at foliage retention of 2 years and ~3300 ft3/ac lower at foliage retention of 1 year. At the same time, western hemlock volume was estimated to increase 500 ft3/ac at foliage retention of 2 years and ~1500 ft3/ac at foliage retention of 1 year (fig. 3). This net reduction in volume would be an even greater reduction in value, given the typically lower log prices for western hemlock relative to Douglas-fir.

Results for the other spacings are relatively similar (fig. 4), with the largest net loss in volume occurring at moderate densities and the smallest net loss at the highest densities.

Although infected mixed stands suffer a net loss of volume relative to their uninfected counterparts, even the most infected mixed stands may produce more standing volume at age 45 than a pure Douglas-fir stand, particularly at higher initial densities (fig. 5).

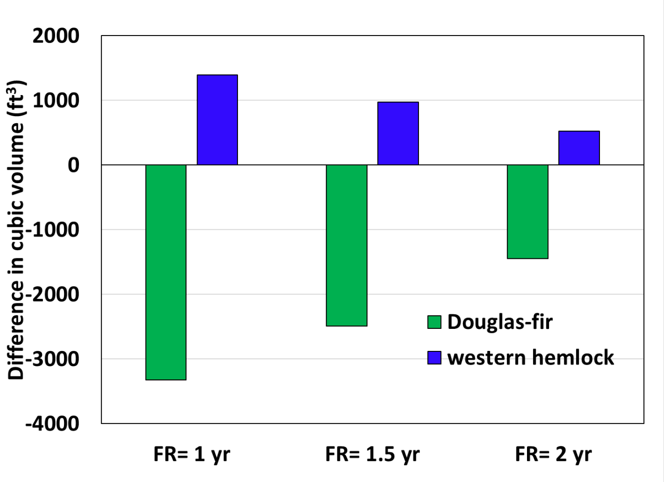

Figure 3. Difference in cubic volume by species between healthy stands (foliage retention=3+ yrs) and those with reduced Douglas-fir foliage retention. Douglas-fir volume is shown to decrease while western hemlock volume increases.

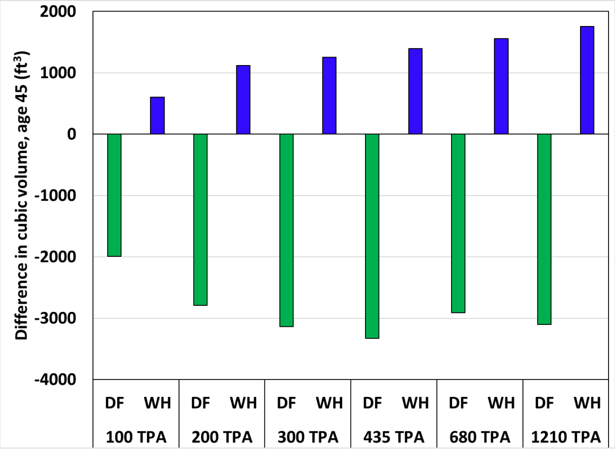

Figure 4. Difference in cubic volume by species for a mixed stand with foliage retention of 1.0 year relative to an uninfected mixed stand at age 45 years.

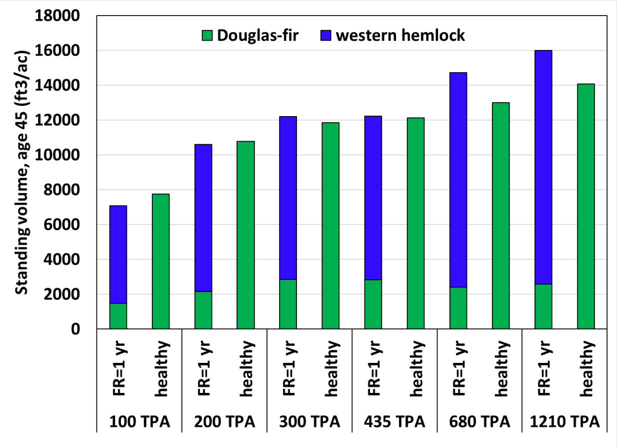

Figure 5. Cubic volumes for mixed stands with foliage retention of 1.0 year relative to an uninfected pure stand of Douglas-fir at six different planting densities.

A more detailed glance at the effects of SNC on differentiation can be seen by comparing the height-diameter relationship of the species mixes at age 45 years. Figures 6 and 7 show the results at one of the sites after 35 years of projection at foliage retention of 3 or 1 year, respectively. Of the three sites from which data was available, the site represented in figures 6 and 7 was the one most closely conforming to the expected dominance of Douglas-fir in the absence of Swiss needle cast (Nigh 1995). Different differentiation patterns would be expected where the relative productivity rates were more similar, as was the case on the other two sites in this analysis.

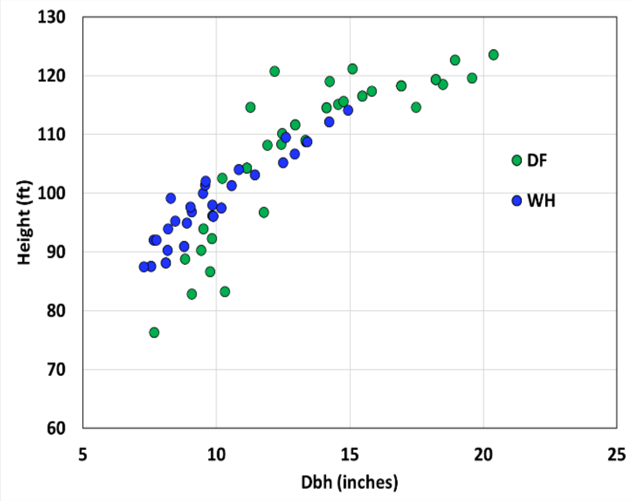

Figure 6. Height-diameter relationship of Douglas-fir and western hemlock from one site, based on a projection with a Douglas-fir foliage retention of 3 years. Douglas-fir is the dominant species.

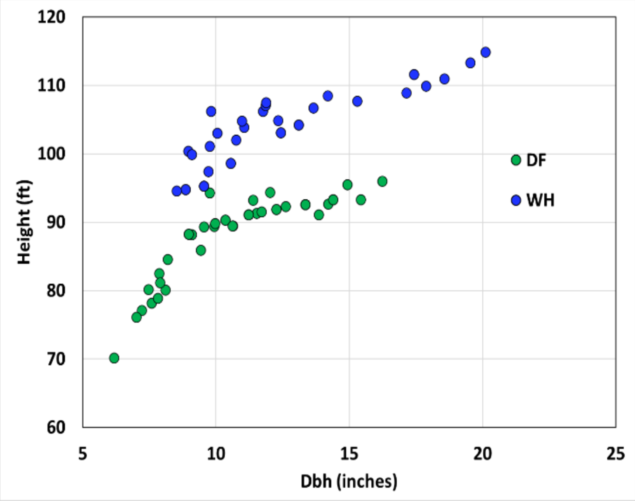

Figure 7. Height-diameter of Douglas-fir and western hemlock from one site, based on a projection with a Douglas-fir foliage retention of 1 year. Douglas-fir is the subordinate species.

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2021 Swiss Needle Cast Ground Sampling in Washington

Rachel Brooks, Daniel Omdal
Department of Natural Resources

Nothophaeocryptopus gaeumannii, the fungus that causes Swiss needle cast (SNC), is found wherever its only host, Douglas-fir (*Pseudotsuga menziesii*), is planted. This foliar disease rarely causes tree mortality but can cause premature needle shed, resulting in sparse tree crowns and reduced growth. This native pathogen became a priority in the coastal forests of Washington and Oregon in the late 1980s and early 1990s and, more recently, has impacted forests in Canada. These areas have likely seen damage due to the fungi-favorable topographic and climatic conditions (such as mild winters and wet springs), historical plantings using off-site seed sources, and increases in Douglas-fir numbers due to forest management practices.

Ground and aerial surveys monitoring this disease have been conducted in Washington State for many years. The Washington State Legislature provided funding in the 2019-2021 biennium to conduct aerial and ground surveys in spring 2020 in Washington's coastal forests. These surveys were canceled due to COVID-19 operating restrictions, and instead, efforts focused on increased ground surveys during 2021.

During the spring of 2021, two study areas in Washington were selected for assessment: (1) the alpha-convex hull containing all marked regions during the 2016 SNC coastal aerial survey ("coastal region") and (2) an area in the Northwest Region representing the active timberland between the cities of Mount Vernon, Darrington, Concrete, Bellingham, and Sumas ("NW region"), as shown in Map 1. The first area represents the location that SNC has been previously monitored for. The second location represents an area not previously surveyed. Ground sampling locations in each area were separately selected with a uniform spatial weighting function using a Balanced Acceptance Sampling method (BAS; Robertson et al., 2013). Based on time availability, fifty sampling locations were chosen randomly in the coastal region and 17 in the NW region. Each selected point was visited once between March and May. An accessible and appropriate stand (dominated by suitably sized Douglas-firs) no greater than four miles away from the random point was chosen for sampling. Points that had no appropriate or accessible sites within four miles were excluded. In total, 48 sites in the coastal region and 15 sites in the NW region were sampled.

At each site, ten trees were selected for sample collection and measurements. Foliar retention (the amount of needles retained from each cohort year) was visually estimated on each tree. One-year-old and two-year-old foliage was collected from each tree's fourth or fifth whirl and taken back to the lab for examination under a microscope. SNC incidence (presence) and severity (percent stomata obstructed by the fungal reproductive structures - pseudothecia) was counted.

Due to differences in sampling density of the two areas (one point per 77 square miles in the coastal region and one per 69 square miles in the NW region), summary calculations (averages and standard errors) for each site were done separately before comparison using a t-test. Standard errors were calculated using the design-based estimators provided by the package 'Spsurvey' (Kincaid et al., 2019) to account for the site selection method.

Though SNC and needle retention varied at each site, some trends were observed. The mean percentage of pseudothecia occluded on 2-year-old needles at a site was 21.1% in the coastal region and 35.9% in the NW region. While mean foliar retention at each site was 2.52 in the coastal region and 2.93 in the NW region (Table 1). Using a t-test, both measurements were significantly different between the areas ($p<0.001$), with the coastal region having lower pseudothecia densities despite worse foliar retention ratings than the NW region. This is noted since stomata are responsible for gas and water exchange within a plant. Significant obstruction of these features can result in imbalanced carbon costs and subsequent needle loss. This lack of association indicates other factors besides SNC likely influence needle retention at these sites. Other spatial trends can be seen on Map 1.

Table 1: Number of sites, the average percentage of occluded stomates on 2-year-old needles (%), and average foliar retention (0 indicates there were no needles retained and 3.6 indicating full retention of 4-years of foliage) for each region surveyed.

Region	Number of sites	The average percentage of occluded stomates*	Average foliar retention *
Coastal	48	21.1 ± 1.2 (2.8 - 53.2)	2.52 ± 0.04 (1.82 - 3.16)
NW	15	35.9 ± 3.0 (12.5 - 62.6)	2.93 ± 0.05 (2.43 - 3.31)

*mean value ± standard error (minimum site value – maximum site value)

Previous surveys occurred throughout the coastal range (Table 2) but never in the NW region. The mean percentage of occluded stomates measured in the coastal region in 2021 is within the previously recorded ranges, while mean foliar retention is slightly higher. This indicates there have been no substantial changes in the incidence and severity of SNC over this period.

Table 2: Previous ground survey results from 2018, 2016, 2015, and 2012.

Year	Number of sites	The average percentage of occluded stomates	Average foliar retention
2018	26	16	2.3
2016	63	22.1	2.4
2015	47	22.5	2.3
2012	75	15.5	2.2

Given that Douglas-fir is the only host of SNC, forest managers may select for or plant other non-host species, such as western redcedar, western hemlock, Sitka spruce, or red alder in areas where disease pressure is high. However, if Douglas-fir is retaining more than three years of foliage on its branches, growth loss is likely to be minimal.

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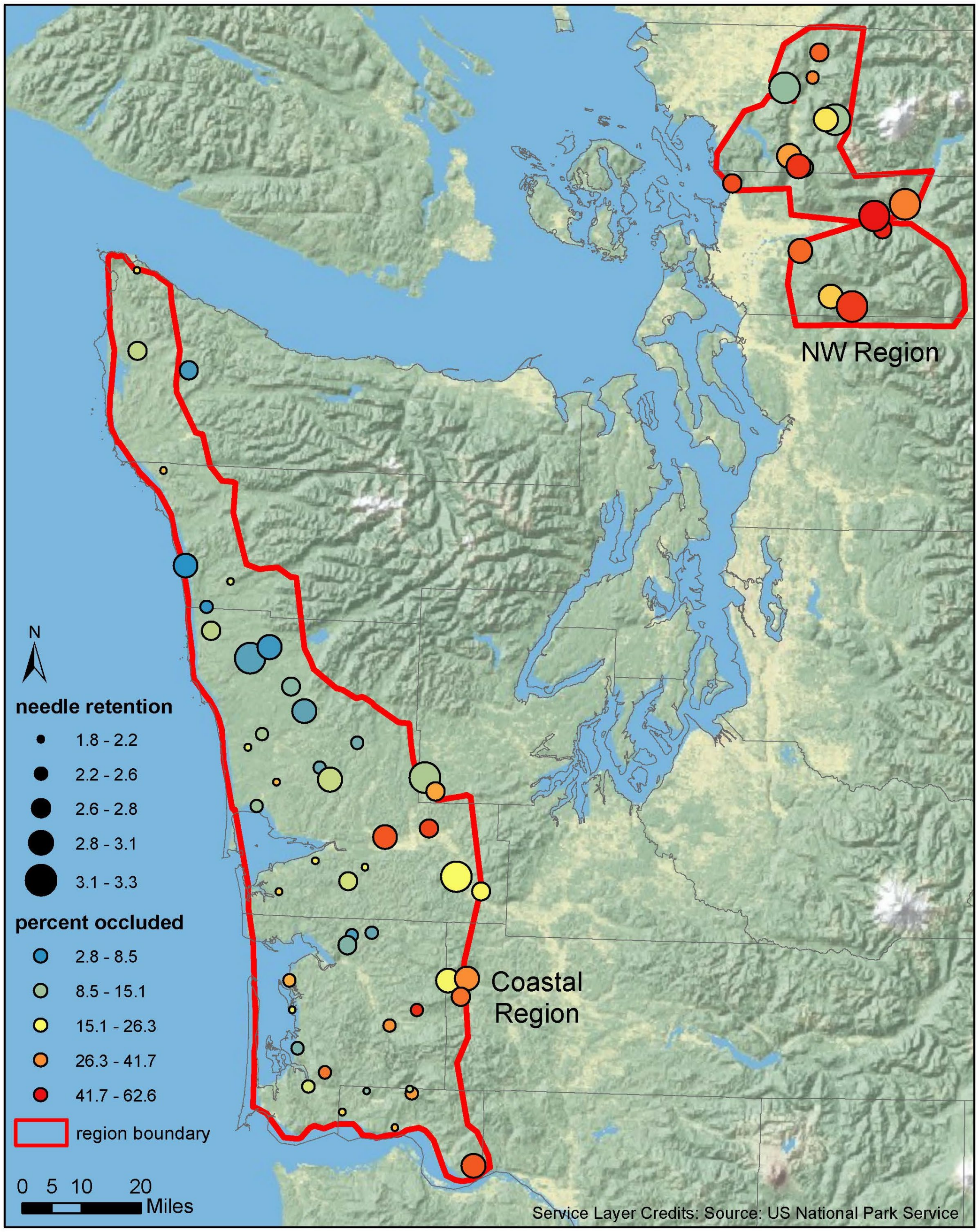

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NRC Research Press

ARTICLE

Douglas-fir foliage retention dynamics across a gradient of Swiss needle cast in coastal Oregon and Washington

Gabriela Ritóková, Douglas B. Mainwaring, David C. Shaw, and Yung-Hsiang Lan

Abstract: Swiss needle cast (SNC) is an important foliage disease of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) caused by the native pathogen *Nothophaeocryptopus gaeumannii* (T. Rohde) Videira, C. Nakash., U. Braun & Crous, which has been present in epidemic proportions in coastal Douglas-fir forests since the 1990s. Under conducive environmental and stand conditions, the fungal fruiting bodies emerge on young needles, inhibiting gas exchange and causing premature needle casting and subsequent growth losses. Using a new regional plot network, which extends and approximately doubles the area of SNC-susceptible coastal forest sampled, we investigated the distribution of SNC disease indices across the region and throughout individual tree crowns. Foliage retention varied from 1.15 to 3.9 years, and disease severity index (incidence × % occluded stomata) ranged from 0.05% to 52.11%. Foliage retention was positively correlated with distance from the coast and elevation, while foliage retention and disease severity were negatively associated across the study area. Within crowns, disease severity was negatively associated with crown depth, and foliage retention was positively associated with crown depth, regardless of distance from coast. Across the entire study area, foliage retention was found to decrease and disease severity increase with latitude, all else being equal. Tree growth metrics are positively associated with increasing foliage retention, and normal growth occurs greater than ~3.2 years.

Key words: Swiss needle cast, *Nothophaeocryptopus gaeumannii*, foliage retention, Douglas-fir.

Résumé : La rouille suisse (RS) est une importante maladie de feuille du douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) causée par le champignon pathogène indigène *Nothophaeocryptopus gaeumannii* (T. Rohde) Videira, C. Nakash., U. Braun & Crous, qui est présent de façon épidémique depuis les années 1990 dans les forêts côtières de douglas de Menzies. Lorsque les conditions du milieu et les caractéristiques des peuplements sont favorables, les fructifications du champignon se développent sur les jeunes aiguilles et inhibent les échanges gazeux, ce qui entraîne la perte prématurée des aiguilles et des baisses subséquentes de croissance. Grâce à un nouveau réseau régional de placettes, qui élargi et approximativement double la superficie de forêt côtière sensible à la RS qui a été échantillonnée, nous avons étudié la répartition des symptômes de la maladie partout dans la région et dans la cime d'arbres individuels. La rétention des aiguilles variait de 1,15 à 3,9 années et la sévérité de la maladie (fréquence × % de stomates obstrués) variait de 0,05 % à 52,11 %. La rétention du feuillage était positivement corrélée avec la distance depuis la côte et l'altitude. La rétention du feuillage et la sévérité de la maladie étaient négativement associées partout dans l'aire d'étude. À l'intérieur des houppiers, la sévérité de la maladie était négativement associée à la profondeur du houppier peu importe la distance de la côte. Dans toute l'étude, toutes choses étant égales la rétention du feuillage diminuait et la sévérité de la maladie augmentait avec la latitude. Les mesures de croissance des arbres sont positivement associées à l'augmentation de la rétention du feuillage et la croissance devient normale lorsque les aiguilles persistent pendant au moins ~3,2 années. [Traduit par la Rédaction]

Mots-clés : rouille suisse, *Nothophaeocryptopus gaeumannii*, rétention du feuillage, douglas de Menzies.

Introduction

Swiss needle cast (SNC) is a species-specific foliar disease affecting Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) that is caused by *Nothophaeocryptopus* (=*Phaeocryptopus*) *gaeumannii* (T. Rohde) Videira, C. Nakash., U. Braun & Crous (Mycosphaerellaceae), a recently reclassified ascomycete fungus (Videira et al. 2017). Pacific coastal forests have seen SNC emerge as a significant threat to Douglas-fir plantation productivity since the 1990s (Hansen et al. 2000; Shaw et al. 2011; Ritóková et al. 2016). The pathogen causes growth and volume reduction of Douglas-fir through inhibition of gas exchange (Manter et al. 2000) and premature casting of needles (Hansen et al. 2000; Maguire et al. 2002, 2011), although disease-caused tree mortality is rare (Maguire et al. 2011).

Nothophaeocryptopus gaeumannii is a fungus that grows internally in the leaf. Disease occurs when spore-producing fungal structures plug the stomata. Based on observations of heavily colonized live needles, it has been estimated that needles are cast when ~25%–50% of the stomata are plugged (Hansen et al. 2000; Manter et al. 2003). Disease severity is determined by measuring the percentage of plugged stomata on 2-year-old needles, which reflects the potential for young needles to be cast. Estimates and modeled growth impacts from SNC have been based on foliage retention in years, that is, the number of retained annual needle cohorts (Maguire et al. 2002, 2011). Quantifiable volume growth losses have been apparent when fewer than 3 years' worth of foliage is retained. While 10- to 30-year-old Douglas-fir plantations in

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the northwestern Oregon Coast Range have been estimated to have a mean annual cubic volume growth loss of ~23%, mean cubic volume growth losses can exceed 50% on the most severely infected sites (Maguire et al. 2011). Foliage retention has previously been shown to be correlated with disease severity in limited ranges within the zone of the SNC epidemic (Hansen et al. 2000; Manter et al. 2005).

Foliage retention in conifers varies naturally on the landscape, especially along site-productivity and elevation gradients, although tree age and stand dynamics are also influential (Schoettle 1990; Reich et al. 1995; Xiao 2003). In general, conifer foliage retention is lowest for the highest-productivity sites, and increases with decreasing productivity and increasing elevation and latitude (Reich et al. 1995; Balster and Marshall 2000; Xiao 2003). The interaction of foliage disease with foliage retention complicates the natural patterns on the landscape by reducing foliage retention in certain geographic locations (Shaw et al. 2014). Weiskittel et al. (2006) found that at the tree level, *N. gaeumannii* reduced the amount of foliage mass in each age class, increased the relative amount of foliage in younger age classes, and increased the relative amount of foliage mass toward the base of the live crown.

Disease severity and symptoms of SNC (low foliage retention and leaf area, chlorotic foliage, and reduced tree growth) are most severe at lower elevations near the coast, and lessen with increasing elevation and distance from the coast (Hansen et al. 2000; Rosso and Hansen 2003), with these two factors being partially co-linear in the Coast Range. Ritóková et al. (2016) also demonstrated that foliage retention increased with increasing elevation on the western slope of the Cascade Mountains in Oregon where SNC is present, but where disease symptoms are limited to moist low-elevation stands.

Climate in the Oregon Coast Range is influenced by the longitudinal elevation profile and is a highly significant factor related to SNC severity. Winter temperature and leaf wetness during spore dispersal from May through August have been identified as the main epidemiological factors positively associated with the disease (Michaels and Chastagner 1984; Hansen et al. 2000; Manter et al. 2005). Consistent with epidemiological models, Zhao et al. (2011, 2012) found correlations between coastal Douglas-fir foliage retention and a temperature-based continentality index as well as a suite of other variables encompassing seasonality of both temperature and precipitation (Manter et al. 2005). Lee et al. (2017) used tree ring width chronologies to show that SNC can impact growth across the region and is not limited to the coastal fog zone. The study found that these impacts were synchronous and linked to winter and summer temperatures and summer precipitation, with the specific influential factors dependent on regional location.

Visible symptoms of SNC (chlorotic foliage and thin crowns) have been assessed by Aerial Detection Survey (ADS) in Oregon annually from 1996 to 2016, and again in 2018, by the US Forest Service - Forest Health Protection and the Oregon Department of Forestry. The Washington Department of Natural Resources (WADNR) has performed ADSs in 1998, 2000, 2012, 2015, 2016, and 2018, and the British Columbia Ministry of Forests' inaugural flight took place in 2018.

Aerial surveys have generally found few visible SNC symptoms in southern coastal Oregon. In 2009, the SNCC conducted limited sampling of Douglas-fir growing in coastal stands of southern Oregon (Shaw and Woolley 2009), where it was found that foliage retention was generally greater than that in northern coastal Oregon for a given distance from the coast. Though these measurements were ultimately used within a larger dataset for correlating climate variables with foliage retention, they were not subject to further analysis. Correlations between climate and foliage retention, extrapolated to unsampled areas along the southern Oregon coast, have predicted lower foliage retention than the aerial survey results have coarsely implied (Coop and Stone 2007), making region-wide assessments of disease impact questionable and greater sampling within these areas valuable.

A substantial body of published research has been produced since the onset of epidemic conditions across coastal Pacific forests in the 1990s, spearheaded and financed through industry and agency collaboration within Oregon State University's Swiss Needle Cast Cooperative (SNCC). This effort, encompassing the first 15 years of focused SNC research, was primarily based on conditions in northwestern coastal Oregon (>44.6°N), where epidemic conditions were first identified (Coop and Stone 2007; Hansen et al. 2000; Maguire et al. 2011; Manter et al. 2005; Rosso and Hansen 2003; Shaw et al. 2014). With further spread of the disease evident, subsequent efforts have been made to expand the geographic range of monitored sites, culminating in the establishment of a new research and monitoring plot network installed by the SNCC (http://sncc.forestry.oregonstate.edu/). The network extends from the northern California border to southwestern Washington (560 km (338 miles) and 56 km (35 miles) inland; Fig. 1) and complements the ADS survey (Fig. 2). It also provides an opportunity to investigate how foliage retention and disease severity vary on both small and large scales, that is, within crowns and geographically throughout Douglas-fir plantations across a gradient of disease symptomatology.

Previous work by the SNCC using a dataset geographically limited to the northwestern Oregon Coast Range found that SNC reduced Douglas-fir cubic volume growth and foliage retention across the western slopes of the Coast Range. Because symptom severity is correlated with climate variables, and because climate change may be a persistent agent, periodic updating of sampling and analysis is considered valuable, particularly with a geographically expanded dataset. Our objectives were to validate the following predictions: (*i*) foliage retention increases and disease severity decreases with elevation and distance from the coast; (*ii*) foliage retention decreases with increasing disease severity; (*iii*) disease severity decreases and foliage retention increases from the top of the crown to the bottom of the crown; and (*iv*) foliage retention decreases and disease severity increases with increasing latitude.

Methods

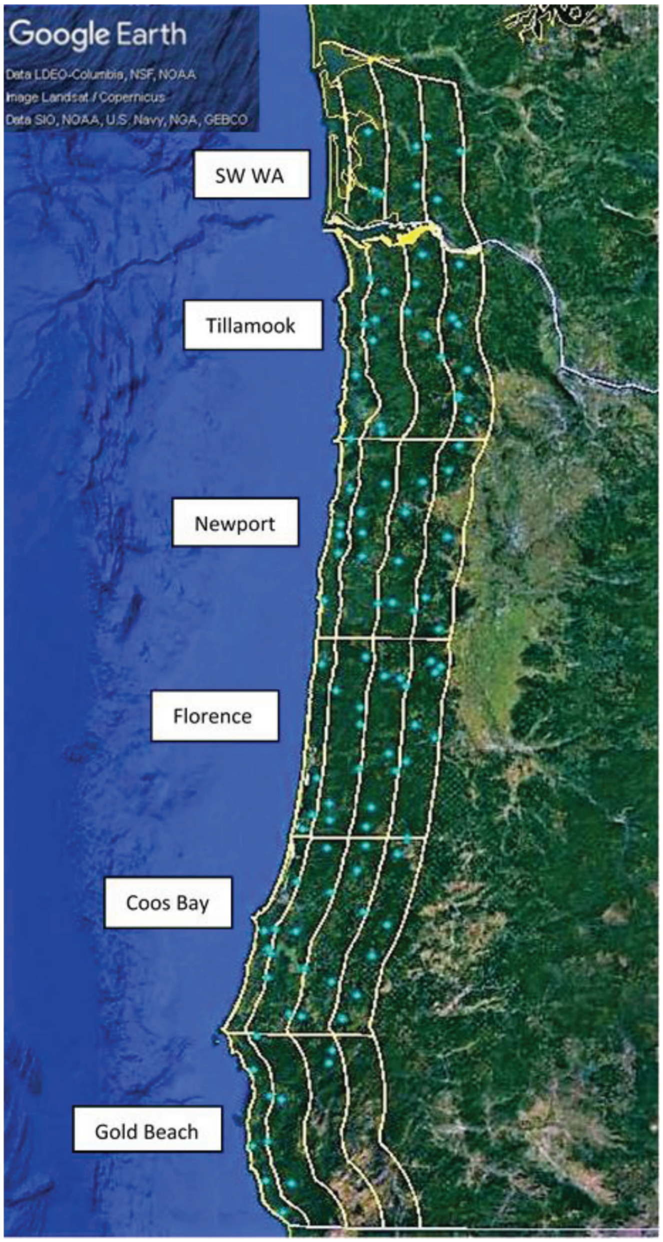
Study area

Dominant forest types within the study region were Douglas-fir and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) with a narrow zone of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) along the Pacific Northwest coast (Franklin and Dyrness 1973). The geographic setting includes the Oregon Coast Range and the Willapa Hills in southwestern Washington. Precipitation and temperature vary across the region owing to elevation, latitude, and rain shadow on the eastern slope of the Coast Range. Annual precipitation ranges from 1200 to 4800 mm (47–190 inches), with the majority falling as rain from October through May. Mean annual temperature ranges from 13 to 18 °C (55–64 °F). Elevation of the research plots ranges from 48 to 807 m a.s.l. (157–2657 feet).

Plot network and field methods

To capture a range of healthy to severely diseased stands, a sampling matrix was created for the Oregon Coast Range and southwestern Washington, extending from the California border to Aberdeen, Washington, and 56 km (35 miles) inland from the Pacific Ocean. The region was divided into four longitudinal panels from west to east: an 8 km-wide strip closest to the Pacific Ocean, where stands are severely affected by SNC, and three 16 km-wide strips. Each of the six latitudinal panels oriented north–south was ~92 km (57 miles) long, resulting in 24 sample blocks (Fig. 1). The SNCC research and monitoring plot network includes 106 plots, with 98 of these plots located in coastal Oregon and 8 plots in southwestern Washington. Five study plots on average were

Fig. 1. Distribution of 106 research plots established in 2013–2015 by the Swiss Needle Cast Cooperative (SNCC) in western Oregon and southwestern Washington (Ritóková et al. 2016). Latitudinal sampling zones from north to south are southwestern Washington (SW WA), Tillamook, Newport, Florence, Coos Bay, and Gold Beach. Map data were obtained from Google, Landsat/Copernicus. [Colour online.]



located within each sample block. The four southernmost west–east blocks did not have a suitable selection of target Douglas-fir plantations and were therefore limited to 11 plots. Plots were established in the fall of 2013, 2014, and 2015 and sampled for disease severity and foliage retention in spring of the following year (2014, 2015, 2016).

The plot installation protocol followed the Maguire et al. (2011) methodology to allow for integration with the growth impact sampling methodology of 1998–2008. Square plots were 0.08 ha (28.45 m × 28.45 m) with a 10 m buffer around the perimeter of each plot. The target age of Douglas-fir plantations was 10–25 years old, with older trees (20–25 years) acceptable in heavily infected areas where SNC-related height growth losses resulted in crowns that were sufficiently accessible for sampling. The target basal area composition was 80% Douglas-fir, and preferred stem density was 800–1000 trees·ha^{-1}. At the time of establishment, all plot trees >5 cm at breast height were tagged and measured at a height of 137 cm. A subset of 40 trees was measured for total height and height to crown base, including the 10 largest and four smallest by diameter at breast height (dbh), with the remainder distributed across the diameter distribution. All plots were established in plantations that had not been precommercially thinned or fertilized in the 5 years before establishment.

Laboratory methods

The SNC disease severity index was determined following the methods of Mulvey et al. (2013). For each crown position on selected trees, 50 needles from year-2 cohorts (branchlets) of each sample branch were removed and attached to an index card. Each needle was visually inspected with a dissecting microscope to determine the presence or absence of pseudothecia. Incidence represented the percentage of 50 needles with pseudothecia present. The first 10 needles with pseudothecia were measured for length (mm) and used to determine pseudothecial density by counting 100 stomata from a starting point randomly located within three zones (tip, middle, and base) on each needle and averaging to determine the percent pseudothecial density. The SNC disease severity index was calculated by multiplying the incidence by the pseudothecial density.

Statistical analysis

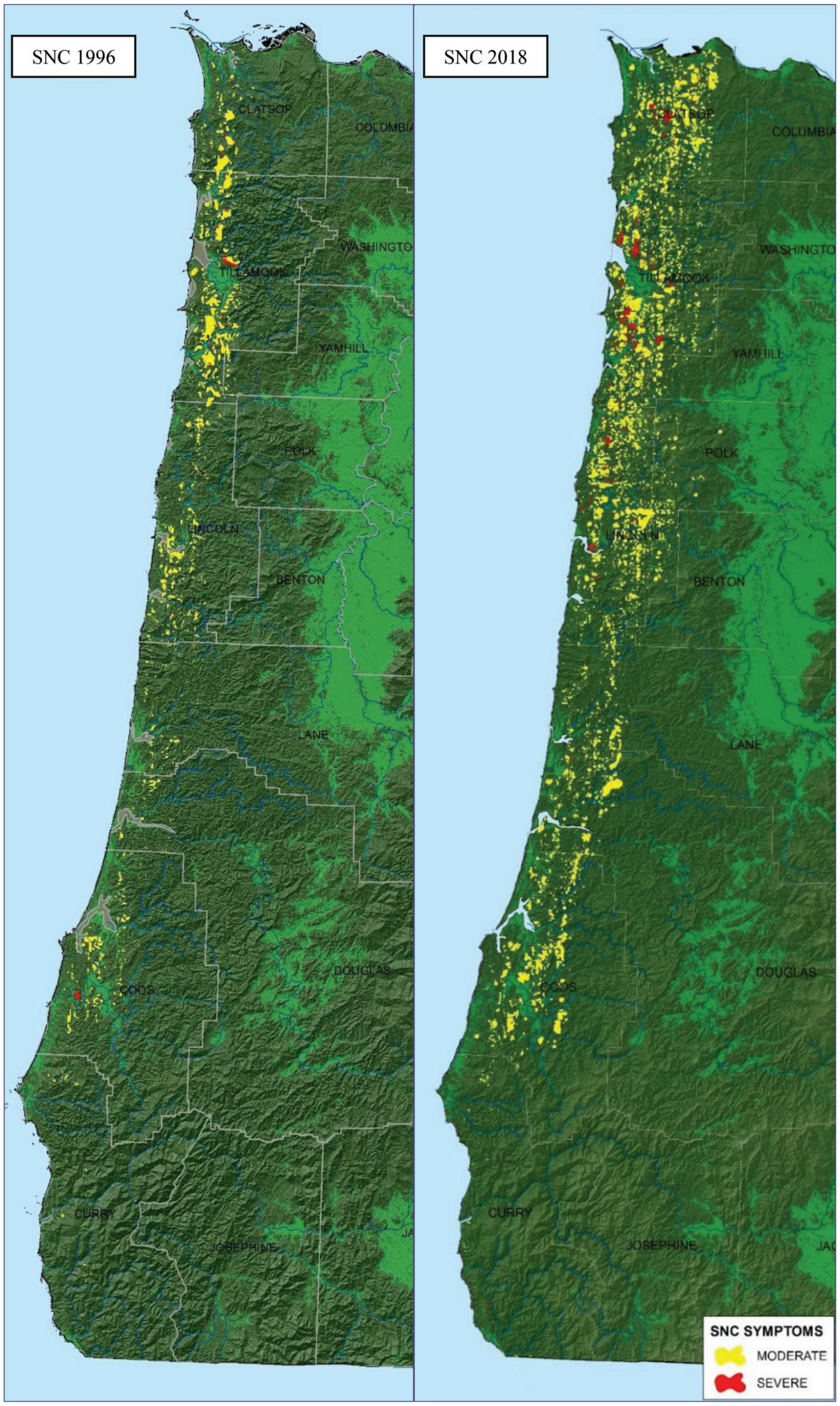
Tests of significance for assessing differences in mid-crown foliage retention or disease severity index across the landscape were conducted using analysis of variance (ANOVA) or analysis of covariance (ANCOVA) within SAS PROC GLM. Distance from coast, elevation, January temperature, or June precipitation were used as either individual or combined covariates, and latitudinal sampling zone was included as a categorical variable. Tests of significance for assessing differences in foliage retention or SNC disease severity index by crown position (upper, middle, or lower) and zone — representing distance from the coast (0–8 km, 8–24 km, 24–40 km, or 40–56 km (0–5 miles, 5–15 miles, 15–25 miles, or 25–35 miles)) — were conducted using ANOVA within SAS PROC GLM, where crown position, zone, and their interaction were treated as separate categorical variables.

Results

The sample region encompassed a range of elevation (48–807 m), foliage retention (1.15–3.9 years), and disease severity (0.05%–52.11%) values (Table 1). Foliage retention increased along a west–east gradient, with the lowest measured values found along the northern coastline. Disease severity index was more variable, exhibiting a decreasing gradient to the south. On the southernmost Oregon coast, plantations currently exhibit very little disease severity and higher foliage retention.

Mid-crown foliage retention regressed against either distance from coast or elevation showed significant positive relationships (R^2 = 0.415 or 0.211, respectively, for models 1 and 2; Table 2); accounting for both variables, the model resulted in R^2 = 0.489 (model 3, Table 2). Additional use of a categorical variable to differentially account for the latitudinal sampling zones resulted in R^2 = 0.574 (model 4, Table 2). Distance from coast and elevation are usually thought of as coarse descriptors of topography that in turn influence climate. When simple climate variables previously found to be associated with foliage retention (mean June precipitation and January temperature since 2000; http://prism.oregonstate.edu/explorer/bulk.php) were added to the full model, the latitudinal sampling zone categorical variable remained significant, but both distance from coast and elevation were

Fig. 2. Areas of Douglas-fir forest with Swiss needle cast (SNC) symptoms in western Oregon detected by aerial survey in 1996 and 2018. Map created by the Oregon Department of Forestry using ESRI 2018, ArcMap 10.6. [Colour online.]



rendered insignificant, and the correlation was slightly improved (R^2 = 0.582 for model 5; Table 2). Model-implied mean foliage retention increased from north to south (Fig. 3).

Disease severity was found to have a significant negative relationship with elevation (R^2 = 0.199 for model 6; Table 2), elevation and January mean temperature (R^2 = 0.244 for model 7; Table 2), and a full model of elevation, January mean temperature, and latitudinal sampling zones (R^2 = 0.422 for model 8; Table 2). No significant relationship with distance from coast or June precipitation was found. Model-implied mean disease severity (full model) decreased from north to south (Fig. 4).

Disease severity was found to be negatively associated with mid-crown foliage retention (R^2 = 0.179 for model 9; Table 2; Fig. 5), though this predictive relationship was improved by accounting for elevation (R^2 = 0.26 for model 10; Table 2) or elevation and latitudinal sampling zone (R^2 = 0.442 for model 11; Table 2).

Foliage retention varied by crown position ($p < 0.0001$), zone ($p < 0.0001$), and their interaction ($p = 0.0314$ for model 12; Table 2), indicating that the relative vertical trends in foliage retention within the crown varied by distance from the coast (Fig. 6). In the two zones within 24 km of the coast, there was a distinct increase in foliage retention from the top to the bottom of the live tree

Table 1. Summary statistics by site and sampling block for Swiss needle cast in Douglas-fir forests of the Oregon Coast Range and southwestern Washington.

Site	Zone	Mean elevation (m a.s.l.)	Foliage retention (years)	Disease severity index (%)*
SW_WA	8–24 km	166	1.93	25.96
	24–40 km	204	2.95	22.73
	40–56 km	313	3.05	22.63
Tillamook	0–8 km	256	1.78	22.32
	8–24 km	302	1.66	29.04
	24–40 km	457	2.68	13.29
	40–56 km	420	3.02	20.02
Newport	0–8 km	106	1.76	24.59
	8–24 km	334	2.29	18.47
	24–40 km	273	3.08	15.62
	40–56 km	263	3.16	15.73
Florence	0–8 km	123	1.61	20.4
	8–24 km	286	2.01	8.73
	24–40 km	263	2.79	12.73
	40–56 km	330	3.05	13.93
Coos Bay	0–8 km	124	2.12	18.15
	8–24 km	223	2.34	16.71
	24–40 km	285	2.61	11.61
	40–56 km	486	2.78	8.8
Gold Beach	0–8 km	402	2.56	9.84
	8–24 km	498	2.83	0.89
	24–40 km	753	3.3	1.57

*Disease severity is measured as incidence × % occluded stomata.

crown, with each third of the crown having a significantly different mean foliage retention. In the two zones furthest from the coast, the upper third of the crown had a significantly lower foliage retention than the middle and lower thirds, but the two lower thirds of the crown did not differ significantly from one another.

Disease severity differed significantly by crown-third ($p < 0.0001$; model 13, Table 2). When analyzed separately by zone, disease severity of 2-year-old needles invariably increased from the bottom to the top of the crown, and significantly so in the three zones furthest from the coast (Fig. 7). Disease severity tended to decrease with increasing distance from the coast for each crown-third but was greater in the lower and middle thirds of the crown of trees located in the zone furthest from the coast.

Discussion

In accordance with our expectations, foliage retention increased with elevation and distance from the coast, and disease severity decreased with elevation. The positive correlation between foliage retention and distance from the coast and elevation was not surprising given previously published work from smaller-scale studies (Hansen et al. 2000; Rosso and Hansen 2003) as well as correlative climate models (Zhao et al. 2011). Although decreased foliage retention in the coastal zones implies increased disease severity, a regional analysis of disease severity has not been previously published in the literature. While elevation was a significant predictor of disease severity, distance from the coast was not, with or without the southernmost zone included in the analysis. This result is consistent with the high variation in pseudothecial occlusion observed across the region as well as the high rates of occlusion observed by the authors in stands as far east as the western Cascades, >100 km east of the Pacific Ocean. Unaccounted for in the examination of disease severity and occlusion are those needles that have been cast as a result of excessive occlusion, underscoring the interdependence of disease severity and foliage retention and the fact that a true qualitative assessment of SNC severity must also account for both. Likewise, it suggests that the estimation of volume growth loss using foliage retention as an index of SNC severity (Maguire et al. 2011) could be further refined by accounting for differences in occlusion (Fig. 5).

Table 2. Results of analysis of variance (ANOVA) and analysis of covariance (ANCOVA) for Swiss needle cast mid-crown foliage retention (MID_CROWN_FOLRET), disease severity for 2-year-old Douglas-fir needles (DIS_SEV, 2-year-old), foliage retention by crown position (FOLRET by crown position), and disease severity by crown position (DIS_SEV by crown position).

Dependent variable	Model	Independent variable	*F*	*p*
MID_CROWN_FOLRET	1	DFC	73.73	<0.0001
	2	ELEV	27.77	<0.0001
	3	DFC	55.93	<0.0001
		ELEV	14.84	0.0002
	4	DFC	71.45	<0.0001
		ELEV	4.48	0.0368
		SITE	3.92	0.0028
	5	DFC	2.47	0.1194
		ELEV	2.49	0.1175
		SITE	4.95	0.0004
		PPT_June	3.17	0.0782
		TEMP_Jan	7.22	0.0085
DIS_SEV, 2-year-old	6	ELEV	25.89	<0.0001
	7	ELEV	31.42	<0.0001
		TEMP_Jan	6.14	0.0148
	8	ELEV	7.01	0.0094
		TEMP_Jan	5.32	0.0232
		SITE	6.01	<0.0001
	9	FOLRET	22.68	<0.0001
	10	FOLRET	8.39	0.0046
		ELEV	11.21	0.0011
	11	FOLRET	9.15	0.0032
		ELEV	8.59	0.0042
		SITE	6.43	<0.0001
FOLRET by crown position	12	CR_POS	73.36	<0.0001
		Zone	26.07	<0.0001
		CR_POS × Zone	2.35	0.0314
DIS_SEV by crown position	13	CR_POS	26.87	<0.0001

Note: DFC, distance from coast; ELEV, elevation; SITE, plot site location; PPT_June, mean precipitation in June; TEMP_Jan, mean temperature in January; FOLRET, foliage retention; CR_POS, crown position (lower, middle, upper).

On the individual-tree level, foliage retention was found to be positively associated with depth into crown, and disease severity was found to be negatively associated with depth into crown, consistent with the top-down pattern of infection originally identified in Hansen et al. (2000) and described quantitatively in Weiskittel (2003). Finally, models accounting for latitudinal sampling zone consistently found it to be a significant predictor of disease, with foliage retention increasing and disease severity decreasing at lower latitudes.

Foliage retention on the landscape

Landscape-level predictions of foliage retention can be useful for managers seeking to assess risk prior to establishing Douglas-fir plantations, likely current or future potential volume growth losses, or the effects of SNC on future harvest schedules. Recognizing the association between precipitation, temperature, SNC germination success, and pseudothecial development (Manter et al. 2005), numerous models have associated foliage retention with various climate variables (Coop and Stone 2007; Latta 2009; Zhao et al. 2011) with varying degrees of success.

While these models offer the potential of predictive flexibility that could be expected under changing climate scenarios, the amount of explained variability in foliage retention by Coop and

Fig. 3. Implied foliage retention for the six coastal latitudinal zones based on a mean June precipitation of 7 cm and a mean January temperature of 5 °C. Different letters indicate a statistical difference between latitudinal sampling zones. Error bars denote standard error. [Colour online.]

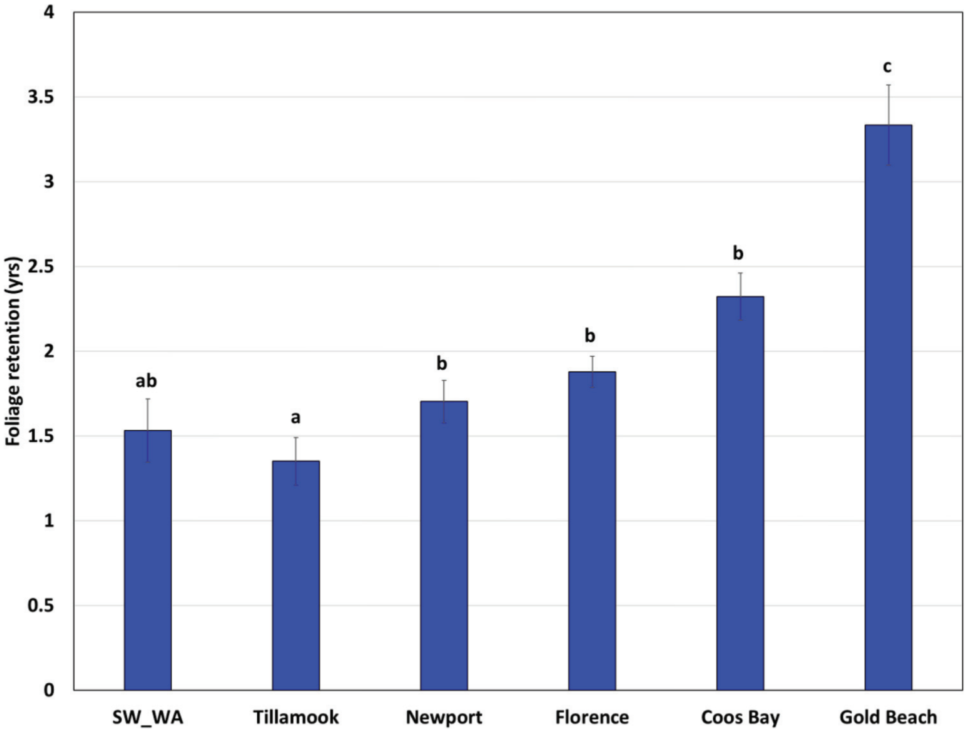
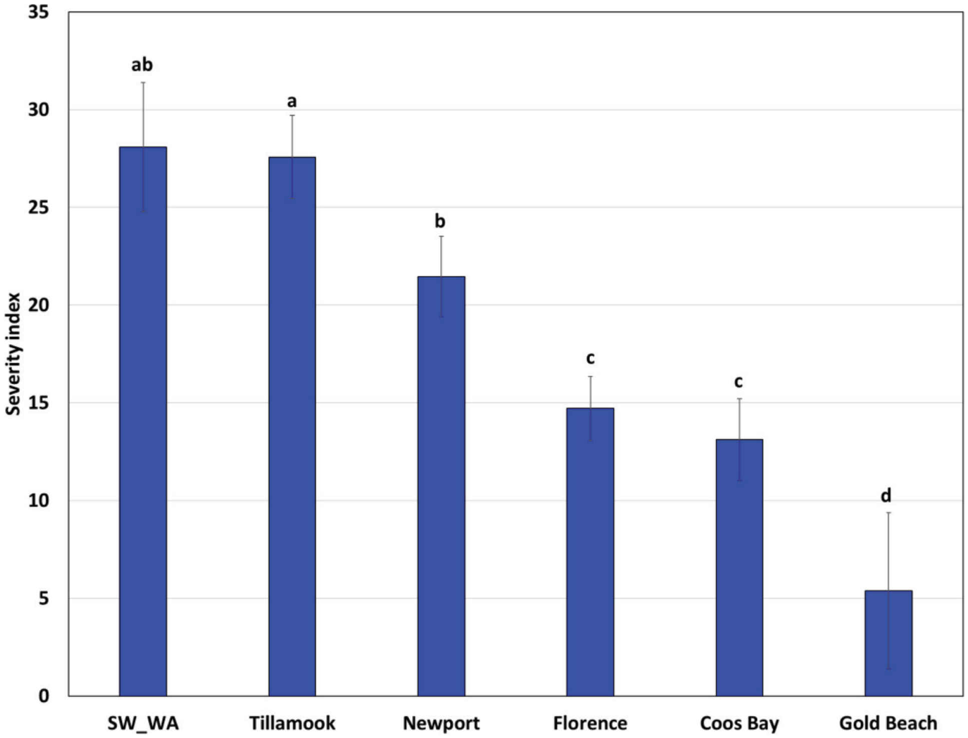
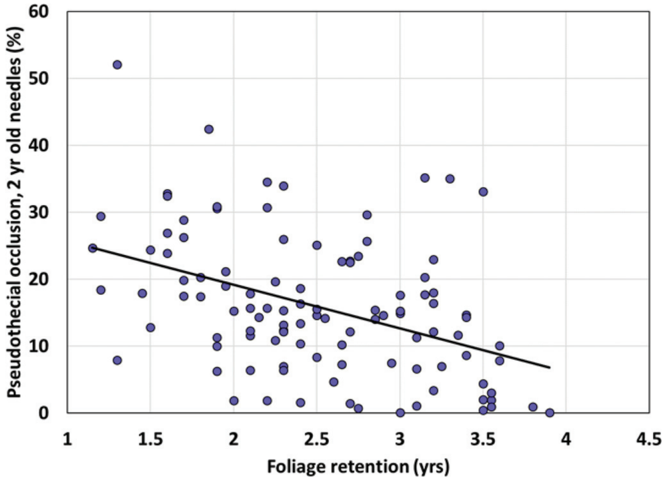


Fig. 4. Implied disease severity ratings for the six coastal latitudinal zones based on an elevation of 100 m and a mean January temperature of 5 °C. Different letters indicate a statistical difference between latitudinal sampling zones. Error bars denote standard error. [Colour online.]



Stone (2007) (R^2 = 0.56) and Latta (2009) (R^2 = 0.52) is not much greater than that explained by coarse geographic variables such as distance from coast, elevation, and the categorical latitudinal sampling zones (R^2 = 0.489) described here. The three aforementioned models did not have the benefit of copious foliage retention data collected from the southern half of the Oregon Coast Range, in some cases resulting in south coast foliage retention predictions that are inconsistent with the data collected as part of this study.

Fig. 5. Distribution of occlusion percentage on 2-year-old Douglas-fir needles versus the mean plot-level mid-crown foliage retention (years). [Colour online.]



Such inconsistencies also underscore the fact that climate is just one of the factors controlling successful fungal infection and development.

The addition of climate variables to the foliage retention model improved the explanation of variation, in that the coarse geographic variables were replaced with the specific variables for which they are surrogates. Nonetheless, in each case the categorical latitudinal variable for site remained significant, with foliage retention predicted to increase and disease severity predicted to decrease from north to south after accounting for distance from coast, elevation, June precipitation, or January temperature. A likely explanation for the misidentified risk of low foliage retention along the southern Oregon coast (Zhao et al. 2011) is to be found in PRISM climate data (https://prism.oregonstate.edu/) from these plots, where mean June precipitation is 8.8 cm in the plots making up the two zones closest to the coast in the Gold Beach region and mean January temperature is 8.0 °C, while the values for the Newport and southwestern Washington regions average 8.1 cm and 5.3 °C. Correlations between these variables and foliage retention as presented in Zhao et al. (2011) would predict lower foliage retention, which is not supported by the data presented here.

The monitoring results from the southernmost zones of the study area demonstrate the greatest benefit of having expanded the original SNC monitoring network (Maguire et al. 2011). The results also raise questions about why SNC symptoms decrease despite a significant component of Douglas-fir and warmer winters. Conditions along the southern Oregon coast differ from those in the north in a number of ways, with the most apparent being contrasting soil types and relative fertility (Heilman et al. 1979). In previously studies, resource availability, manipulated in thinning or fertilization experiments, have been found to influence conifer needle length (Brix and Ebell 1969; Raison et al. 1992; Tang et al. 1999). Among stands with healthy levels of foliage retention (≥3 years), mean needle length was significantly lower in the southern latitudinal sampling zones, with a whole-crown mean of 23.65 mm in the four northern zones, 21.68 mm in the Coos Bay zone, and 18.96 mm in the Gold Beach zone, suggesting limits to growth along the southern Oregon coast. Furthermore, when associations between mean needle length and foliage retention were assessed separately by latitudinal sampling zone, the associations were significantly positive in the four northernmost zones, consistent with the results found by Weiskittel (2003), but insignificant in the Coos Bay zone and negative in the Gold Beach zone. In other words, in the north, diseased trees had shorter needles, suggesting that disease-related decreases in productivity could be limiting needle development. However, in the southernmost zone, diseased trees had longer needles, raising the question of whether some resource limitation somehow provided enhanced resiliency against disease. This possibility has been raised in a previous study (El-Hajj et al. 2004).

The incongruency between a lack of SNC symptoms and the presumed SNC-conducive climate along the southern Oregon coast found in climate models (Zhao et al. 2011) has been of interest to SNC researchers and is one of the reasons the SNCC research plot network was extended to include the entire Oregon coast. In the entire 0–8 km sampling strip closest to the ocean, the five plots of the Gold Beach zone exhibited milder SNC symptoms than those exhibited by plots at other latitudes, significantly so for all but the Coos Bay zone. The five plots in the Gold Beach coastal zone had a mean foliage retention of 2.56 years and a mean disease severity index of 9.84% versus 1.72 years and 22.6% for the three northernmost Oregon zones. Looking closer, of the five Gold Beach plots, two (GB_Infected) had characteristics similar to those of northern zones — a mean foliage retention of 1.93 years and a disease severity index of 23.28%. The three other plots in the same zone (GB_Uninfected) had a mean foliage retention of 2.98 years and a disease severity index of 0.88%, providing an opportunity to draw contrasts between the two plot groups. Deployment of a combination of fungal spore traps, climate and leaf wetness sensors, and soil chemistry analysis may provide clues as to the reasons for the difference.

Factors influencing foliage retention

Most conifers depend on a 2- to 11-year complement of needles (Goheen and Willhite 2006) for healthy development and maximum productivity. Loss of older needles in conifers occurs annually and is not considered damaging. However, a large proportion of foliage loss results in growth loss and sometimes mortality. Several biotic and abiotic factors cause foliar loss, and foliage retention among Douglas-fir trees in Coastal Oregon and southwestern Washington plantations is influenced by numerous environmental factors, including foliage disease. Particularly in coastal zones where SNC occurs, salt spray (Burkhardt 1995) or high winds (Ozolinčius and Stakėnas 1996) can affect foliage retention, as can biotic factors such as foliar pathogens and defoliating insects (Kurkela et al. 2009).

Nutrition has also been shown to influence foliar retention (Balster and Marshall 2000). The soil nitrogen gradient in the Oregon Coast Range exhibits a generally negative association with the SNC symptom gradient (Perakis et al. 2013), making it difficult to partition how much the pattern of demonstrated here — increasing foliage retention with distance from coast and increasing elevation — is based on a fertility gradient, spore concentration, or the interaction of the two, as demonstrated previously (Lan et al. 2019; El-Hajj et al. 2004). However, unlike SNC-influenced levels of foliage retention, fertility-influenced foliage retention does not result in sparser crowns and the estimable growth losses that have been found among Coast Range Douglas-fir plantations (Maguire et al. 2011).

Foliage retention in the crown

Relatively similar levels of mean disease severity regardless of distance from the coast (Fig. 7) underscore the primacy of foliage retention as an index of SNC disease intensity. The greater increase in mean foliage retention with distance from the coast (Fig. 6) relative to other crown depths, coupled with the greater foliage mass (Weiskittel et al. 2006), validates the Maguire et al. (2002, 2011) application of mid-crown foliage retention as the best representative of disease levels upon which to estimate cubic volume growth in young Douglas-fir plantations. Shaw et al. (2014) also found the lowest retention in the upper crown

Fig. 6. Differences in plot-level mean foliage retention within the crown-thirds of Douglas-fir trees within each longitudinal sampling zone. Different letters indicate significantly different levels of foliage retention within each sampling zone. Error bars denote standard error. [Colour online.]

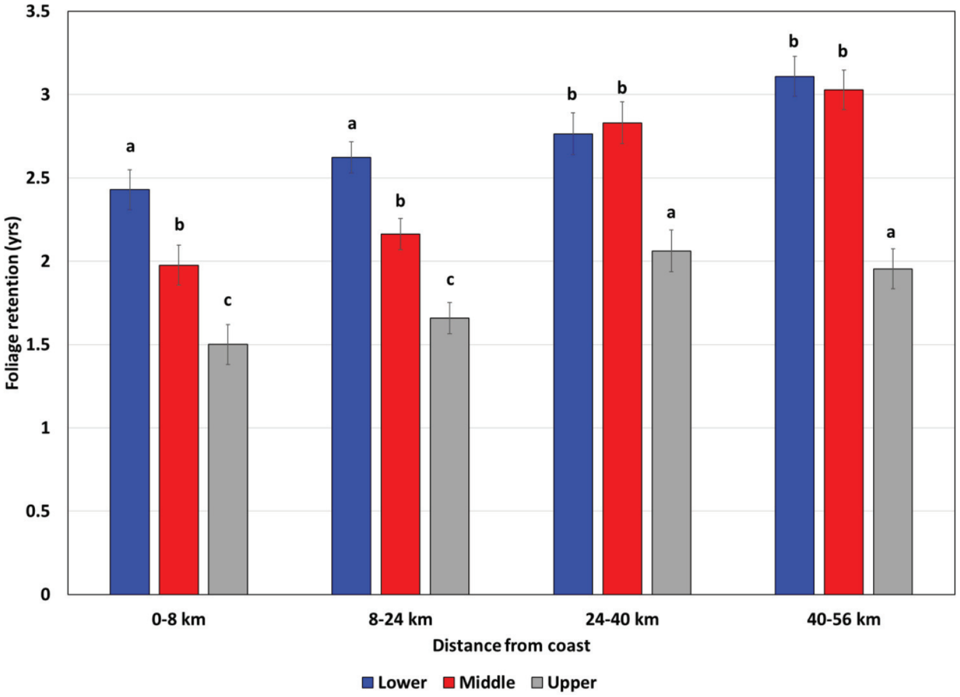
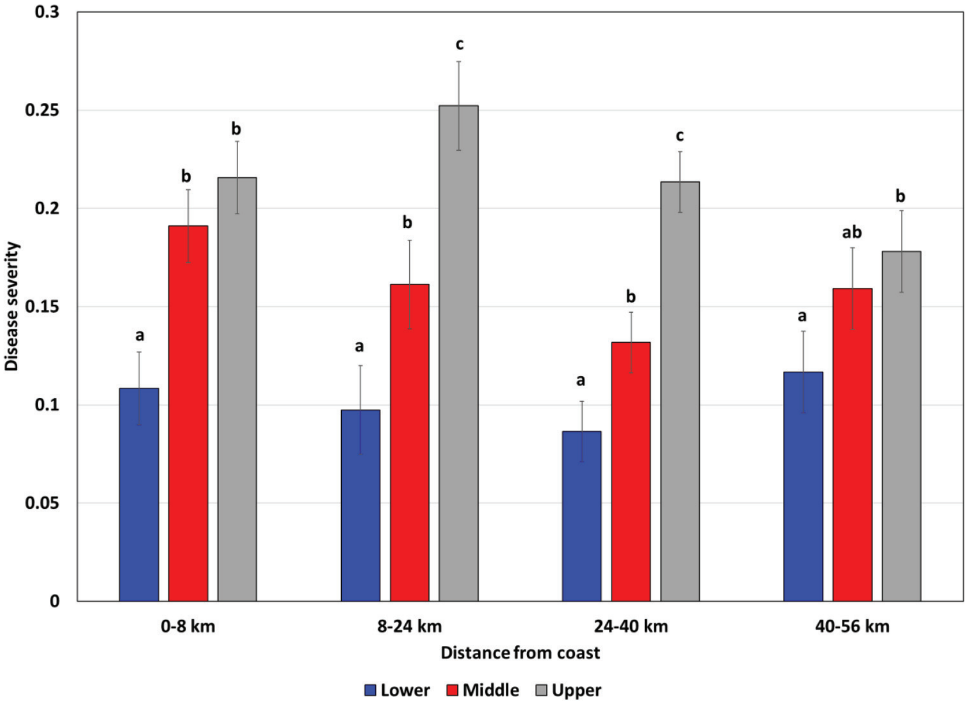


Fig. 7. Differences in plot-level mean disease severity within the crown-thirds of Douglas-fir trees within each longitudinal sampling zone. Different letters indicate significantly different levels of foliage retention within each sampling zone. Error bars denote standard error. [Colour online.]



and highest retention in the lower crown across 76 permanent growth impact plots (GIS) in the northern Oregon Coast Range. Our anecdotal observations suggest that needles in the lower canopy position might be affected by other foliar pathogens such as *Rhizoctonia* and *Phytophthora* (Buhl et al. 2016) or needle mortality due to limited light, resulting in imprecise association between SNC severity and foliage retention in the lower canopy. The upper crown of younger trees often lacked 4-year-old lateral branches, not allowing for comparable estimates of foliage retention with the other crown-thirds.

The SNCC (Shaw et al. 2011) has prepared recommendations for managers interested in maintaining productive stands within the SNC infection zone. For timber managers, Douglas-fir has traditionally been the preferred species owing to its high productivity and market value. Planting decisions made under the assumption that salable forest products in 40 years resemble those of the present must be informed by growth rates and market values of currently available species. In areas subject to high SNC pressure, there has been a notable shift toward increasing the amount of western hemlock on the landscape because of fears that the current SNC epidemic will not wane, and that regardless of its lower value in the current market, it will at least ensure a stand with a merchantable product in a financially realistic time frame. Geneticists have advised the use of SNC-tolerant Douglas-fir families under moderate disease levels (Johnson 2002; Jayawickrama et al. 2012).

Acknowledgements

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Review Article - forest threats

Persistence of the Swiss Needle Cast Outbreak in Oregon Coastal Douglas-Fir and New Insights from Research and Monitoring

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Abstract

Swiss needle cast (SNC), caused by *Nothophaeocryptopus gaeumannii*, is a foliage disease of Douglas-fir (*Pseudotsuga menziesii*), that reduces growth in native stands and exotic plantations worldwide. An outbreak of SNC began in coastal Oregon in the mid-1990s and has persisted since that time. Here we review the current state of knowledge after 24 years of research and monitoring, with a focus on Oregon, although the disease is significant in coastal Washington and has recently emerged in southwestern British Columbia. We present new insights into SNC distribution, landscape patterns, disease epidemiology and ecology, host-pathogen interactions, trophic and hydrologic influences, and the challenges of Douglas-fir plantation management in the presence of the disease. In Oregon, the SNC outbreak has remained geographically contained but has intensified. Finally, we consider the implications of climate change and other recently emerged foliage diseases on the future of Douglas-fir plantation management.

Study Implications: Douglas-fir tree growers need to consider Swiss needle cast (SNC) and other emerging foliage diseases as SNC has not abated over the past 24 years, and along with other emerging diseases, it continues to pose a threat to Douglas-fir plantation productivity. Douglas-fir management in western Oregon remains important, such that a knowledge of disease impacts and effective silvicultural responses is key. Managers should carefully consider whether alternative species may be ecologically or economically beneficial in some situations while tree improvement programs must continue to breed for tolerance to SNC. Research shows that regional scale foliage disease outbreaks can result in trophic cascades and hydrologic changes that affects more than just the trees. The environmental controls on the SNC epidemic imply that climate change could strongly influence future directions of the outbreak, with the greatest threats to trees at higher elevations.

Keywords: Swiss needle cast, *Nothophaeocryptopus gaeumannii*, Douglas-fir, foliage disease, Oregon

Swiss needle cast (SNC) is a foliage disease of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) caused by the fungus *Nothophaeocryptopus gaeumannii* (T. Rohde) Videira, C. Nakash., U. Braun & Crous (Mycosphaerellaceae) (Videira et al. 2017). The Pacific coastal forests of Oregon, Washington, and southwestern British Columbia have seen SNC emerge as a significant threat to Douglas-fir plantation productivity (Hansen et al. 2000, Shaw et al. 2011, Ritóková et al. 2016, Montwé et al. 2021). The pathogen causes growth and volume loss of Douglas-fir because of reductions in gas exchange (Manter et al. 2000) and premature casting of foliage (Hansen et al. 2000, Maguire et al. 2002, 2011), although disease-caused tree mortality is rare (Maguire et al. 2011) (Figure 1). The fungus is present wherever Douglas-fir occurs but causes significant disease only in certain geographic, climatic, and management settings (Shaw et al. 2011, Lee et al. 2016, 2017, Mildrexler et al. 2019). The pathogen is native to western North America but was first described in Switzerland (Boyce 1940), hence the name, Swiss needle cast.

Nothophaeocryptopus gaeumannii is a fungus that does not directly kill the leaf. Spores land on the leaf surface, germinate, and grow hyphae into the leaf via an appressorium in a stomate (Stone et al. 2008a). Disease expression (leaf chlorosis, foliage casting and reduced diameter growth) (Figure 1a, b) is associated with spore-producing bodies (pseudothecia) that plug the stomates. Foliage is cast when approximately 25% to 50% of the stomates are plugged (Hansen et al. 2000, Manter et al. 2003). Disease severity is associated with conditions where stomatal plugging occurs on one- and two-year-old foliage, causing premature foliage casting. Foliage retention has been correlated with disease severity (Hansen et al. 2000, Manter et al. 2005, Ritóková et al. 2020), and estimates of growth impacts from SNC have been based on foliage retention in years (i.e., the number of retained annual foliage cohorts; Maguire et al. 2002, 2011). Quantifiable volume growth losses occur when fewer than three years of foliage are retained (Figure 2). Annual volume growth losses averaged ~23% for 10- to 30-year-old Douglas-fir plantations in the northwestern Oregon Coast Range, and average cubic volume growth losses can exceed 50% on the most severely infected sites (Black et al. 2010, Maguire et al. 2011).

Swiss needle cast symptoms are most severe at lower elevations near the coast and lessen with increasing elevation and distance from the ocean in western Oregon (Hansen et al. 2000, Rosso and Hansen 2003, Shaw et al. 2014). Ritóková et al. (2016) also demonstrated that foliage retention increased with increasing elevation on the west slope of the Cascade Mountains in Oregon where SNC is present, but where disease symptoms and apparent volume growth losses are limited to moist low elevation stands and follow short-term climate fluctuations. Climate in the Oregon Coast Range is influenced by the west–east elevation profile and is

Figure 1. Symptoms of Swiss needle cast. (a) Swiss needle cast disease symptoms (chlorotic foliage, low foliage retention) in Douglas-fir. (b) The impacts of Swiss needle cast on growth can be seen in two 40-year-old stands planted at the same time ~3 miles from the coast. Douglas-fir is the stand on the right versus western hemlock, the stand on the left. Note the western hemlock trees are larger and have created more shade, whereas the Douglas-fir are smaller and have thin crowns allowing full light to increase understory vegetation growth. The western hemlock stand was a fenced first-generation progeny test site. Photo by Gabriela Ritóková.

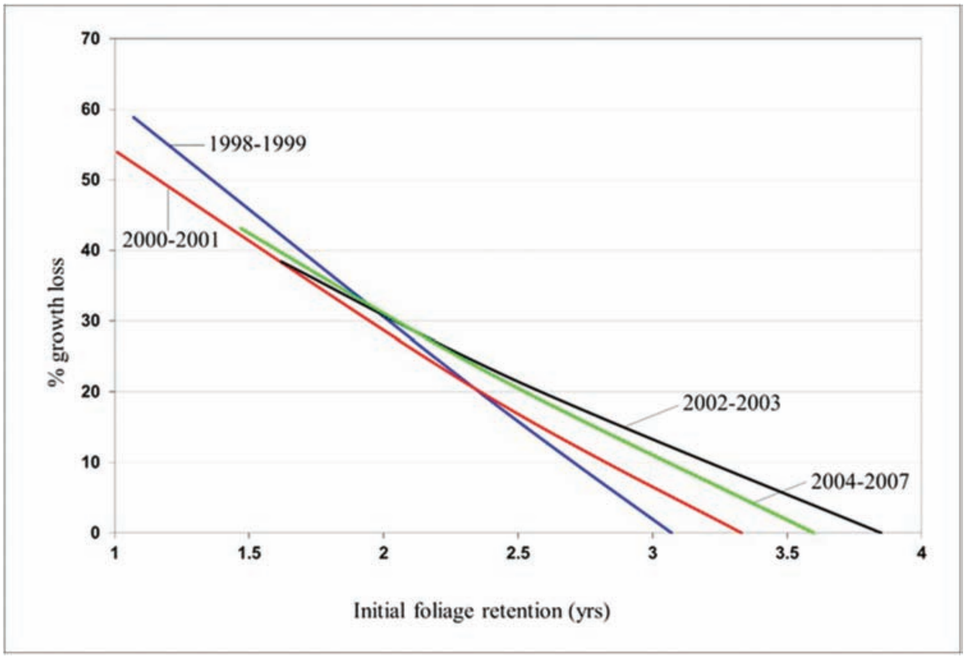

Figure 2. The relationship observed between foliage retention and percent volume-growth loss over four separate growth periods from 1998 to 2008 within 76 Douglas-fir stands in north coastal Oregon. Different color lines represent the foliage retention-growth loss relationship during a specific measurement period. In general, growth loss peaks at about 50–60%, and no growth loss is expected when trees retain more than three foliage cohorts.

a significant factor related to SNC severity. Mild winter temperatures and leaf wetness during spore dispersal in May through August have been identified as the main environmental factors positively associated with the disease expression (Michaels and Chastagner 1984, Hansen et al. 2000, Manter et al. 2005). Dominant forest types within this region are Douglas-fir and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) with a narrow zone of Sitka spruce (*Picea sitchensis* [Bong.] Carr.) along the coast (Franklin and Dyrness 1988). The epidemic has long been associated with Douglas-fir plantations within the coastal fog belt of the Sitka spruce zone immediately adjacent to the coast, but the disease is not limited to that zone (Rosso and Hansen 2003, Ritóková et al. 2016).

Here we update the current state of knowledge after 24 years of research and monitoring, with a focus on Oregon, although the disease is significant in coastal Washington and has emerged in southwestern British Columbia. We have new insight into the spread of the disease, landscape patterns, epidemiology, ecology, and host-pathogen interactions, as well as trophic and hydrologic influences. Silviculture and management remain nuanced and closely associated with local site conditions, especially stand age (Mildrexler et al. 2019). We conclude with a synthesis of our understanding of SNC and climate change and discuss the three additional foliage diseases considered threats to Douglas-fir plantations of western Oregon.

Is the Disease Spreading in Oregon?

An aerial detection survey (USDA Forest Service, Oregon Department of Forestry Cooperative Aerial Survey, hereafter ADS) has been flown for SNC symptoms annually from 1996 to 2016, and again in 2018. Observed SNC symptoms extend inland from the coast approximately 35 km (22 miles) (Figure 3). We evaluated the SNC ADS from 1996 and 2016 except 2008 when the surveys were incomplete (Figure 4). The surveys were performed from an observation plane flown at 460 to 610 m above the terrain, following north–south lines separated by 3.2 km (Ritóková et al. 2016). Observers looked for areas of Douglas-fir forest with obvious yellowing (chlorotic) foliage and thin crowns. Polygons of forest with these symptoms were sketched onto topographic maps or ortho-photos, originally on paper and eventually on computer touchscreens. The survey area extended from the Columbia River in Oregon south to the California border and from the coastline eastward until obvious symptoms were no longer visible (Figures 3, 4).

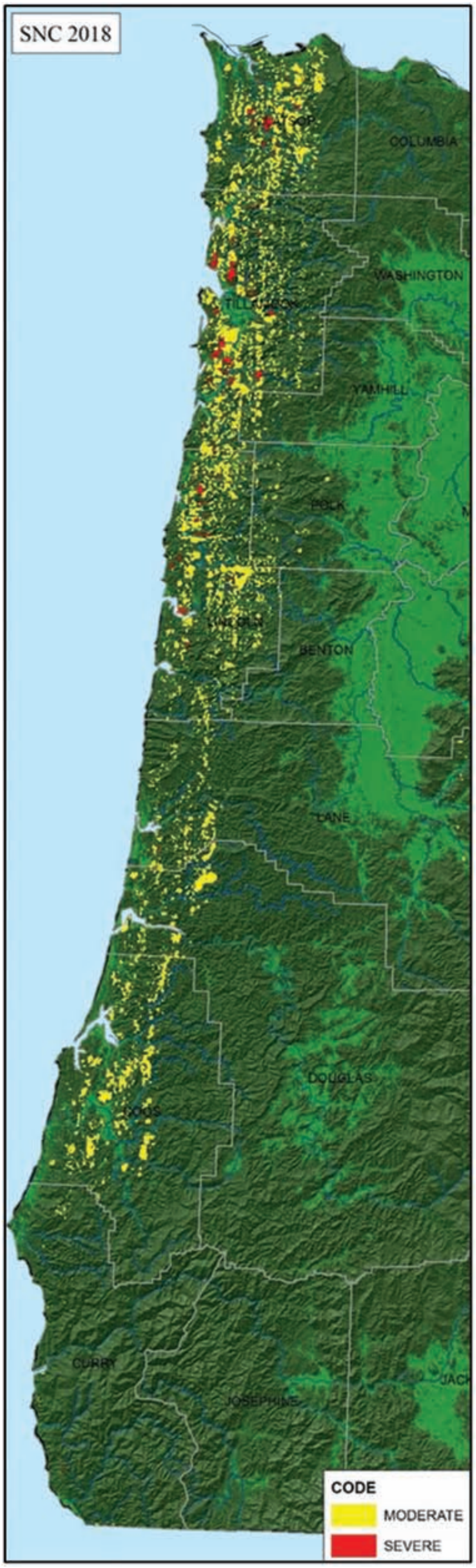

Figure 3. Map of Aerial Detection Survey results for Swiss needle cast in Oregon for 2018 indicating 167,165 hectares were symptomatic with chlorotic foliage and thin crowns visible from the airplane. Yellow polygons are considered moderately infected, and red are severely infected. Note the distinct regional pattern associated with distance from coast. Map source: Oregon Department of Forestry.

To determine if the disease has spread further east from the coast, we used the ArcGIS software to locate the area and centroid for each symptomatic polygon delineated by ADS. The distance from the coast to each polygon centroid was then identified. A polygon was defined as the individual area drawn on the map by the observer. For each year, the distance from the coast that contained 50%, 75%, and 95% of the total symptomatic area was determined and compared across all annual aerial surveys. The 50th, 75th, and 95th percentile distances were intended to outline the proximity of the symptomatic stands to the coast for each year. A simple linear regression was performed to predict the distance from the coast from 1996 to 2016 for each percentile.

Symptomatic hectares expanded eastward for the first few years of the study; however, very little net change occurred after that (Figure 5), even while the total symptomatic area in the coast range rose from 57,235 hectares in 1999 to 221,056 hectares in 2016 (Figure 4). The trendlines for the three percentile marks are nearly flat and none of the percentiles had an R^2 value greater than 0.04. A similar pattern occurred when the years were arranged by total infected area (not shown). Though initial increases in total statewide symptomatic area were correlated with expansions eastward, once the total symptomatic area passed 80,000 hectares, the trendlines were nearly flat again and none of the percentiles had an R^2 greater than 0.02. These results indicate that SNC disease has a strong geographic pattern that has remained remarkably stable.

Mapping Disease Severity and Foliage Retention for Plantations

Douglas-fir plantation management requires a knowledge of where SNC is a problem and what the growth losses are. A new research and monitoring plot network installed by the Swiss Needle Cast Cooperative (http://sncc.forestry.oregonstate.edu), extending from the northern California border to southwestern Washington (560 km [338 miles]), and 56 km (35 miles) inland, complements the ADS survey with ground based measurements and provides an opportunity for epidemiology studies while monitoring stand volume growth impacts across a gradient of disease symptoms (Ritóková et al. 2020). The geographic setting

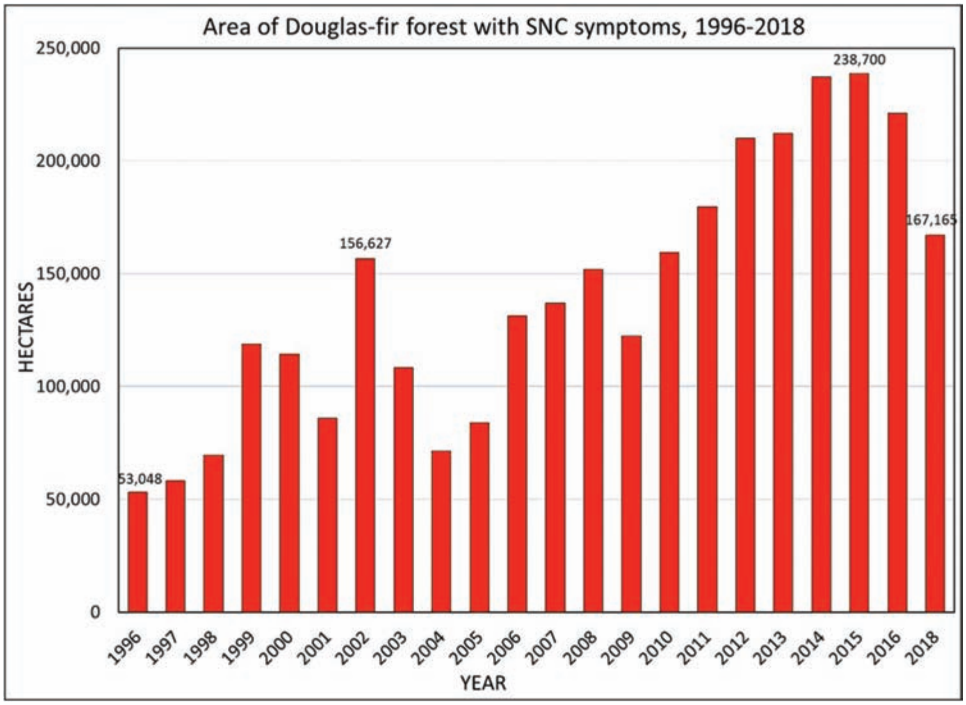

Figure 4. Aerial Detection Survey results for Swiss needle cast in coastal Oregon 1996–2018. In 2017, aerial detection survey was not flown.

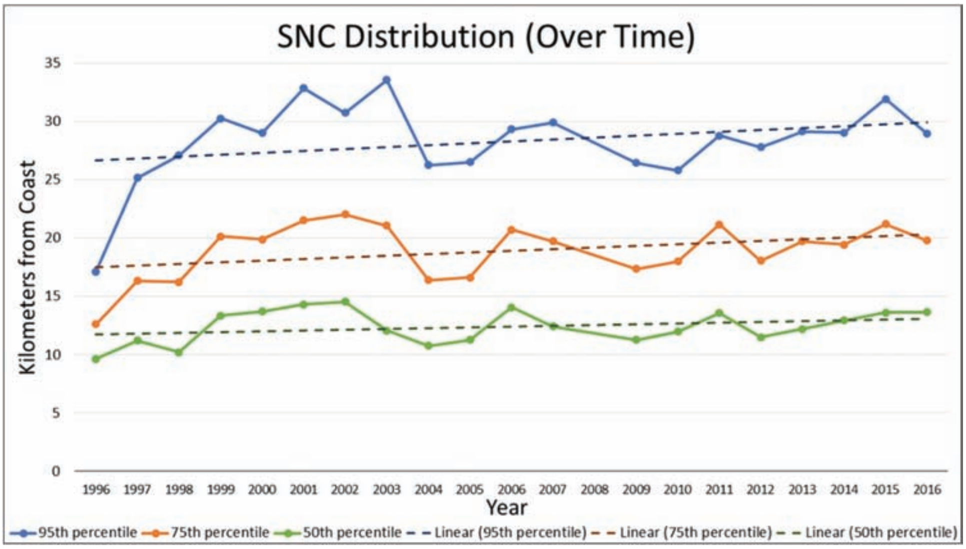

Figure 5. Distance from the coast that contains 50%, 75%, and 95% of all Aerial Detection Survey Swiss needle cast (SNC) symptomatic polygons from 1996 to 2016 arranged by year with data from 2008 excluded.

of the new plot network includes the coastal portion of the Klamath-Siskiyou Mountains, the Oregon Coast Range, and the Willapa Hills in southwestern Washington. Precipitation and temperature vary across the region because of elevation, latitude, and rain shadow on the eastern slope of the Coast Ranges. Annual precipitation ranged from 1,200 to 4,800 mm (47–190 inches), with the majority falling as rain from October through May. Mean annual temperature ranged from 13°C to 18°C (55–64°F). Elevation of the research plots ranged from 48 to 807 m (157–2,657 feet) above sea level (Figure 6a).

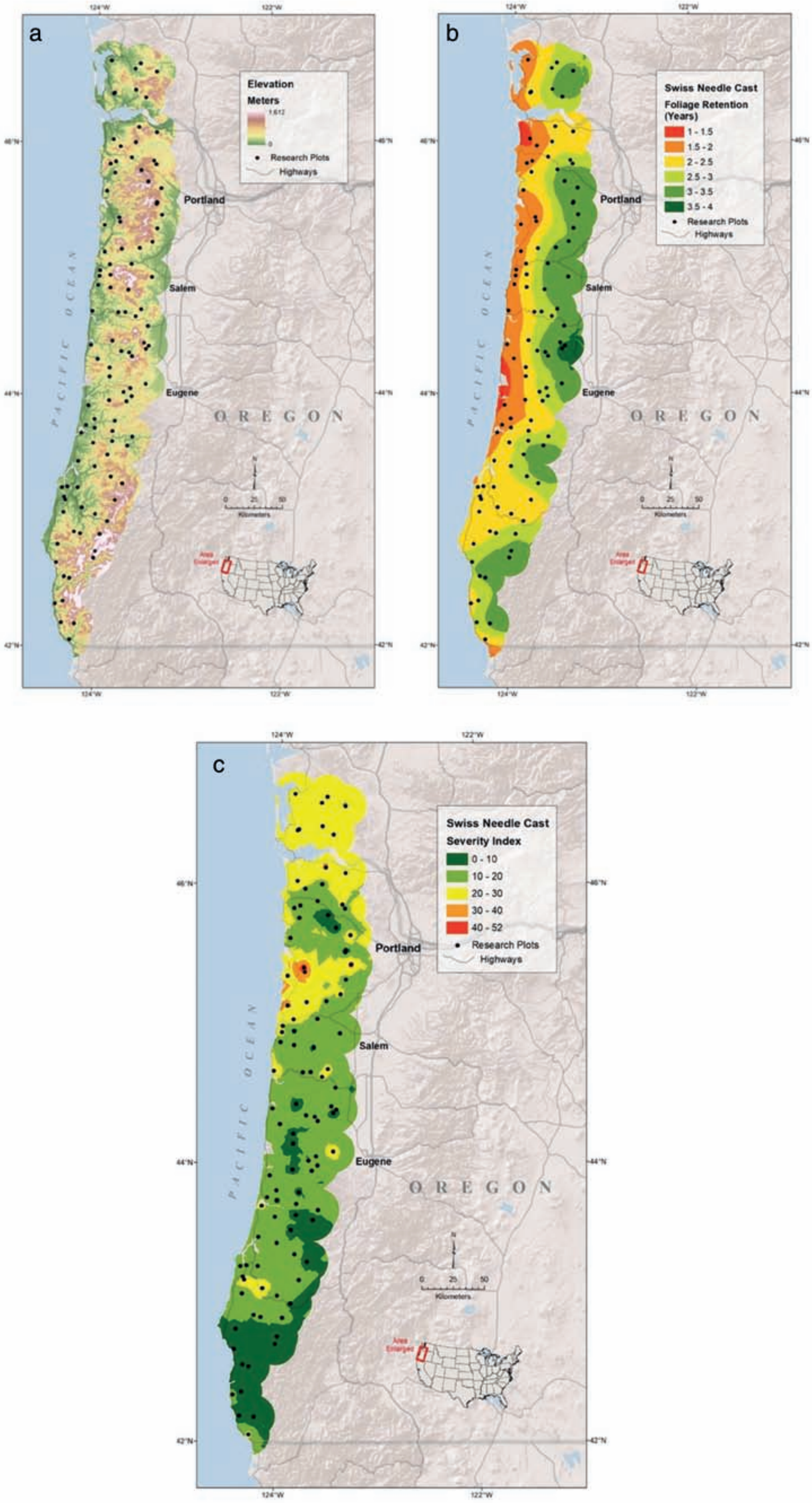

Figure 6. Maps of Swiss needle cast research and monitoring plot area. (a) Map of elevation across the Oregon Coast Range and location of 106 Swiss needle cast research and monitoring plots. (b) Foliage retention in years of retained

Methodology

The plot installation protocol followed the Maguire et al. (2011) procedures to remain compatible with the original growth impact sampling methodology and is described by Ritóková et al. (2020). All plots were established in plantations (10–30 years old) that had not been precommercially thinned or fertilized within five years prior to establishment. Foliage samples were collected just prior to budbreak (March–May) in the spring following plot installation in 2014, 2015, and 2016. Foliage sampling methods, including assessment of foliage retention and disease severity followed the methods of Mulvey et al. (2013b) and Ritóková et al. (2020). The SNC disease severity index was calculated by multiplying the incidence of leaves with pseudothecia by the percent pseudothecial density on individual leaves.

SNC foliage retention and disease severity continuous surface maps were created by interpolating data from 106 research plots using ordinary kriging (Figure 6b, c). The spatial extent of each surface interpolation was limited to the average distance (17 km) between the nearest five research plots used in interpolation search neighborhoods. Final maps were created by classifying continuous surface maps. All geostatistical analyses were completed using ArcGIS geographic information system (GIS) software (ESRI, 1995–2017, ArcMap version; ESRI, 2014, ArcGIS Desktop: Release 10.7.0. Environmental Systems Research Institute, Redlands, CA).

Results

Our sample region encompassed a range of disease severity (0.05–52.11) and foliage retention (1.15 years to 3.9 years) (Figure 6b, c). Within crowns, disease severity was greater in the upper crown, foliage retention was greatest in the lower crown, and the pattern was consistent regardless of distance from coast (Ritóková et al. 2020). The potential site hazard maps indicate a clear distance-from-coast and elevation pattern in foliage retention (Figure 6b) and a less clear pattern in disease severity (Figure 6c). There is a strong latitudinal gradient with foliage retention decreasing and disease severity increasing from the California border to the northern coast of Oregon and into southwestern Washington State (Ritóková et al. 2020). Although we consider foliage retention to be closely related to disease severity, there are distinct differences in the maps which indicates that there is an inconsistent relationship between needle retention and disease severity (Montwé et al. 2021). However, foliage retention and disease severity are strongly related to elevation (Figure 7a, b).

New Insights into Epidemiology, Ecology, and Host-Pathogen Interactions

Epidemiology is the study of the distribution, patterns and cause of disease focusing on why and how a disease agent is causing problems. Ecological perspectives shed light on how the patho-system relates to forest management. Although *N. gaeumannii* is found everywhere Douglas-fir grows, the fungus causes SNC disease in a subset of specific geographic regions associated with mild winter temperatures and late spring–summer rainfall or fog-causing leaf wetness and increased humidity. Leaf wetness during the spore dispersal period (May–August) allows good fungal colonization of the needle while warm winter temperatures appear to accelerate the timing of pseudothecia development so that pseudothecia form in one- and two-year-old foliage and cause needle casting.

Zhao et al. (2011, 2012) found correlations between coastal Douglas-fir foliage retention and a temperature-based continentality index as well as a suite of other variables encompassing seasonality of both temperature and precipitation that is consistent with epidemiological models (Manter et al. 2005). In addition, Lee et al. (2017) used tree ring width chronologies to show that SNC can affect growth across the region and is not limited to the coastal fog zone. They also found that impacts were regionally synchronous and linked to winter and summer temperatures, and summer precipitation, and the specific factor (temperature or moisture) that was more influential varied with geographic location.

Tree Age

The question of tree age and disease severity has recently been investigated by Lan et al. (2019a) who compared SNC disease severity between young (20- to 30-year-old) and mature Douglas-fir (120- to 470-year-old) across seven sites in western Oregon; three sites in the Coast Range in the epidemic area, and four sites in

foliage across the Oregon Coast Range. (c) Disease severity (incidence × pseudothecia-plugged stomate density) across the Oregon Coast Range. Black dots note the location of Swiss needle cast research and monitoring plots used as data points to make the maps b and c.

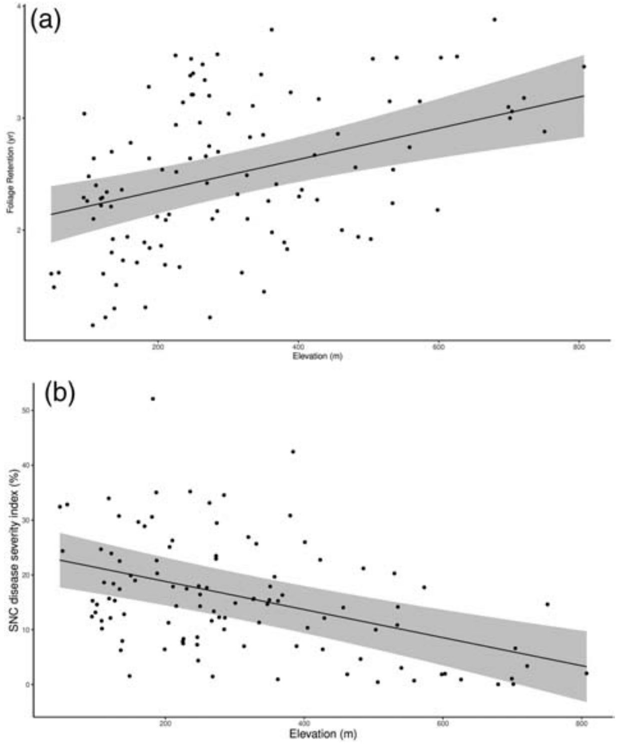

Figure 7. Elevation and disease severity and foliage retention. (a) Relationship between foliage retention and plot elevation across coastal Oregon and southwestern Washington based on the Swiss needle cast (SNC) research and monitoring plot network. Mixed linear models were applied to test the association of plot elevation with foliage retention by using R (v. 3.4.3, R Core Team 2017) packages dplyr (Wickham et al. 2017), ggplot2 (Wickham 2009), and nlme (Pinheiro et al. 2017). The association between foliage retention and plot elevation is significantly positive ($p < .001$). Gray area indicates 95% confidence interval. (b) Relationship between SNC severity index and plot elevation across coastal Oregon and southwestern Washington based on the SNC research and monitoring plot network. Mixed linear models were applied to test the association of plot elevation with SNC severity index by using R (v. 3.4.3, R Core Team 2017) packages dplyr (Wickham et al. 2017), ggplot2 (Wickham 2009), and nlme (Pinheiro et al. 2017). The association between SNC severity index and plot elevation is significantly negative ($p < .001$). Gray area indicates 95% confidence interval.

the Cascade Mountains outside the epidemic area. The authors found that young plantation trees had consistently higher disease severity than nearby mature/old-growth forests. In addition, SNC disease incidence (% needles with pseudothecia) was evaluated for all age classes of foliage. Incidence peaked at age two for young trees and ages three to five for mature trees. These differences are related to timing of pseudothecial development and emergence in stomates. Theories for earlier pseudothecial emergence in young trees include temperature of tree crowns, factors related to age, or differential tree genetics.

The association of SNC with younger plantations in the Oregon Coast Range is supported by Mildrexler et al. (2019), who have shown that SNC is more likely to be mapped by aerial detection surveys in the intensively managed plantations more typical of private ownership. However, older stands can exhibit substantial disease impacts. Black et al. (2010) used dendrochronological techniques to investigate SNC in mature stands at both low- and high-elevation sites near Tillamook, Oregon, and found nearly 85% growth reductions in several low elevation trees with more than 10 missing growth rings. In recent visits to the sites, it was discovered that many trees >90 years old that have been chronically infected for over 20 years died during the 2015–2018 drought (Figure 8a, b). This area has long been considered the most severely affected by SNC, such that western hemlock has supplanted Douglas-fir as the preferred plantation species.

Short-Term Climate Trends and Persistence of Coastal Fog

Mildrexler et al. (2019) also found that short-term climate trends were correlated with a significant rise in symptomatic hectares documented from aerial detection survey. For the period from 2003 to 2012,

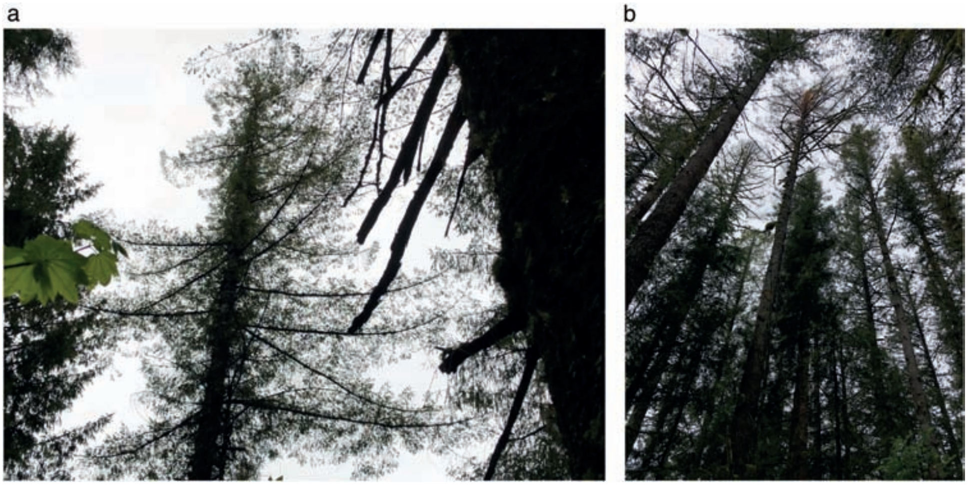

Figure 8. Mature Douglas-fir trees affected by Swiss needle cast. (a) Chronically affected mature Douglas-fir (~85 years) northeast of Tillamook Oregon in 2018 at Tillamook Lower (Black et al. 2010). Individual live crown; note the epicormic branching along the bole, low foliage retention, and thin crown. (b) Tree mortality associated with long term impacts of Swiss needle cast perhaps interacting with drought.

they used canopy energy and water exchange data calculated from Modis Land Surface Temperature and evapotranspiration data, and PRISM (parameter-elevation relationships on independent slopes model) derived precipitation data to estimate climate trends. During this nine-year period, June and July recorded cool and moist conditions, conducive to disease development. ADS validated this presumed SNC intensification, with a reported low of 71,465 hectares in 2004, increasing to 210,184 hectares in 2012 (Figure 4).

The link with the coastal region has often been associated with summer fog (Rosso and Hansen 2003), but quantification of fog and low clouds across the region has remained elusive. Dye et al. (2020) have recently developed the first documentation of low clouds for the entire region over the 22-year period 1996–2017. Their analysis shows that occurrence of low clouds (including fog) in May, June, and July are a significant characteristic of the lower elevations of the coastal strip along the west side of the Oregon Coast Range. The subsequent moist conditions, in combination with ocean-moderated mild winter temperatures could explain why the SNC outbreak area has remained geographically contained during that period with distance from coast defining the epidemic (Figure 5). Whether the results of Dye et al. (2020) constitute a change in conditions relative to prior periods is unknown.

Seed Source

Wilhelmi et al. (2017) investigated a seed source movement trial that used coastal Douglas-fir seed sources from southwestern Washington, western Oregon, and northwestern California to determine the susceptibility to foliage diseases. *N. gaeumannii* and *Rhabdocline* species (cause of Rhabdocline needle cast) were important within the study and seed source was shown to affect susceptibility to these diseases. Trees grown from seed sourced from drier habitats moved to wetter habitats, and from higher elevations to lower elevations showed increased SNC and Rhabdocline needle cast. This is consistent with the hypothesis expressed in Hansen et al. (2000) that establishment of Douglas-fir in coastal zones previously dominated by Sika spruce, western hemlock, and red alder, and establishment of Douglas-fir stands using seeds sourced from drier areas further east have a role in the origins of the epidemic. Douglas-fir shows genetic tolerance to *N. gaeumannii*, in that all seed sources have leaves that are equally susceptible to infection no matter what the environment. Tolerant trees have greater foliage retention and crown fullness, however.

Lineages of *Nothophaeocryptopus gaeumannii*

There are two, noninterbreeding lineages of *N. gaeumannii* (Lineage 1 and Lineage 2) (Winton et al. 2006, Bennett and Stone 2019) in coastal Pacific Northwest forests, and a third lineage (Lineage 1i) has been identified in the interior of British Columbia, Canada, and the Northern Rocky Mountains, USA (Hamelin and Feau, University of British Columbia, 2020, pers. commun.). Although these lineages are noninterbreeding, they require molecular analysis to determine the differences.

In Oregon, Lineage 2 is closely associated with the coast, and Lineage 1 is more widespread, reflecting the gradient of environmental conditions (Winton et al. 2006, Bennett and Stone 2019). Investigations into whether any of these lineages are more pathogenic than the other are inconclusive (Bennett and Stone 2019).

Effects on the Tree

The implications of *N. gaeumannii* infection on nonstructural carbohydrates associated with stomate blockage was investigated by Saffell et al. (2014b). The study provides insight into carbon dynamics because water stress was low, and carbon uptake was not influenced by drought. In a highly diseased stand, mean basal area increment growth decreased by about 80% and nonstructural stem carbohydrates decreased by about 60% across a gradient of foliage mass reduction. However, twig and foliage nonstructural carbohydrate concentrations remained constant with decreasing foliage mass. Douglas-fir trees retained nonstructural carbohydrates in the crown at the expense of trunk radial growth which allowed for foliage growth and shoot extension in the spring.

In a study of tree-ring stable isotopes in a fungicide treated plantation versus an adjacent untreated plantation, Saffell et al. (2014a) showed that isotopes record the impact of *N. gaeumannii* on CO_2 assimilation and growth. Fungicide only protects current year foliage from infection and the fungicide treatment occurred for five consecutive years in the treated plantation. As foliage retention increased following treatment, the annual basal area increment doubled by the fifth year compared with the untreated stand. After treatment stopped, it took about four years of steady growth reductions before increment in the two stands were similar, indicating that *N. gaeumannii* was the cause of growth impacts. The ability of Douglas-fir to discriminate against carbon stable isotope ($\Delta^{13}C$) increased in the treated stand, supporting the contention that *N. gaeumannii* is causing carbon starvation. The authors also found that tree ring $\Delta^{13}C$ was negatively correlated with relative humidity during the two previous summers, supporting the contention that summer climate is important.

Hydrologic and Trophic Interactions

In the first study to show a forest pathogen can influence watershed hydrologic regimes, *N. gaeumannii* was shown to influence catchment scale hydrology in the Oregon Coast Range (Bladon et al. 2019). Bladon and colleagues investigated 1990–2015 annual streamflow, runoff ratio, and the magnitude and timing of peak flows and low flows for 12 catchments in areas with 0 to 90% of the catchments mapped with SNC symptoms by ADS surveys. They found that in catchments with >10% ADS area mapped, that the runoff ratios increased. However, in the two most heavily affected catchments, with ~50–90% of the area mapped by ADS, there was no effect. They hypothesized that this was due to vegetation compensation—that is, growth of non-Douglas-fir conifers, hardwoods, and shrubs increased because of the negative impact of SNC on Douglas-fir (Zhao et al. 2014a).

Studies also indicate that trophic interactions are altered by *N. gaeumannii*, including mycorrhizae and the Douglas-fir beetle (*Dendroctonus pseudotsugae*) (Coleoptera: Curculionidae). Luoma and Eberhart (2014) investigated the relationship between Swiss needle cast and ectomycorrhizal fungus diversity in the Oregon Coast Range across a gradient of disease severity. They found that ectomycorrhizal diversity varied 10-fold across the sites and ectomycorrhizal species richness varied about 2.5-fold. Both ectomycorrhizal diversity and species richness were positively related to increasing foliage retention. Carbon starvation may be the reason for the reduction in ectomycorrhizal fungi diversity and abundance, and this likely causes a trophic cascade below ground.

The lack of evidence for SNC-induced mortality in Douglas-fir plantations (Maguire et al. 2011) is partially because of the decreased likelihood of secondary mortality agents. For example, the Douglas-fir beetle is not attracted to SNC diseased Douglas-fir trees (Kelsey and Manter 2004). Carbon starvation and lack of tree resources for production of protective chemicals and ethanol may be the reason. Kelsey and Manter (2004) found that woody tissue ethanol concentrations, wound-induced resin flow, and beetle attraction were reduced as the severity of SNC increased. Because there has not been increased Douglas-fir beetle activity associated with the SNC outbreak, the authors speculate that pioneering beetles do not recognize stressed SNC infected trees because of a lack of an ethanol signal.

Silviculture and Plantation Management

Management of SNC-infected stands can be coarsely directed by the known gradient of disease severity on the landscape (Figure 6). A one-size fits all approach ignores opportunities for effectual production of Douglas-fir throughout the coastal region (Shaw et al. 2011, Mulvey et al. 2013a, Zhao et al. 2014b). Integrated pest management is recommended and the suggested approach to SNC stand management includes three steps. First, a site hazard assessment should incorporate ADS and models of SNC impacts on foliage retention (Figure 6b), to assess the current and future likelihood of disease impacts. Second, stand impact assessments should be made using average stand foliage retention, verification of *N. gaeumannii*, and quantitative growth impact assessments. Determining whether growth reductions are occurring is a key step because deviating from normal plantation management practices should be based on knowledge of whether growth reductions are occurring. Finally, silvicultural decisions should be site specific, informed by both biological and economic risk factors.

Precommercial and commercial thinning can be used in conjunction with species selection to improve the stand (Zhao et al. 2014b). Variation in disease tolerance within individuals is observed in the field (Zhao et al. 2014a); therefore, thinning from below can remove Douglas-fir with sparse crowns and small sizes indicative of low disease tolerance. Western hemlock is a codominant species in the near-coastal region of Oregon that naturally seeds into Douglas-fir plantations. In severely affected Douglas-fir stands, western hemlock can outcompete Douglas-fir even seeding in two or three years later (Figure 1b). Some landowners use a diameter-minus rule for precommercial thinning where western hemlock is common (Zhao et al. 2014b), dictating the retention of small hemlocks and removal of larger neighboring Douglas-fir in expectation of better long-term results for hemlock. The size difference in diameter dictating such decisions (diameter-minus) depends on absolute tree size, and SNC intensity.

Silvicultural techniques that are traditionally used to reduce foliage disease by drying the canopy through increased air circulation, including thinning, vegetation management, and pruning, are not effective at reducing SNC within a planation (Mainwaring et al. 2005, Shaw et al. 2011). Thinning and vegetation management have been shown to increase individual Douglas-fir tree growth in diseased stands, but growth rates will be reduced relative to healthy stands (Mainwaring et al. 2005). Fungicides have been shown to be effective in plantations (Stone et al. 2007, Saffell et al. 2014a), but their use is neither cost effective nor environmentally friendly, requiring annual applications because only current-year foliage is colonized by *N. gaeumannii*.

Species choice at planting is generally driven by economic factors and management familiarity, but alternative species such as western hemlock, currently less valuable, can be included in increasing proportion as the known or expected disease severity of the site increases. The seed source of planted stock is important, with sources from drier regions moved to wetter regions, or higher elevations moved to lower elevations, being particularly susceptible to both SNC and Rhabdocline needle casts (Wilhelmi et al. 2017). Traditional tree improvement focused on genetic tolerance is an important part of the overall goal of managing Douglas-fir for Swiss needle cast (Jayawickrama et al. 2012, Montwé et al. 2021), but some locations exhibit such high disease severity that Douglas-fir is not advised and western hemlock has emerged as a preferred species (Kastner et al. 2001).

Although the hypothesis that higher foliage N increases disease is still unclear (Mulvey et al. 2013b), fertilization of diseased stands with N is not advised, with multiple fertilizer trials in diseased stands having repeatedly shown no positive growth responses (Mainwaring et al. 2014). Lan et al. (2019b), using the SNC research and monitoring network, recently confirmed that higher N in foliage is associated with higher disease, but this covaries with climate factors and distance from coast, so it is difficult to disassociate from epidemiological factors.

Climate Change

Seasonal changes in precipitation and temperature rather than increasing tree stress will influence SNC, as well as other foliage diseases (Kliejunas et al. 2009, Agne et al. 2018). Temperature is a key non-growing-season epidemiological factor described by Manter et al. (2005). Stone et al. (2008b), Watt et al. (2010), and Lee et al. (2017) suggest that winter temperatures will influence SNC impacts in future climate scenarios, and that if conditions in late spring to midsummer result in some periods of leaf wetness, SNC impacts will increase at higher elevations and higher latitudes. A dendrochronological investigation of heavily affected mature stands in the Tillamook area found that SNC-associated basal area growth reductions became evident in the 1980s and have persisted since that time (Black et al. 2010). According to the Oregon Coastal Climate Division of NOAA, the average minimum

November–April temperatures since the mid-1980s have generally been above the 1901–2000 average (Figure 9), possibly indicating that warming winter temperature has already played a role in the SNC epidemic of coastal Oregon.

Late spring and summer precipitation and fog that wets Douglas-fir leaves is key to disease intensification. Mildrexler et al. (2019) have shown that consistently cool and wet weather in the coastal Oregon during May–July from 2004 to 2014 correlated with an increase in SNC ADS area (Figure 4). However, drought, drier spring and summer weather, and longer, drier, and hotter growing seasons will reduce SNC presence or impacts because of poor colonization of foliage when conditions are dry. Precipitation changes are difficult to predict along the coast, but spring precipitation may remain similar and summers will likely be drier, for the period 2010–2039 compared with 1971–2000 (MACA Summary Projections using higher emissions, RCP 8.5, https://climate.northwestknowledge.net/MACA/tool_summarymaps2.php), so that the disease may persist along the coast into the future even if the inland sites dry out more as predicted.

The Suite of Foliage Diseases in Coastal Douglas-Fir

Over the past decade, two new foliage diseases have emerged as potential threats to Douglas-fir plantations (LeBoldus et al. 2019). These include web blight (*Rhizoctonia butinii*) (Chastagner and LeBoldus 2018) and Phytophthora needle cast (*Phytophthora pluvialis*) (Williams and Hansen 2018) of Douglas-fir. Rhabdocline needle cast (several *Rhabdocline* species) (Stone 2018) is a well-known disease associated with off-site plantings and may emerge if assisted migration is employed without field testing (Wilhelmi et al. 2017). Although these new diseases do not currently appear to be affecting forest plantation management to the degree that SNC does, this complex of diseases could threaten Douglas-fir management as environmental and management conditions change.

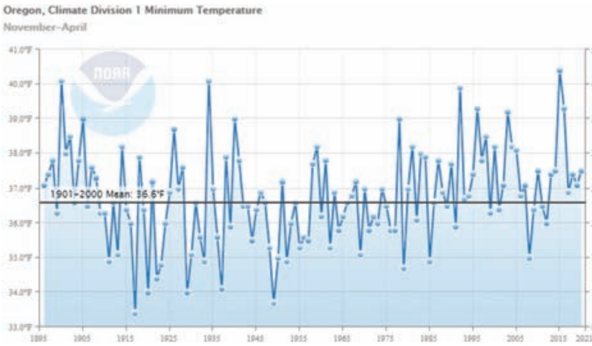

Figure 9. Minimum temperature time series from 1895 to 2020 for the six-month period, November–April for Division 1, Coastal Oregon. Note that since the 1980s, temperatures have tended to be warmer. Source: NOAA National Centers for Environmental Information. Divisional Time Series, Division 1 (coastal) Oregon Climate.

Phytophthora needle cast, also called red needle cast in New Zealand, is a foliage Phytophthora recently described in western Oregon and about the same time observed in Douglas-fir and radiata pine in New Zealand where is it causing significant damage (Hansen et al. 2015, Williams and Hansen 2018). Although it is widespread in western Oregon, it does not appear to be causing significant damage in Douglas-fir plantations (Hansen et al. 2017). Gómez-Gallego et al. (2019) contrasted pathogen loads in coexisting populations of *P. pluvialis* and *N. gaeumannii* in New Zealand and the Pacific Northwest, USA. They found that both pathogens were more abundant in New Zealand than the Pacific Northwest, and that in the Pacific Northwest, their abundance in the same leaf was negatively correlated.

Web blight is widespread and more commonly observed than Phytophthora needle cast, but anecdotal observations suggest it is most important in lower crowns of dominant and codominant canopy class Douglas-fir trees in plantations and understory trees such as western hemlock in mixed and older stands (Chastagner and LeBoldus 2018, LeBoldus et al. 2019; personal observations by the authors). In general, our knowledge of the role of Phytophthora needle cast and web blight in natural and managed forests of western Oregon is in its infancy, and epidemiological and ecological studies are needed. It is generally believed that *P. pluvialis* is native to western Oregon (Hansen et al. 2017), and it is not known if *R. butinii* is native or not.

Conclusions

Swiss needle cast will continue to be an issue for coastal Douglas-fir into the near future, and the lower elevations of the western Cascade Mountains are also a region of potential SNC impacts. Warmer winter temperatures combined with leaf wetness during May–July will lead to disease intensification and increased impacts at increasingly higher elevations. The scale of the disease on the landscape is influencing forest productivity, hydrologic regimes, as well as trophic interactions and biodiversity belowground. Continued research and development of genetically improved, tolerant Douglas-fir for plantations is critical to long-term management, while care must be taken in moving seed sources from drier regions into the coast range of Oregon. Although disease severity and needle retention can be estimated from models and maps (Figure 6), individual stand management is quite nuanced, site specific, and entails an informed approach based on how the disease is actually influencing the stand.

The tree microbiome is the new frontier of forest pathology, and knowledge of the dynamics of the entire microbial community of Douglas-fir foliage could lead to major breakthroughs in our understanding of SNC because interactions with other fungi and bacteria in the leaf may influence *N. gaeumannii*. At the leaf level, there is also a need to understand more about the internal nutrient acquisition of the fungus. Other key research needs include the role of temperature in the timing of pseudothecial development and investigations of whether temperature of the leaf is distinct in young, even-aged plantations versus mature and older stands, and whether this can be explained by stand structure. The influence of soils and foliage chemistry and linkages to climate and distance from coast require more inquiry to try to separate these confounding factors.

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REVIEW ARTICLE

Applications of a conceptual framework to assess climate controls of forest tree diseases

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Abstract

A conceptual framework for climate involvement in forest tree diseases was applied to seven examples to demonstrate its suitability for different disease types: cases where climate favours pathogen biology which then leads to tree mortality or where diseases are caused primarily by climate-driven physiological injury or stress to trees. Hypotheses for climate involvement are derived from detection and monitoring data to express associations of weather or climate factors with disease development at several spatial and temporal scales. Research findings contribute to an understanding of temperature, precipitation and related climate variables that influence biotic and abiotic diseases. To demonstrate use of the framework, we accessed information from the literature which exposed data and information gaps. Among various simulated approaches to test associations of climate and disease, we found disease risk factor models that use climate inputs derived from monitoring and research provide the best understanding of climate–disease relationships. These model outputs project future disease scenarios that can be used to inform climate adaptation strategies. Conservation and management implications for current and likely future climatic conditions are provided for each disease example. The most common guidance in managed landscapes is to move the imperilled tree species to areas of lower projected climate risk and to favour non-host, climate-adapted tree species where the disease is occurring.

Paul E. Hennon, James J. Worrall and Charles G. Shaw are retired.

1 | INTRODUCTION

As Hepting (1963) predicted, climate and climate change have profoundly affected forest tree diseases with consequent impacts on ecological dynamics, species viability and provision of multiple forest resource values. Atmospheric changes and their impacts on tree diseases present complex management challenges (Seidl et al., 2017). The disruption of forest diseases (pathosystems) is considered among the earliest and most severe climate change impacts on forests (Mahony et al., 2018) and may be particularly difficult to predict in novel climates (Woods, 2011). The body of literature documenting cases of a changing climate affecting forest diseases continues to grow (Allen et al., 2015; Brasier, 1996; Delgado-Baquerizo et al., 2020; Desprez-Loustau et al., 2006, 2007; Hennon et al., 2012; La Porta et al., 2008; Sturrock et al., 2011; Woods et al., 2005; Worrall et al., 2013; Wyka et al., 2017). But forecasts on how these relationships will unfold are uncertain because of the critical role that precipitation plays in most pathosystems and expected rapid swings between opposite precipitation extremes in the future (Cai et al., 2015). Increased monitoring of biotic and abiotic disturbances in both managed and unmanaged forests is needed to help close the information gaps surrounding forest condition and threats (McDowell et al., 2015). Forest managers must incorporate adaptation to climate change in the development of management plans to ensure that forests are sustained, and species remain viable (Jandl et al., 2019). The great puzzle is to determine how best to adapt forest management, and what conditions to adapt to, given sustained climate change. A key piece is a better understanding of how forest diseases will respond to climate change and how they will alter future forest dynamics.

To address these questions, we proposed “A framework to evaluate climate effects on forest tree diseases” (Hennon et al., 2020) to provide concepts and methods for demonstrating climate as a cause of tree disease development. The framework, based on the plant disease triangle, calls for an examination of ways that weather or climate can influence disease outbreaks. Diseases are divided into two fundamental categories, Type 1, where the dominant influence is on the pathogen (climate-pathogen disease), and Type 2, where the primary climate effect occurs directly on the forest tree (climate-stress disease). Climate-stress diseases, in some cases, are largely abiotic where the stress alone can kill the tree (Type 2a). In others, secondary pathogens and/or insects take advantage of the stressed trees and kill them where the abiotic stress alone may have been insufficient to cause mortality (Type 2b).

Because experimentation with mature trees across landscapes is impractical or impossible, to demonstrate causality, the framework relies primarily on associations between weather or climate and disease, as well as the hosts and pathogens (Hennon et al., 2020). The associations are both spatial (varying weather or climate over geographic area drives disease distribution) and temporal (varying weather or climate over time drives disease frequency or severity). Spatial variation is considered at different scales: tree, stand, landscape or range wide. At fine spatial scales, individual tree, stand and site factors (e.g., tree age, density, basal area, soils, aspect, elevation) can affect climate-influenced diseases as predisposing factors. Temporal perspectives cover a range from short-term hourly and daily weather events to long-term climate and multi-decadal climate regime shifts (climate change).

Here we present applications of the framework with examples from western North America where a climate element is considered a driver of disease, thereby testing our conceptual framework with available data. We discuss similarities and differences that emerge from these disease examples including modelling for future predictions and management implications. Our objective is to facilitate use of this framework on other tree diseases where climate is suspected to be a major factor, thereby allowing for improved understanding and management of forest diseases. A longer-term goal is to improve integration of forest disease information into global dynamic vegetation models to more accurately reflect the role of forest diseases and other biotic disturbance agents under changing environmental conditions.

2 | APPLYING THE CONCEPTUAL FRAMEWORK OF CLIMATE INVOLVEMENT TO EXAMPLE FOREST TREE DISEASES

Below, the conceptual framework (Hennon et al., 2020) is applied to seven forest tree diseases that have increased during this or the previous century, and for which there is an adequate body of knowledge to enable analysis. A hypothesis is stated to explain climate involvement for each disease. The relationship between climate and each of the main factors in the conceptual framework is examined (Table 1). Climatic and other environmental conditions, including management history, are considered at several spatial scales along with temporal factors (i.e., alignment of temperature and moisture levels at locations with disease outbreaks). Then an assessment of the certainty of assumptions is made to gauge the strength of causality. Where weather or climate appear to be drivers, climate projection models are used to predict future disease activity.

2.1 | Dothistroma needle blight in British Columbia

Disease: Dothistroma needle blight (Figure 1a–d).

Forest tree: Lodgepole pine (*Pinus contorta* var. *latifolia*), shore pine (*P. contorta* var. *contorta*), and other pine species.

Type of climate effect: Type 1, climate-pathogen disease.

Pathogen: *Dothistroma septosporum* (Dorog.) Morelet.

Climate hypothesis: The pathogen, *D. septosporum*, is strongly controlled by the weather, so disease expression can change rapidly due to shifts in weather patterns. The disease spreads and intensifies quickly during periods of increased summer precipitation combined with warmer overnight minimum or optimal (i.e. warmer) daytime temperatures.

TABLE 1 Factors considered in the conceptual framework (Hennon et al., 2020) to evaluate hypotheses for climatic conditions that elicit increases or decreases in forest tree diseases

Elements to associate with climate	Approach, monitoring, analysis and research
Disease expression—spatial scales	Evaluate the climate–disease relationship at tree, stand, landscape and range-wide spatial scales
Disease expression—temporal scales	Evaluate the climate–disease relationship at weather (daily or seasonal), yearly to decadal, and multi-decadal to centuries time scales
Predisposing factors	Evaluate site and stand conditions that exacerbate or alleviate disease expression
Forest tree vulnerabilities	Evaluate climate impacts directly to forest trees, especially tree physiological stress
Pathogens	Evaluate climate-controls directly on pathogen reproduction, infection and virulence. Evaluate endophytic fungi that may change behaviour as climate changes

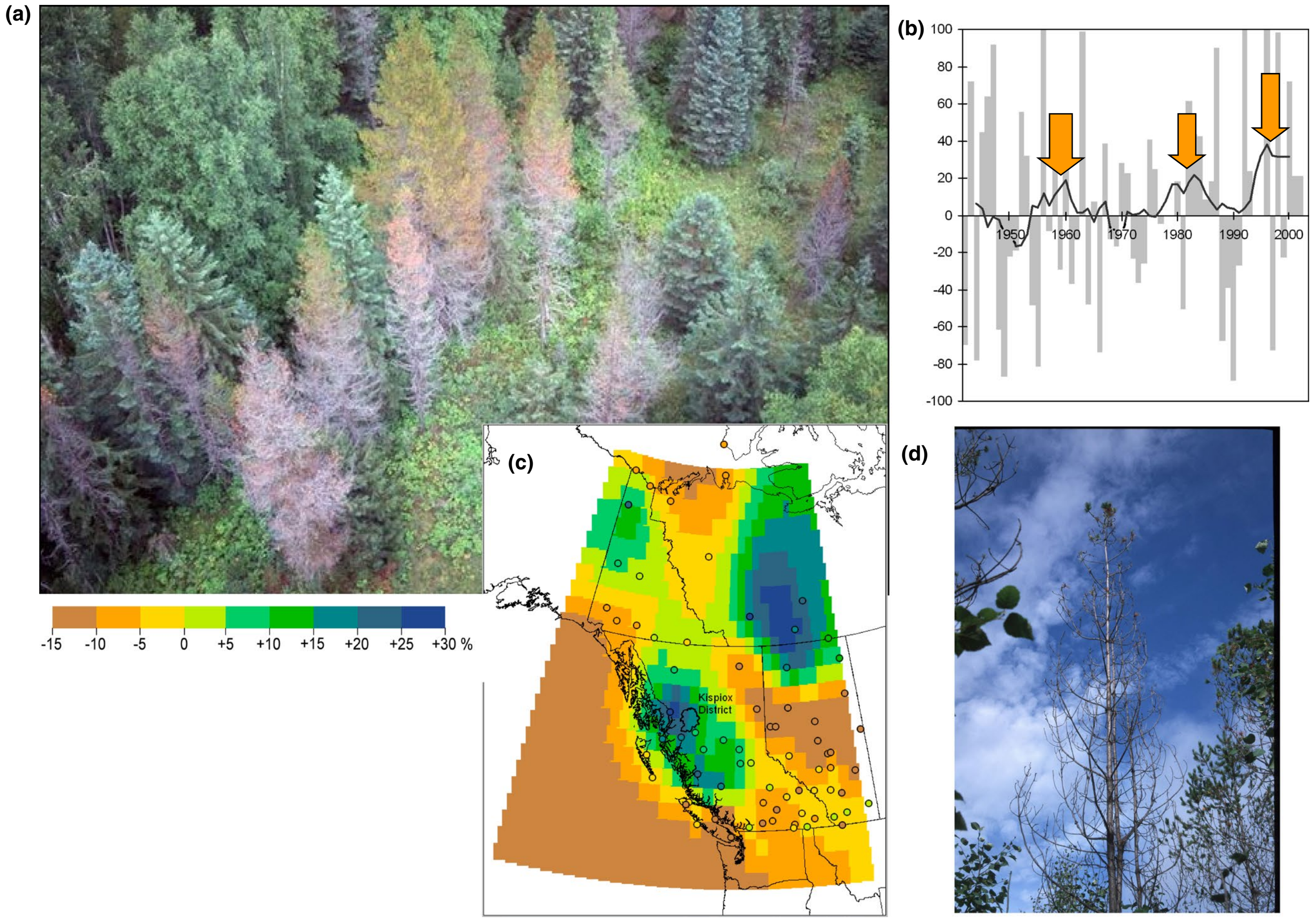

FIGURE 1 Dothistroma needle blight. (a) Photo of severe Dothistroma needle blight infestations killing mature lodgepole pine trees in the Kispiox District, British Columbia. (b) Deviation from 1961 to 1990 normal mean summer precipitation in nearby Smithers, BC (10-year moving average is added to visualize trends in noisy data) and timing of previous reports of Dothistroma outbreaks in the area based on Forest Insect and Disease Surveys (orange arrows) and Woods et al., 2005.(c) Changes in mean summer precipitation for British Columbia, Canada, displaying the percent increase in mean summer precipitation during the period of current Dothistroma epidemic initiation, 1998–2002, over the climate normal of 1961–1990. (d) Photo of young lodgepole pine severely impacted by Dothistroma needle blight

Summary: The Dothistroma epidemic in northwest British Columbia began in the late 1990s following a series of wet summers, 1997 being one of the wettest summers since the 1950s. Above-normal summer precipitation combined with warmer overnight minimum summer temperatures continued into the early 2000s, favouring this foliar pathogen in lodgepole pine stands throughout the region and beyond in a band across central British Columbia (Welsh et al., 2009). By 2001, in addition to cases of complete plantation failure in the most heavily impacted areas, mature lodgepole pine trees were observed succumbing to the foliar disease—an unprecedented phenomenon (Woods et al., 2005).

Climate–disease spatial. At the fine scale (individual tree and stand level), *Dothistroma* first attacks the lower portion of tree crowns. Most susceptible are trees located in depressions and cool air-ponding sites, such as stream draws. Species composition of the stand appears to have little influence on infection; *Dothistroma* attacks host pine trees whether they are a prevalent or minor stand component. At the middle spatial scale (landscape level), lower elevation stands in valley bottoms are the first to be attacked, but when favourable environmental conditions persist over broad areas, this spatial pattern can break down. The influence of soil and other stand or site attributes in this host/disease relationship is minor compared to the overwhelming influence of weather conditions, but thinning treatments have been shown to reduce disease severity in several areas including New Zealand and the UK, at least temporarily (Bulman et al., 2016). At the range-wide scale, Dothistroma needle blight has severely impacted lodgepole pine plantations and natural stands in wetter interior environments throughout BC. *Dothistroma* does not yet extend to the coldest northern limits of the range of lodgepole pine in the Yukon Territory although over time, with continued warming, this is likely to change. To the south and east of BC, recent evidence suggests an expansion of the range for this pathogen (Barnes et al., 2014). Dothistroma needle blight occurs throughout the range of the shore pine in Alaska.

Climate–disease temporal. This Dothistroma epidemic example covers the temporal spectrum from daily warm-rain weather events triggering short-term outbreaks, to climatic patterns of weather over multiple years dictating disease activity in association with weather drivers such as El Niño events. An increase in the frequency and magnitude of El Niño/Southern Oscillation (ENSO) events has been forecast (Cai et al., 2015) which could influence disease expression. The strong El Niño of 1996/97 is thought to have been a critical climate turning point for the current epidemic (Woods et al., 2016). Weather events consisting of five consecutive days of rain with average high temperatures above 18°C occurred only four times from 1950 to 2002 but occurred twice in 1997 (Woods, unpublished data). This combination of precipitation and temperature is near optimal for *Dothistroma* (Gadgil, 1967; Peterson, 1967). Past outbreaks of *Dothistroma* reported in the area were associated with increased summer precipitation, but these earlier, less severe outbreaks subsided once drier conditions returned (Woods et al., 2005). Based on dendrochronological evidence, it appears periodic outbreaks of the disease have been responsible for episodic growth reductions in pines in northwest British Columbia for several hundred years (Welsh et al., 2009). These same investigations have revealed the importance of relatively warm August minimum temperatures as a determining factor in past *Dothistroma* outbreaks (Welsh et al., 2014). The increase in summer overnight minimum temperatures is one of the clearest climatic trends in northern British Columbia, increasing by 7°C at the Fort St. James weather station from 1895 to 2019 (V. Foord, pers comm., June 2, 2020).

Climate-forest tree. The host tree species, lodgepole pine, is native to the area, present for at least the past 9000 years based on pollen evidence (Gottesfeld et al., 1991). However, forest management has increased its prevalence over the past four to five decades (Woods, 2003). The impacts of *Dothistroma* on lodgepole pine growth have not been quantified in BC but in New Zealand, van der Pas (1981) found volume growth of radiata pine (*Pinus radiata*) was reduced in proportion to the percent of infected crown. At the peak of the epidemic in northwest British Columbia, over 90% of pine plantations had suffered some degree of defoliation and over 7% of the surveyed area contained trees killed by *Dothistroma* (Woods et al., 2005).

Climate-pathogen. The incidence and severity of *Dothistroma* outbreaks are strongly controlled by precipitation and temperature and are thus highly sensitive to yearly differences in weather conditions (Peterson, 1973). Each year, the first splash-dispersed conidiospores of the fungus are released in the spring from persistent dead needles infected the previous year (Bradshaw, 2004). Conidiospores continue to be released and new infections initiated throughout the year, provided temperatures are above 5°C and moisture is present (Sinclair et al., 1987). The specific environmental conditions that favour disease development are well understood (Gadgil, 1967; Peterson, 1967). Higher rates of summer precipitation combined with increased overnight minimum temperatures and warm rain events are associated with past outbreaks of Dothistroma needle blight in the US Midwest (Peterson, 1973) and Chile (Gibson, 1974).

Secondary agents are not important drivers of increased damage or mortality associated with this disease.

Certainty of climate involvement: Confirmed.

Given the consistent alignment of documented pathogen outbreaks with past favourable weather events, there are few alternative explanations for the change in disease behaviour in British Columbia. Each aspect of the disease triangle (host, pathogen, and environment) suggests a changing climate remains the best explanation for the increased disease severity in this area, making this clearly a climate-pathogen disease.

An analysis of the genetic structure of *D. septosporum* in northwest British Columbia indicates that sexual reproduction is a regular part of its life cycle, contributing to high levels of genetic diversity in the pathogen population (Dale et al., 2011). Findings from this work suggest the fungus has likely been present in the ecosystem for a considerable time. There is no evidence of a recent introduction of a new virulent strain of the pathogen that could serve as an alternate hypothesis for the cause of these outbreaks. Recent research has raised concern that tree breeding programs and material transfers of planting stock farther east in the province could increase the risk of new disease epidemics (Capron et al., 2020).

Management implications. Lodgepole pine in northwest British Columbia has shifted from being considered a favoured species, planted extensively, to a major restoration liability (Woods et al., 2005). Forests managers in BC would benefit from diversifying managed stands to mitigate previously unexpected negative effects of climate change on forest productivity. Growth forecasts need to be adjusted to account for increased lodgepole pine volume losses due to *Dothistroma*.

Information gaps/needed research. There remains considerable uncertainty as to how climate change will affect precipitation patterns in BC and elsewhere in the range of susceptible pines. Precipitation forecasting is difficult. Extreme rain events and seasonal extremes, rather than trends, will drive disease expression. In 2018 a severe, hot, drought throughout BC led to the worst wildfire season in the history of the province; two years later, summer precipitation in northwest British Columbia was the highest in the past 70+ years. Given the importance of environmental factors in the behaviour of this pathogen, continued monitoring of forest conditions is essential.

2.2 | Swiss needle cast in the Pacific Northwest

Disease: Swiss needle cast (SNC) (Figure 2a–c).

Forest tree: Douglas-fir, *Pseudotsuga menziesii*.

Type of climate effect: Type 1, climate-pathogen disease.

Pathogen: *Nothophaeocryptopus gaeumannii* (T. Rohde) Videira, C. Nakash., U. Braun & Crous.

Climate hypothesis: In the Pacific Northwest (PNW), two climatic conditions are associated with increased Swiss needle cast (SNC) disease severity: high humidity in spring/early summer, and warm winter temperatures. Increased mean winter temperatures, evident since the 1980s, are driving disease outbreaks; warming speeds up the colonization within the needle by the fungus which appears to increase earlier formation of the stomatal blocking-fruiting bodies on Douglas-fir needles, and stomatal blockage causes disease.

Summary: Swiss needle cast was first detected on Douglas-fir along the northern Oregon Coast in the 1980s and reached epidemic proportions by the 1990s (Shaw et al., 2011). Leaf wetness during the spring/early summer sporulation period and mild winter temperatures have been identified as the two climatic factors positively correlated with disease development, with the latter likely the key in coastal Oregon and Washington (Manter et al., 2005). Since the epidemic was first identified in the mid-1980s, the mean minimum daily winter temperature in the last decade has been consistently greater than the 1961–1990 normal (~+0.8°C, ClimateNA, Wang et al., 2016). *Nothophaeocryptopus gaeumannii*, the causal agent of SNC, incites disease through stomatal plugging of infected needles by fungal pseudothecia (Manter et al., 2000). This leads to carbon starvation and subsequent needle casting in the tree host, resulting in sparse crowns and reduced growth. Due to the centrality of Douglas-fir to wood production in the region, the economic impact of SNC is substantial.

Climate–disease spatial. At the fine scale within the epidemic area, SNC is most severe in the upper crown and least severe in the lower crown of individual trees (Hansen et al., 2000; Ritóková et al., 2020). This is due to leaf wetness levels sufficient for leaf colonization in the upper crown and warmer ambient temperatures due to higher sunlight exposure. Susceptibility of Douglas-fir foliage to fungal colonization is not affected by stand species composition or density, but tolerance to *N. gaeumannii* varies across individual trees (Wilhelmi et al., 2017). Stand age is influential, as trees in older stands (120–400 years) experience consistently lower disease severity than nearby younger (20–30 years) plantation trees (Lan et al., 2019).

At the mid-scale, SNC disease severity varies across landscapes; plantations within a few miles of each other often have quite different disease severity levels. Distance from the coast is a significant factor for the Oregon epidemic, but disease severity distribution is complicated, likely due to topographic effects on weather patterns (Ritóková et al., 2020).

At the broad, geographic scale, SNC in western Oregon develops primarily within about 35 km of the Pacific Coast, with greater disease severity in the north and west. SNC is also present in southwest coastal Washington, and the disease has recently intensified in southwest coastal British Columbia (Montwé et al., 2021; SNCC, 2018, 2019). Despite a large increase in disease incidence over the last 25 years, the geographic bounds of the epidemic within Oregon have remained relatively unchanged (Shaw et al., 2021), suggesting that climatic conditions are a limiting factor (Rosso & Hansen, 2003).

Climate–disease temporal. Mildrexler et al. (2019) showed that short-term climate trends were correlated with an increase in disease expression in Oregon from 2004 to 2014; the decade was consistently cool and wet in the Pacific coastal strip from May to July. Looking to the future, average annual precipitation is not predicted to change significantly in this area (USGCRP, 2017), so SNC will likely persist even if inland sites become drier. Tree-ring studies have been used to predict and understand relationships between disease expression and climatic conditions over time. Black et al. (2010) focused on trees near Tillamook, Oregon, where SNC impacts mature forests. The study found that Douglas-fir growth reductions began in the mid-1980s and intensified in the 1990s through to the present. Decreased tree growth was correlated with increased mean temperature from March to August. Lee et al. (2017) contend that anticipated climate change in Oregon will sustain SNC development throughout the region, and disease may increase at higher elevations due to the increases in temperature as long as sufficient needle wetness is maintained during the sporulation period.

Climate-forest tree. Genetic tolerance of Douglas-fir to *N. gaeumannii* is linked to the climatic conditions at the seed source; trees grown from seed sources from higher elevations and drier regions are more susceptible to SNC when grown in common garden studies (Wilhelmi et al., 2017). Douglas-fir is well adapted to the region along the western slope of the Oregon Coast Range within the *Tsuga heterophylla* (western hemlock) vegetation series (Franklin & Dyrness, 1973). However, the near-coastal environment is in the *Picea sitchensis* (Sitka spruce) vegetation series where the current SNC epidemic is believed to have initiated (Hansen et al., 2000) and where Douglas-fir was historically a minor component. Conversion of coastal stands of non-susceptible species (e.g., *T. heterophylla*, *P. sitchensis*, *Alnus rubra* (red alder)) to Douglas-fir and large-scale reforestation of the ~150,000 ha, mid-20th century Tillamook Burn

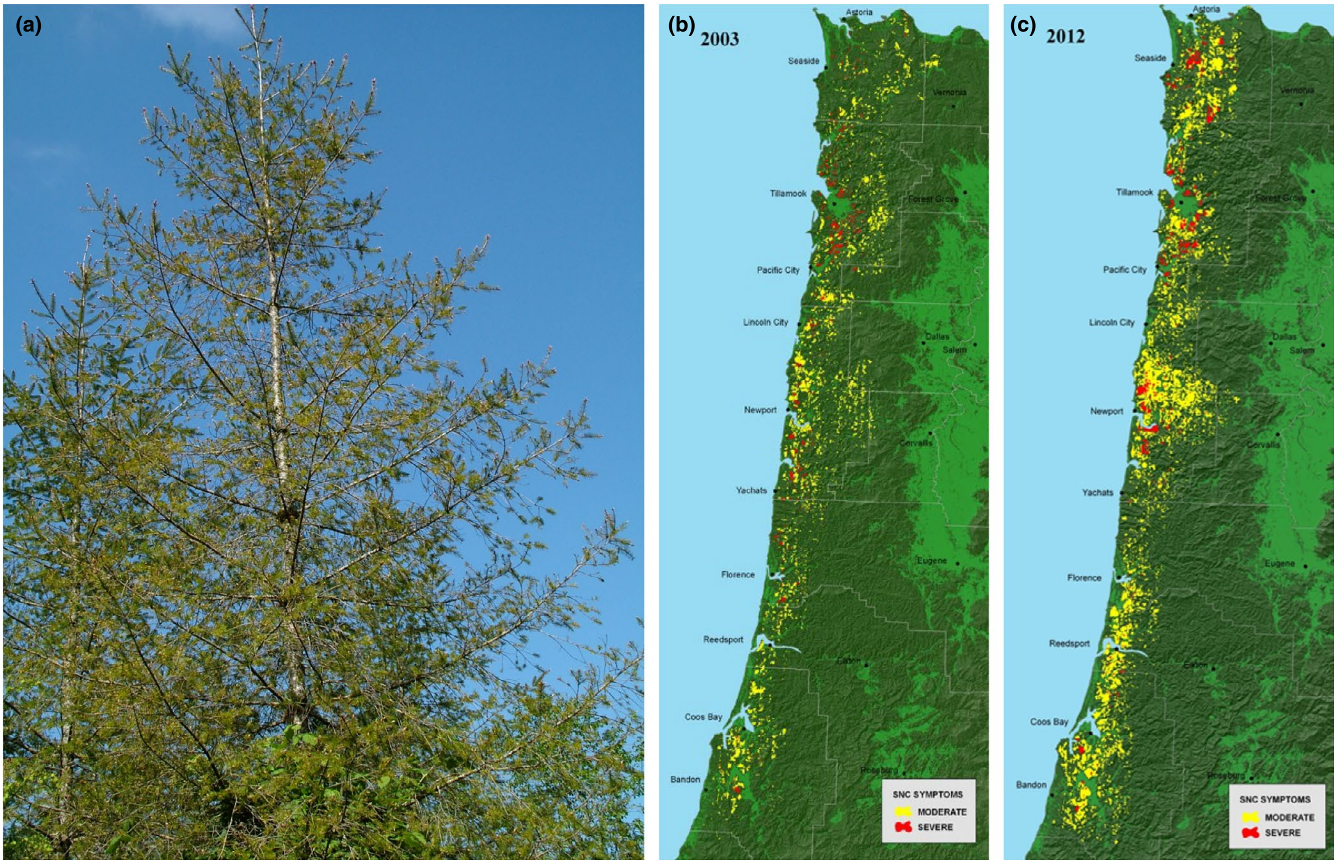

FIGURE 2 Swiss needle cast. (a) Douglas-fir infected with the Swiss needle cast pathogen near Hemlock, Oregon. Photo: Dave Shaw, 2006. (b, c) Maps from aerial detection survey for Swiss needle cast along the Oregon Coast in 2003 (108,369 ha mapped with symptoms) and 2012 (210,184 ha mapped with symptoms). This is the period of study used by Mildrexler et al. (2019) which showed that decade was cooler and moister in May–August. Figure from Oregon Department of Forestry

with seemingly inappropriate seed sources resulted in stands highly susceptible to this native pathogen.

Climate-pathogen. Leaf wetness during May-August promotes needle colonization and subsequent inoculum buildup, while mild fall and winter temperatures appear to facilitate early fruiting of pseudothecia on young needles due to faster colonization within the needle by the fungus (Manter et al., 2005).

Climate models for this disease have used Douglas-fir needle retention as a surrogate for disease severity and are based on precipitation during the spore dispersal period (May–August) and temperatures in winter (non-growing season). Higher precipitation during spore dispersal and warmer winter temperatures decrease needle retention and increase disease severity (Lee et al., 2017; Manter et al., 2005; Rosso & Hansen, 2003; Stone et al., 2008; Watt et al., 2010; Zhao et al., 2011, 2012). Models have had considerable variation in specific months used for climate variables, and this may be related to geographic (elevational) variation causing a shift in which climate variables are most influential (Lee et al., 2017).

Certainty of climate involvement: Confirmed.

The association of mean winter (non-growing season) temperature with disease development has been supported by several studies (Lee et al., 2017; Manter et al., 2005; Stone et al., 2008; Watt et al., 2010). NOAA records indicate that winter temperatures have increased within the symptomatic area during the epidemic (1985 to the present). Additionally, disease expression requires spore germination, which research has associated with spring/early summer leaf wetness (Manter et al., 2005). The amount of low cloud cover in the near coastal area has remained consistent since 1996 (Dye et al., 2020) so is not considered responsible for changes in disease incidence.

Management implications. Douglas-fir remains the most economically valuable timber resource in the PNW due to its abundance, normally short crop rotation interval, and high log prices. Nonetheless, the presence of stagnating or unproductive, diseased Douglas-fir stands has resulted in some liquidation of pre-merchantable stands and reforestation with non-susceptible but less valuable timber species.

Planting of alternative tree species (e.g., *T. heterophylla* and *Thuja plicata* (western redcedar)) is increasing and is recommended in areas prone to severe disease, with Douglas-fir included in planting mixes in increasing proportion as disease pressure decreases. Breeding for tolerance guides tree improvement efforts, with disease-tolerant stock recommended for areas with moderate to low disease levels.

Information gaps/needed research. The role of temperature at the stand and foliar scale needs more attention. SNC severity (expressed as amount of foliage retention) has been modelled across the landscape with interpolated climate variables (Zhao et al., 2011). Still, there remains a great deal of unexplained variation, probably due to the complex topography of the Oregon coastal mountains. Furthermore, forests along the southern Oregon Coast exhibit limited disease despite a climate conducive to SNC. It is thought that anomalies within the disease zone may be due to wind patterns that reduce spore loads or spring moisture levels. To better understand these factors, leaf wetness sensors and spore trapping will be employed in otherwise similar areas exhibiting contrasting disease levels.

2.3 | Hard pine rusts

Disease: Hard pine rusts (comandra, stalactiform and western gall rust) in western North America (Figure 3).

Forest tree: Lodgepole pine, *P. contorta* var *latifolia*; ponderosa pine, *Pinus ponderosa*; Jack pine, *Pinus banksiana*.

Type of climate effect: Type 1, climate-pathogen disease.

Pathogen: *Cronartium comandrae* Peck, *Cronartium coleosporioides* Arthur, *Cronartium harknessii* (JP Moore) E. Meinecke.

Climate hypothesis: Hard pine rust pathogens are very responsive to weather conditions with narrow environmental windows for portions of their life cycles. These narrow windows have resulted in 'wave years' where most infections are restricted by the timing of a few key climatic events. However, due to climate warming, increasing overnight minimum temperatures have eliminated a critical environmental barrier that had been restricting infection frequency. The result is an increased probability of rust infection each year, particularly in environments where cool overnight temperatures had hitherto reduced infection success.

Summary: A trend towards a greater frequency of years with more spring and summer precipitation and higher overnight minimum temperatures in late summer throughout interior BC has reduced the period between rust wave years (Woods, 2011) to as little as three years on some sites (Reich et al., 2015). This represents an apparent change in disease behaviour from that observed earlier in BC and farther south in the Rocky Mountain states where outbreaks of comandra blister rust had been considered rare (Krebill, 1968). Wave years of western gall rust caused by *C. harknessii* have also been relatively rare historically, occurring approximately once a decade (Peterson, 1971).

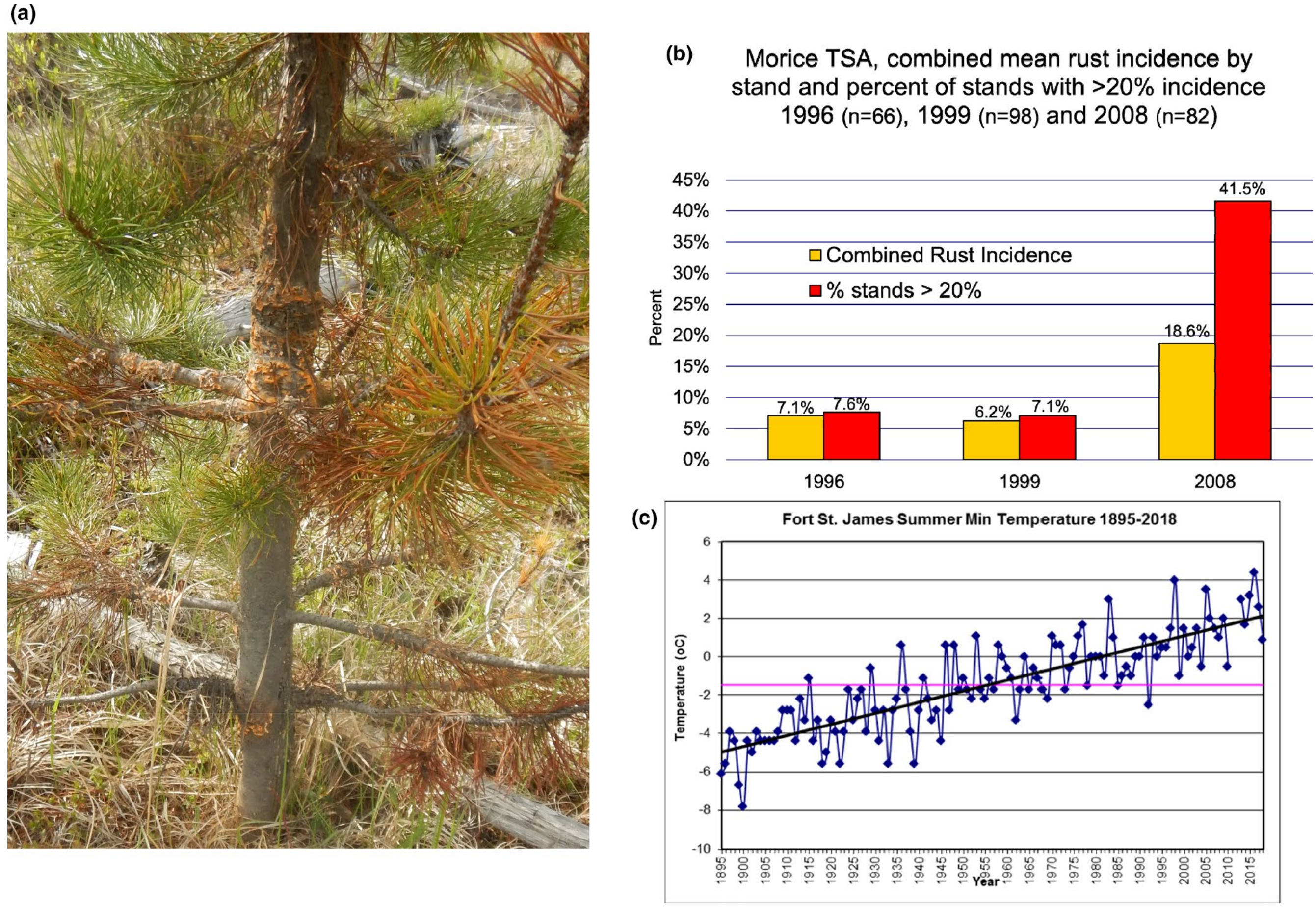

FIGURE 3 Hard pine rusts. (a) Multiple comandra blister rust infections on a young lodgepole pine in British Columbia. (b) Increase in landscape incidence of rust in the Morice timber supply Area (TSA) in central British Columbia. (c) Increase in overnight minimum summer temperatures in the region (Woods, 2011)

Climate–disease spatial. Although a consistent means of recording rust incidence and severity across western North America is lacking, the geographic range of reported increases in disease activity is broad, extending across BC (Heineman et al., 2010; Maclauchlan & Brooks, 2020; Woods et al., 2017) and the western United States (Jacobi et al., 2002). This broad-scale increase in rust incidence has occurred, while the climate across the range of lodgepole pine has warmed, particularly in terms of overnight minimum temperatures in spring and summer. Precipitation patterns across western North America both spatially and temporally are less predictable, so it is difficult to link a trend of increased hard pine rust incidence across broad areas to moisture patterns. The weakening of the jet-stream across North America contributes to this uncertainty (Francis & Vavrus, 2015).

At stand and landscape scales, hard pine rusts are most conspicuous in young stands where the majority of infections occur by age 10 (Blenis & Li, 2005). Stand density appears to have little influence on disease incidence, but lower density pine stands (<1000 sph) suffer greater timber productivity impacts, losing as much as 50% of projected volume at rotation in the most severely rust-affected, lower density stands (Woods et al., 2000). In the lodgepole pine dominated interior plateau of central BC (latitude 52–56°N), hard pine rust incidence is generally higher at lower elevation sites (<800 m). Farther south in the province both the landscape and the forest species composition are more varied and rust incidence generalizations for elevational bands are less clear (Heineman et al., 2010). As widespread warming and more extreme variation in precipitation occurs, prior generalizations about rust incidence levels at different elevational ranges and latitudes, (i.e., hazard ratings) are expected to break down.

Although the influence of stand structural attributes, including host age and the presence of alternate host plants for both comandra and stalactiform rusts, is critical, the influence of weather plays a large part in this host/pathogen relationship (Krebill, 1968; Peterson, 1971).

Climate–disease temporal. The incidence and severity of hard pine rusts are strongly controlled by precipitation and temperature and are thus highly sensitive to yearly differences in weather (Krebill, 1968; Peterson, 1971). A close relationship between comandra blister rust outbreaks and the timing of specific environmental conditions may occur over periods of just a few hours (Krebill, 1968). Wave years for western gall rust require cool moist conditions in late spring (van der Kamp, 1988). Wave years for other stem rusts, including white pine blister rust (*Cronartium ribicola*), comandra and stalactiform blister rust, require moderate temperatures and moist conditions in mid- to late summer (Hunt, 2004; Krebill, 1968; Van Arsdel et al., 1956) during the vulnerable basidiospore stage of the rust life cycle (Peterson, 1971). Optimum overnight minimum temperatures are also critical for wave year events (Reich et al., 2015). Long-term climatic trends at Fort St. James, BC, a weather station located near the centre of the latitudinal range of lodgepole pine in western North America (Wheeler & Critchfield, 1985), indicate a 7°C increase in summer overnight minimum temperatures over the period of 1895–2019 (V. Foord, pers comm., June 2, 2020). The result is an increase in landscape-level rust incidence spatially, as specific infection conditions are met in more locations. Temporally, there is a more even distribution of infection events rather than a concentration in less frequent wave years.

Climate-forest tree: The host tree species, lodgepole, Jack and ponderosa pine, have historically been well adapted to the climate of their respective ranges. Environmental stress on the host trees is, in general, not considered a factor in development of these rust diseases.

Climate-pathogen. The life cycle of most stem rusts has three distinct spore stages which have similar environmental requirements to those well documented for comandra rust (Krebill, 1968) and the introduced pathogen that causes white pine blister rust (*C. ribicola*) (Van Arsdel et al., 1956). The first two spore stages, aeciospores and urediniospores, have relatively wide environmental windows for germination with temperatures ranging from 3 to 28°C, but the most favourable conditions span 8–18°C, provided free water is available (Krebill, 1968). Aeciospores spread from infected pine to alternate hosts in late spring and urediniospores can further increase infection levels spreading among alternate host plants throughout the summer. The narrowest environmental window in the life cycle is when basidiospores are released from alternate host plants that will infect the conifer host, as they require >98% relative humidity, favourable temperatures of 13–23°C and low intensity light in order to germinate (Krebill, 1968). Krebill posits these conditions are only met when warm storm systems remain in areas for several consecutive days in August to early September, resulting in wave years of infection. Wave years for western gall rust require cool moist conditions in late spring during the period of shoot elongation (van der Kamp, 1988).

To date there is no evidence that the native hard pine rust pathogens have increased in virulence due to genetic changes.

Management implications. The extent of lodgepole pine plantations in the central interior landscape of BC has increased significantly since the 1980s. It is possible that the creation of plantations full of young susceptible age classes of trees within a landscape once dominated by mature timber could itself influence rust incidence.

The warmer, wetter conditions and their effect on forest pathogens in central BC are forcing forest managers to consider assisted migration of species such as Douglas-fir (*P. menziesii*) and western larch (*Larix occidentalis*) that are ecologically suitable to these new environmental conditions and immune to these ubiquitous pathogens. The increasingly variable weather conditions across western North American forests call for a greater emphasis on monitoring forest pathogens including hard pine rusts.

Certainty of climate involvement: Probable. A lack of detailed, historic records of disease incidence, and difficulties to precisely date infections, limit our ability to link weather patterns and past climatic conditions with disease expression.

Information gaps/needed research. One of the key information gaps is the translation of stand-level rust incidence in young stands to the volume impact at rotation. A consistent means of long-term monitoring of rust pathogens in operational managed stands coupled with on-site weather stations capable of hourly assessments would add valuable information.

2.4 | Hemlock dwarf mistletoe

Disease: Hemlock dwarf mistletoe (Figure 4a–c).

Forest tree: Western hemlock, *T. heterophylla*.

Type of climate effect: Type 1, climate-pathogen disease.

Pathogen: *Arceuthobium tsugense* (Rosend.) G.N. Jones.

Climate hypothesis: An aspect of the reproductive or dispersal biology of this dwarf mistletoe, likely either fruit and seed survival/maturation or over-winter seed retention in tree crowns, is favoured by a warmer climate with longer growing seasons, reduced snow or alternatively by non-lethal winter temperatures.

Summary: The elevational and north-western (geographic) range distributions of hemlock dwarf mistletoe relative to its primary host, western hemlock, suggests climate limitations on the disease. This is apparent to the north in Alaska where mistletoe brooms recorded in forest inventory plots show the extent of the disease. Interpretation of the plot data in the southern distribution of the tree and pathogen is complicated by the presence of multiple dwarf mistletoe species and numerous susceptible host tree species. Climate controls on pathogen distribution are suspected to be a limiting factor, but the mechanism has not been demonstrated. It is theorized that climate operates as a threshold to constrain distribution, but the pathogen is already well adapted to climate within its range, so further warming and reduced snow are not expected to produce greater disease severity in areas that are currently infested.

Climate–disease spatial. The main evidence for a climate control of hemlock dwarf mistletoe is the restriction of the pathogen and disease to a subset of the host tree range, which occurs from California to south-central Alaska. The mid- and broad-scale spatial distribution of hemlock dwarf mistletoe is limited by elevation and to the northwest range in the northern portion of its range in Alaska. Western hemlock is abundant to about 800 m elevation in Alaska at latitudes 54–59°N where hemlock dwarf mistletoe occurs (Caouette et al., 2016). Near sea level at that latitude, hemlock dwarf mistletoe infects about 20 percent of western hemlock trees, but the pathogen becomes far less common above 200 m and drops to about two percent infection at 400 m in elevation (Barrett et al., 2011). Climate modelling of the host tree and pathogen supports the hypothesis that geographic influences limit disease in Alaska but cannot confirm which aspect of climate is responsible for limiting disease (Barrett et al., 2012). For climatic or other unknown reasons such as the discontinuous presence of susceptible host trees, hemlock dwarf mistletoe does not occur in the continental interior populations of western hemlock in Idaho, Washington, Montana and British Columbia.

Using vegetation inventory plots to determine elevational limits of the disease is more challenging in the southern portion of the range (California through Washington) due to the presence of both multiple subspecies of the pathogen and several susceptible tree species. Here, the best evidence of climate influence on disease extent is from field observations. The mistletoe subspecies that affects western hemlock, *A. tsugense* subsp. *tsugense*, is reported from sea level to 1300 m in Oregon (Hawksworth & Weins, 1996), but susceptible hosts are also found at higher elevations. Observations of elevational limits on the other subspecies of dwarf mistletoe are also reported (Hawksworth & Weins, 1996; Mathiasen, 2021). Climate modelling for this dwarf mistletoe species has not been conducted for its southern distribution.

The occurrence of dwarf mistletoe on western hemlock at the finer spatial scale, within and between stands, is likely controlled more by disturbance history (Trummer et al., 1998), including fire and timber harvest, than by climate or soils. Dwarf mistletoe thrives in late-successional forests because gap-phase dynamics facilitate mistletoe seed dispersal (generally <10 m distance) (Robinson & Geils, 2006; Shaw & Hennon, 1991).

Climate–disease temporal. Dwarf mistletoes are chronic, slow-developing tree diseases. Individual hemlock dwarf mistletoe infections can survive for a century or more. The lack of annual and probably decadal fluctuation of disease complicates attempts to link the disease to recent and mid-term climate data. Relationships between climate and disease severity may be more discernable by examining long durations (i.e., decades), suggesting that bioclimatic niche modelling, based on the association of the pathogen distribution, may be useful. Using several climate scenarios, Barrett et al. (2012) projected a 374–757 percent increase in extent over a century in the potential climate space for hemlock dwarf mistletoe on western hemlock in Alaska; however, slow migration limited by pathogen dispersal will limit the actual extent of broad-scale spread.

Climate-forest tree. The primary host tree, western hemlock, appears well suited to current and future precipitation and warming conditions in northern portions of its range where the species is likely to extend its distribution (Barrett et al., 2012). Short-term droughts may increase dwarf mistletoe damage to western hemlock (Bell et al., 2020) and fire can eliminate both the host tree and disease (Shaw & Agne, 2017).

Climate-pathogen. The main climate effects that increase dwarf mistletoe intensity and range likely influence pathogen reproductive and dispersal biology. Short growing seasons or snow may explain the current climatic restrictions of disease. As these conditions are lifted by a warming climate, there are three likely scenarios for future upslope and north-westward expansion of the disease: (1) longer, warmer growing seasons allow fruit to mature and seeds to disperse before first frost in the fall; and (2) reduced snow due to warmer winters lessens sloughing snow that previously could remove overwintering seeds; (3) freezing damage to seeds no longer occurs. More seeds would persist in canopies to enable spring infection. The basis for the first hypothesis, freezing of mistletoe berries, has been observed in British Columbia (Baranyay & Smith, 1974). Expansion of range of this dwarf mistletoe would serve as a classic example of the lifting of climate restrictions through climate warming; yet, dwarf mistletoe may have a slow rate of migration to the newly suitable

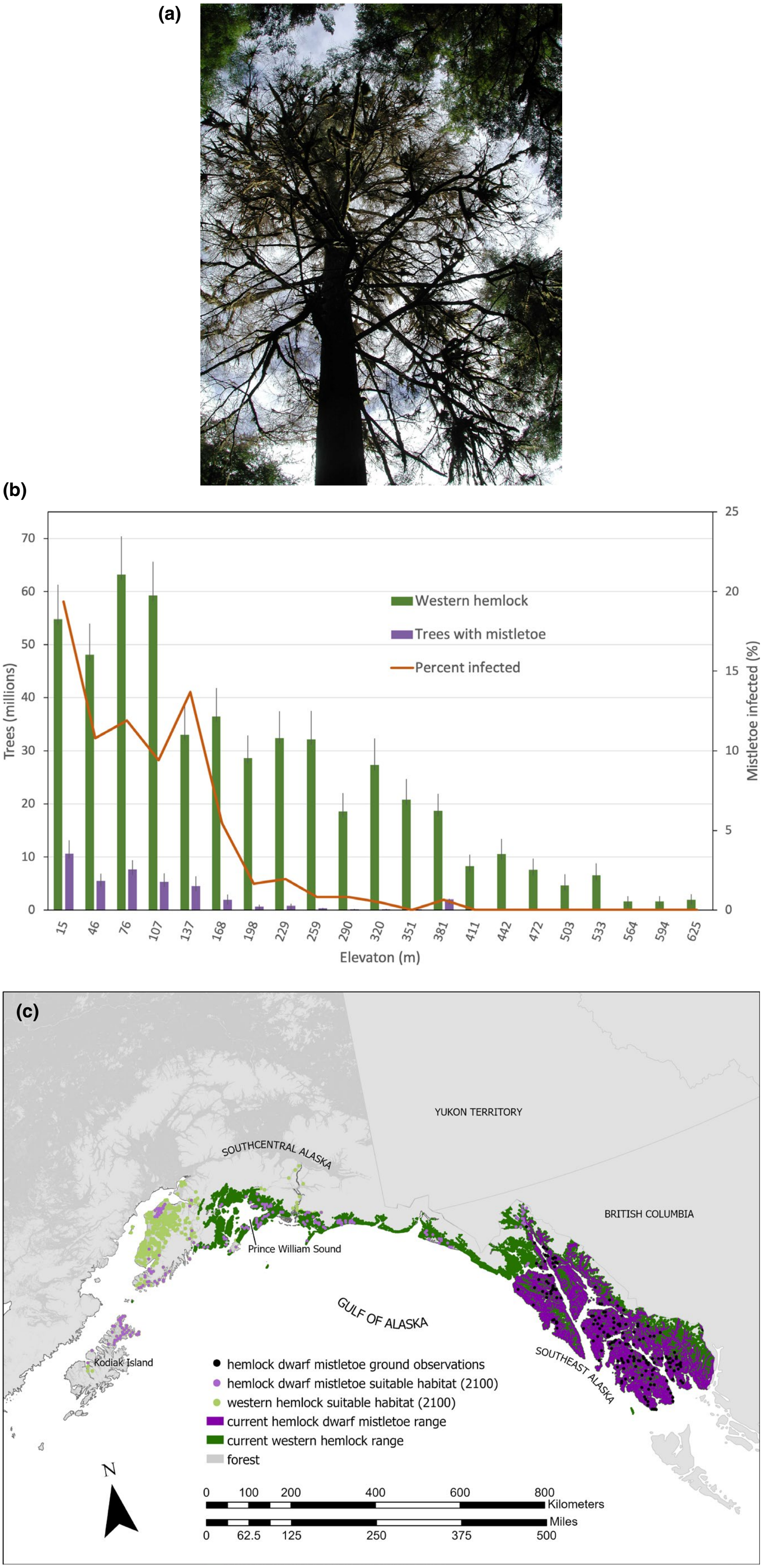

FIGURE 4 Hemlock dwarf mistletoe. (a) Dead mature western hemlock showing numerous hemlock dwarf mistletoe brooms used to detect the disease in forest surveys. Photo: US Forest Service. (b) Estimated numbers of western hemlock and trees with hemlock dwarf mistletoe and percentage of mistletoe-infected western hemlock trees (brown line) in 30 m (100 ft) elevation classes in southeast Alaska, latitude 54.5–59°N. Modified from Barrett et al. (2011). (c) The current ranges of western hemlock in Alaska where hemlock dwarf mistletoe is present (purple) and absent (dark green). Disease presence is based on Forest Inventory and Analysis plots and other ground observations. Projected potential 2100 ranges of the western hemlock habitat with (light purple) and without mistletoe infection (light purple) from bioclimate niche models (Barrett et al., 2012)

climatic habitat within the current and projected potential ranges for the tree (Hawksworth & Wiens, 1996). Analysis and modelling identified a range of environmental factors that currently restrict hemlock dwarf mistletoe in Alaska (growing degree-days, indirect and direct solar radiation, rainfall, snowfall, slope, and minimum temperatures (Barrett et al., 2012)), but because of covariance in these factors, they could not be used to distinguish the actual mechanism that limits the disease.

Management implications. There is a wealth of information on silvicultural treatments (e.g., thinning to foster healthy regeneration) to manage dwarf mistletoes (Hawksworth & Wiens, 1996). Climate change may not be a major factor in disease management decisions because of slow apparent response to changes in atmospheric conditions by the pathogen, and the relative simplicity of the management actions needed in areas where disease impacts are considered unacceptable. For resource managers interested in promoting the positive wildlife and ecosystem values of this mistletoe, increasing fires and drought in the southern portions of hemlock dwarf mistletoe's range due to climate change may be the biggest limit to this disease.

Certainty of climate involvement: Tentative. Climate involvement in hemlock dwarf mistletoe incidence, severity and potential range expansion is provisional. Certainty would be greater if the specific climate mechanisms that limit reproduction or dispersal of this dwarf mistletoe were firmly established through observation or experimentation. A similar scenario of the host extending higher in elevation than the pathogen has been described for lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.) on lodgepole pine (*P. contorta*) in the Rocky Mountains (Hawksworth, 1956; Hawksworth & Wiens, 1996) and western spruce dwarf mistletoe (*Arceuthobium microcarpum* (Engelm.) Hawksw. & Wiens) on Engelmann spruce (*Picea engelmannii*) (Acciavatti & Weiss, 1974; Mathiasen & Hawksworth, 1980).

Information gaps/needed research. Monitoring could be directed to the elevational and northwest limits of the pathogen to detect any migration of the disease consistent with model predictions (Barrett et al., 2012; Muir & Hennon, 2007). The complete absence of the disease in the interior continental western hemlock populations is not well understood (Smith & Wass, 1979) and may be related to geographic gaps in host tree distributions and details of parasite dispersal biology.

2.5 | Sudden aspen decline

Disease: Sudden aspen decline (Figure 5a,b).

Forest tree: Quaking aspen, *Populus tremuloides*.

Type of climate effect: Type 2b, climate-stress disease, important secondary agents.

Pathogen or other associated organisms: *Cytospora* spp., aspen bark beetle (*Trypophloeus populi*), bronze poplar borer (*Agrilus liragus*), and others.

Climate hypothesis: Severe, hot drought stresses aspen, which increases susceptibility to secondary agents. Some agents then become more aggressive due to their increased population density.

Summary: Sudden aspen decline (SAD) occurred following the turn-of-the-century drought in western North America, considered a climate-change type drought because it was hot as well as dry (Breshears et al., 2005). The drought peaked in 2002 and affected a great swath from western Mexico to the prairie provinces of Canada, with record extreme conditions. Branch dieback, crown thinning, and stem and root mortality of aspen occurred on a landscape scale.

Climate–disease spatial: At fine (stand) and middle spatial (landscape) scales, SAD occurs primarily in stands older than about 35 years. Open stands are more vulnerable than dense stands (Worrall et al., 2008, 2010), as the forest floor and stems are exposed to the drying effect of sun and wind. SAD is inversely related to elevation, low elevations having higher temperatures and lower precipitation. It also occurs preferentially on south and west aspects and on upper slope positions, all related to drought vulnerability. At

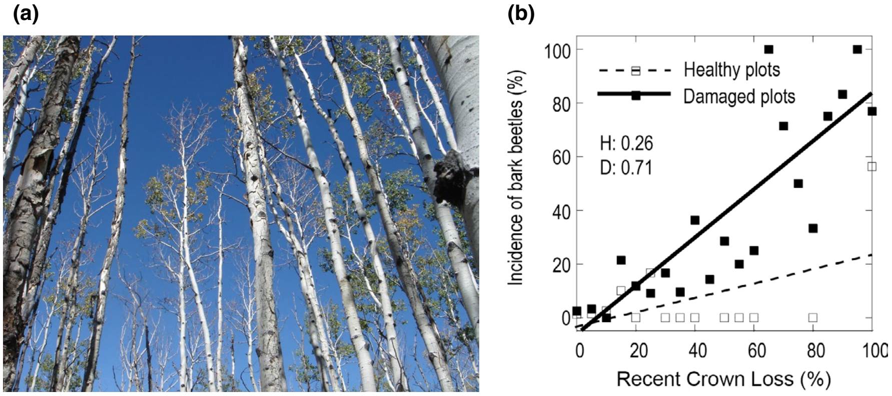

FIGURE 5 Sudden aspen decline. (a) Sudden aspen decline, Colorado, USA, in 2011. (b) Incidence of aspen bark beetles in trees grouped into crown-loss classes, in plots with SAD damage vs. healthy plots. Even in trees with high crown loss, few trees in healthy plots had beetles except for dead ones. In plots with damage, incidence of beetles increased strongly with crown loss. Because beetles were abundant in damaged plots, they could cause more damage for a given amount of stress (as indicated by crown loss) than in healthy plots. From Marchetti et al. (2011)

the range-wide scale, SAD occurred within the swath of the turn-of-the-century drought and where aspen was a dominant species, including the aspen parkland of Alberta and Saskatchewan, southern Wyoming, Colorado, Utah, northern Arizona, and New Mexico (Michaelian et al., 2010; Worrall et al., 2013). All these areas had warm, dry extremes during the drought. In Colorado, areas with SAD had greater moisture deficits in 2002 than did healthy areas (Worrall et al., 2010). A random forests bioclimate model showed that areas where sudden decline occurred are on the fringe of the realized climate niche for aspen and, consequently, are and have been the most vulnerable to such a drought (Rehfeldt et al., 2009).

Climate–disease temporal. The turn-of-the century drought was the most severe in the instrumental record, both locally and west-wide (Schwalm et al., 2012; Worrall et al., 2013). Schwalm et al. (2012) estimated that it was the most severe in over 800 years. It peaked in 2002 and, in most areas, ended by the following winter. What later became known as SAD was first detected in southwest Colorado in 2004 and spread and intensified over the following 4–5 years. However, mortality was already widespread and intense in the aspen parkland of Alberta when surveyed in 2004 (Michaelian et al., 2010). The bioclimate model mentioned showed that, from 1950 to 2006, 2002 had the most extreme deviations in variables most important in determining the distribution of aspen (Rehfeldt et al., 2009). These include an annual dryness index, the ratio of summer to annual precipitation, and an interaction of growing season precipitation with the summer–winter temperature differential.

Climate-forest tree. *Populus tremuloides* has the lowest drought tolerance of all the co-occurring tree species in the southern Rocky Mountains except for *Populus angustifolia*, which has equal tolerance (Niinemets & Valladares, 2006). The latter is strictly a riparian species that depends on water tables rather than upland soil moisture. The stems have a short lifespan, and there is a fair number of pathogens and insects that attack it, either killing stressed trees or killing or weakening vigorous trees.

Climate-pathogen (and other secondary agents). There is no evidence to suggest, and it seems unlikely, that drought directly favours the biotic agents that are important in SAD. Instead, the drought-stressed trees become more susceptible to the agents. In addition, there is evidence that when populations are increased by host stress and mortality, some agents become more aggressive and can then successfully attack healthy trees (Marchetti et al., 2011).

Certainty of climate involvement: Confirmed.

The factors above consistently support the turn-of-the-century drought being the inciting factor for SAD. The drought was considered a climate-change-type drought. The drought was a weather event, but bioclimate models indicated that sites where SAD occurred are climatically vulnerable to drought. SAD distribution was consistent with projections that link the bioclimate model to future climates. In three aspen bioclimate models with different spatial scales and sample data, the most important variables were all relevant to drought (Rehfeldt et al., 2009, 2015; Worrall et al., 2013).

Management implications. Timely coppice cutting, before about 50% of the stand is killed, can stimulate adequate regeneration (Ohms, 2003; Shepperd et al., 2015). Stands < 40 years old were more tolerant, so regeneration of aspen should increase resilience to drought and SAD. However, avoid management for aspen where bioclimate models indicate that future suitability is very low. Instead invest management in areas where suitability is moderate to good. Because of its light, airborne seeds, aspen is more likely than most species to colonize newly suitable climatic habitat, and this can be enhanced by appropriate disturbance.

Information gaps/needed research. Although soil traits should affect drought vulnerability, field assessment of soil pits in healthy and diseased plots revealed no significant soil traits (Worrall et al., 2010); this bears further study. Because the secondary agents are ubiquitous, it is unclear whether, or how commonly, severe drought in poor sites can kill trees directly, without intervention of pathogens and insects. It is also unknown why there is a stand age threshold for SAD of about 35–40 years. Determining why the disease began earlier and advanced more quickly in the aspen parkland than in the southern Rockies would also advance understanding of the disease.

2.6 | Western white pine pole blight

Disease: Western white pine pole blight.

Forest tree: Western white pine (*Pinus monticola*).

Type of climate effect: Type 2a, climate-physiological disease. Abiotic stress is the cause of mortality; secondary organisms also occur but are not considered significant.

Pathogens or other associated organisms: *Armillaria* spp., *Leptographium* sp., and *Dendroctonus ponderosae* (mountain pine beetle) occur on some trees in advanced stages of decline at some locations.

Climate hypothesis: Prolonged stress from severe, multi-year drought at sites with thin soils cause dominant and codominant western white pines in pole-stage stands to undergo slow, whole-tree decline leading to mortality. The disease results from interacting effects of extended or recurrent, severe drought, soils prone to water deficit, and physiological factors including root system and resource allocation characteristics of the tree species.

Summary: Western white pine pole blight (pole blight) is a historically important, but little-recognized climate-stress disease of 40- to 100-year-old western white pine characterized by reduced radial and leader growth, crown thinning, chlorosis, and long, narrow, resinous lesions at the bole cambium, resulting in crown deterioration and mortality (Leaphart, 1958a, 1958b; Leaphart & Gill, 1955; Molnar, 1955; Wellner, 1947) (Figure 6a). Pole blight was first reported circa 1929 in northern Idaho (Leaphart et al., 1957), many years into a severe, prolonged drought that extended from about 1915 to 1960 (Leaphart & Stage, 1971). Since then, pole blight has not been considered a significant disease. However, in 2017–2020, pole-sized white pines with characteristic symptoms were observed at two drought-prone locations in Idaho (P. J. Zambino, personal observations).

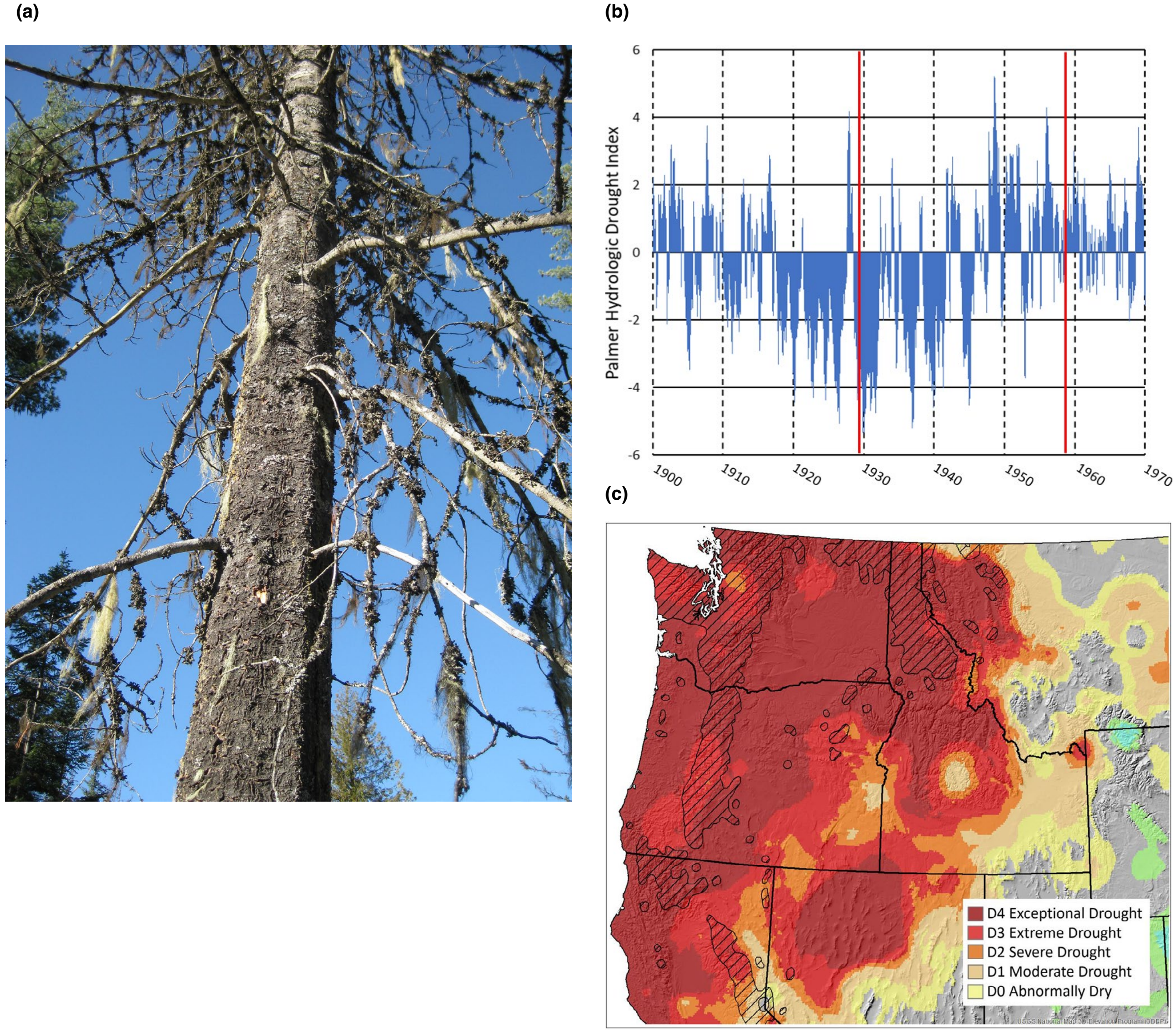

FIGURE 6 Pole blight of western white pine. (a) Recent symptoms in pole-aged trees in a stand that historically had pole blight, including slowed growth and thin crowns progressing to whole-tree mortality and multiple flat faces from long, linear, resinous lesions of the cambium typical of pole blight (Zambino, pers. obs. 2019). (b) Palmer Hydrologic Drought Index for Idaho Climate Division 1 ("Idaho Panhandle Climatological Division") from 1900 to 1970 (NOAA, 2021a). Vertical lines represent the first record of pole blight mortality (Leaphart et al., 1957) and the last surveyed increase in disease extent and severity (Graham, 1955, 1958). (c) Standardized Precipitation Index for the 9-month period ending November 1929 (NOAA, 2021b), the year when pole blight was first recorded (Wright & Graham, 1952). Cross-hatched areas indicate the geographic range of western white pine (Little, 1971)

Climate–disease spatial. Pole blight occurs during prolonged drought. In affected areas in both the panhandle and central mountains of Idaho in the first half of the 1900s, the Palmer Hydrologic Drought Index (PHDI) rarely departed from −1 to −4 for recurrent periods and occasionally reached PHDI-5 (Figure 6b) (NOAA, 2021a). Drought was widespread throughout the PNW (Figure 6c), with pole blight documented in most of the interior range of western white pine including northern Idaho, western Montana, eastern Washington (Graham, 1955, 1958; Wright & Graham, 1952) and interior southern British Columbia (Parker et al., 1950). Only a few affected locations were recorded outside the interior white pine region, including coastal British Columbia (Parker, 1951), where drought also occurred.

Differences in pole blight incidence and severity are discernable at fine, middle, and broad spatial scales. At the middle-to-broad spatial scale, aerial surveys displayed a patchwork of diseased and healthy, naturally regenerated, pole-sized western white pine stands (Wright & Graham, 1952). Differences in disease prevalence between stands were associated with the spatial distribution of soil types and other factors (Copeland & Leaphart, 1955; Leaphart, 1958a, 1958b). Areas with pole blight were characterized as having low soil moisture-holding capacity, less than 12.7 cm available water in the top 81.3 cm of soil (Copeland & Leaphart, 1955; Graham, 1959). At the fine spatial scale (within stands), the disease affected dominant and codominant trees but not suppressed trees (Leaphart, 1958a).

Climate–disease temporal. Pole blight was supported by a mid-scale, temporal, climatic event: a decades-long period of recurring droughts corresponding with Pacific Decadal Oscillation (PDO)-conditions that typically cause warmer and drier winter conditions in coastal and interior areas of the PNW (Newman et al., 2016). Onset and expansion of the disease occurred in the late 1920s–1950s, within the period considered by Leaphart and Stage (1971) as the most prolonged and severe drought in the Inland Northwest over the previous 280 years. The disease appeared several years into the drought and developed and intensified (Graham, 1955, 1958) until drought severity lessened. Some severely affected trees continued to die even after drought abated. Symptoms and mortality generally correlated with the severity and duration of the moisture deficit (Graham, 1958). Current and predicted increased drought severity in the upper reaches of the Missouri basin (Martin et al., 2020) and Inland Northwest (Gutzler & Robbins, 2011; Overpeck & Udall, 2020; Sheffield & Wood, 2008) could increase the threat of pole blight at susceptible locations.

Climate-forest tree. Western white pine is vulnerable to pole blight because of its rooting pattern in thin soils. Western white pine has a low rootlet to structural root ratio; pine rootlets support larger amounts of structural root than other species (Leaphart, 1958b). The species thrives in deep soils, two feet or more in depth. In stands on thin soils that developed pole blight, both symptomatic and asymptomatic western white pines were shown to have dramatically reduced numbers of fine roots and mycorrhizae, with the greatest reductions present on symptomatic trees (Gill et al., 1949). Western white pine is considered more drought intolerant than co-occurring species (Graham, 1990; Leaphart & Wicker, 1966; Minore, 1979); Douglas-fir and western redcedar (*T. plicata*) have total root length per soil volume and fine roots in upper soil layers that are typically many times that of western white pine (Leaphart & Grismer, 1974). In soils conducive to pole blight, these species do not show whole-tree mortality from drought stress.

Climate-pathogen. *Armillaria* and *Leptographium* root pathogens were frequently isolated from trees with pole blight at some sites (Gill et al., 1949; Leaphart et al., 1957; Leaphart & Gill, 1955). There are many unknowns as to how their behaviour in western white pine stands is affected by climatic conditions.

Management implications. In areas within the geographic range of western white pine where drought may be severe, of long duration, or recurrent, land managers should consider planting this species only on sites with deep soils, good water-holding capacity and adequate soil moisture recharge (Leaphart, 1958a). On naturally regenerating sites with less favourable soils, managers may consider retaining a mixture of canopy classes and including tree species with greater drought tolerance.

Certainty of climate involvement: Supported. There is little contemporary literature on pole blight, but research published in the 1950s–1970s demonstrated that drought is the principal factor for pole blight.

Information gaps/needed research. A predictive pole blight risk factor model could be constructed based on current understanding. Such a model would include the geographic distribution of white pine, soil types and age classes as predisposing factors, and potential for drought index extremes as a dynamic climate input factor. Also needed are investigations of root system development for pole-sized trees growing in multi-cohort stands (Jain et al., 2020) versus uniform stands and evaluations to determine if uneven management, with white pines developing in gaps of mature stands, would have less inherent stress and a reduced tendency to develop pole blight.

2.7 | Yellow-cedar decline

Disease: Yellow-cedar decline (Figure 7a–c).

Forest tree: Yellow-cedar, Alaska-cedar, *Callitropsis nootkatensis*.

Type of climate effect: Type 2a, climate-physiological disease.

Pathogen or other associated organisms: *Armillaria* spp., *Phloeosinus* sp. (bark beetles), others, but none are important as a cause of death.

Climate hypothesis: Yellow-cedar trees die from freeze injury when shallow fine roots are killed by temperatures <−5°C during repeated cold weather events on sites that lack protective insulating snowpack to mitigate the disease.

Summary: Research on yellow-cedar decline was initiated in the 1980s to explain the cause of long-term, widespread mortality of this tree species. After ruling out other possible causes, the role of climate in yellow-cedar decline was proposed (Hennon & Shaw, 1994), and research progressed by establishing associations of climate and disease (Hennon et al., 2012) including a range-wide analysis for yellow-cedar (Buma et al., 2017). Root freezing injury was replicated experimentally (Schaberg et al., 2008), and the hypothesis stated above is now generally accepted (Oakes et al., 2016).

Climate–disease spatial. The occurrence of yellow-cedar decline has been mapped by aerial survey in Alaska and British Columbia and placed into a range-wide context for this tree species (Buma et al., 2017). Mortality is centred on landscapes with a modelled mean temperature in the coldest month of −5 to 0°C (Buma, 2018). In Alaska, yellow-cedar decline consistently aligns with climate patterns where annual precipitation as snow is below 250 mm (Hennon et al., 2012). The relationship between this threshold snow level and mortality was observed at spatial scales ranging from fine (stand), watershed (D'Amore & Hennon, 2006) to regional and Alaska-wide (Hennon et al., 2016). In British Columbia, mortality and related climate factors are present at Haida Gwaii, indicating that periodic subfreezing cold temperatures can extend to the most ocean-moderated temperature (hypermaritime) areas to kill trees (Comeau et al., 2019). Soils interact with climate at the fine spatial scale, as water-saturated soils cause shallow soil-root profiles that promote the disease, whereas trees remain healthy where they are deeply rooted—even in areas without adequate snow protection (D'Amore & Hennon, 2006; Hennon et al., 1990). Open-canopy stands on

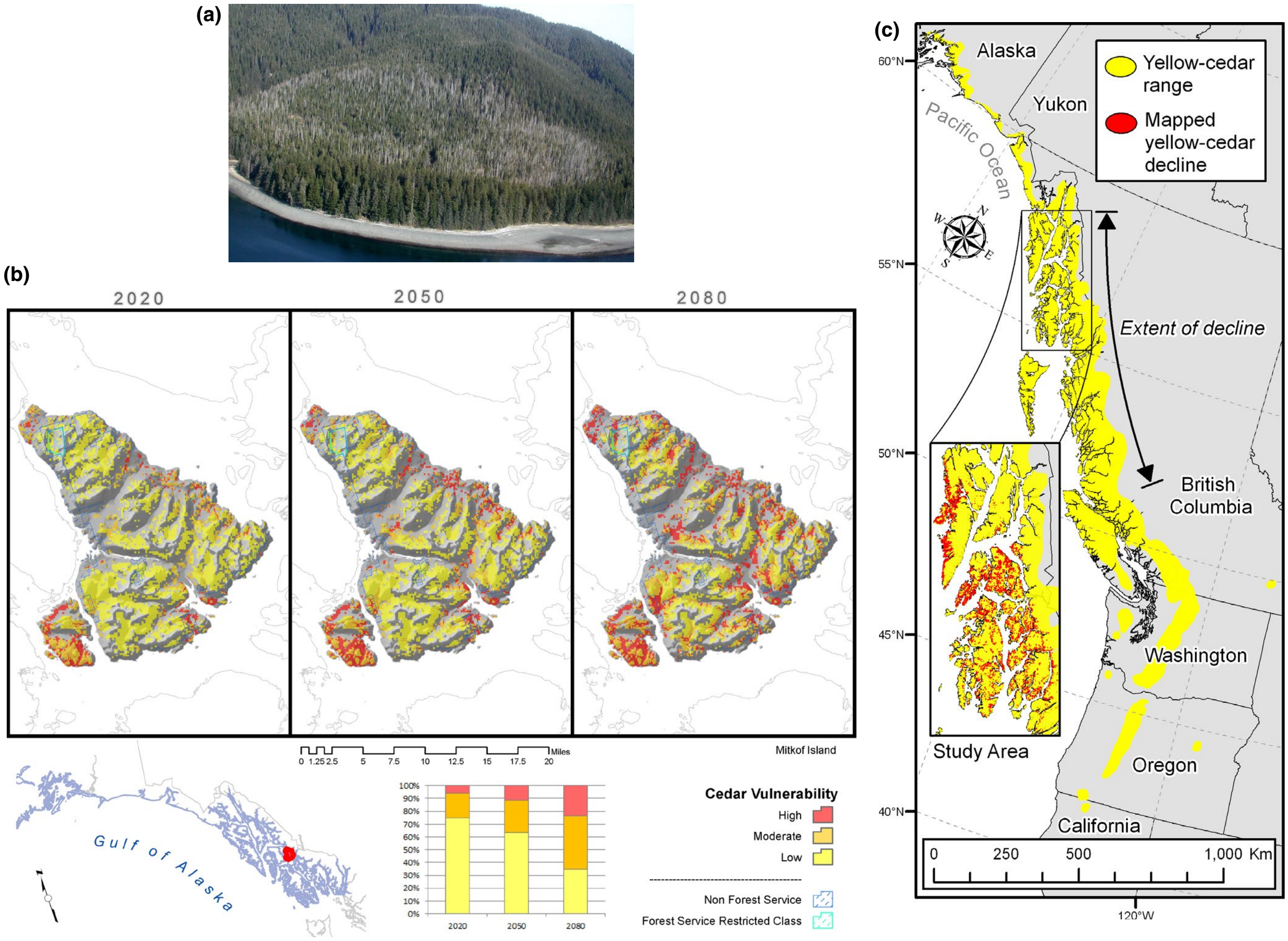

FIGURE 7 Yellow-cedar decline. (a) Patch of yellow-cedar decline at Poison Cove, Alaska, the site of some of the research on fine-scale aspects of decline such as microclimate, soils, and stand structure. Photo US Forest Service, 2004. (b) Risk of yellow-cedar decline at Mitkof Island, one of 33 mid-scale analysis zones in coastal Alaska, modelled at 30 m pixel resolution but displayed at 240 m. Modelled low (yellow), medium (orange) and high (red) risk of decline overlays the occurrence of yellow-cedar; risk categories are derived from equally weighted annual snow accumulation and drainage models. Future projections of snow accumulation from averages of general circulation models with conservative emission scenarios. From Hennon et al. (2016). (c) The range of yellow-cedar showing the latitudinal extent of decline and (inset) mapped yellow-cedar decline in Alaska. From Hennon et al. (2012); see Buma et al., 2017 for a complete mapped distribution of yellow-cedar decline including occurrence in British Columbia

wetter bog soils create conditions conducive to more extreme cold and fluctuating temperature microclimates that exacerbate the disease at the stand scale (Hennon et al., 2010).

Climate–disease temporal. Dating the year of snag creation allowed a reconstruction of tree mortality over time and established that the earliest period of broad-scale mortality coincided with the end of a natural climate cycle—the Little Ice Age—before 1900 (Hennon et al., 1990b). Weather station and cedar dendrochronological data showed that snow decreased throughout the twentieth century, but the frequency of damaging short-term, late-winter freeze events was maintained, so mortality was consistent with the climate hypothesis stated above (Beier et al., 2008). Accelerated mortality in the 1970s and 1980s was associated with a departure from typical climate decadal oscillations to indicate anthropogenic climate change (Hennon et al., 2012). Hourly monitoring of soil temperatures in forests revealed that lethal in situ soil temperatures (<−5°C) do not occur when snow is present, and when snow is absent, temperatures lethal to fine roots are confined to shallow soils during cold weather events (Hennon et al., 2010). Known risk factors for the decline disease (snow and drainage) were incorporated into a general risk model with climate projections to predict future spread of the disease (Hennon et al., 2016). Northerly spread of the disease, consistent with these models, has been confirmed by field observation (Oakes et al., 2014). A 'transitional mortality', where a climate window for tree vulnerability that moves across geographic space, explains this spatio-temporal movement of the disease appearing and abating through time at the range-wide scale (Buma, 2018).

Climate-forest tree. Cold tolerance hardening and dehardening of yellow-cedar are driven by weather conditions more than by photoperiod (Schaberg et al., 2005). Yellow-cedar fine roots are more vulnerable to freeze injury than co-existing tree species (Schaberg et al., 2011) which explains why yellow-cedar is the tree that is impacted. Hypothetical root freeze injury to trees has been replicated experimentally as has the mitigation-protection afforded by snow (Schaberg et al., 2008). Fine roots, which are the initial tissues affected in the disease (Hennon et al., 1990c), are killed by soil temperatures <−5°C as established by cold tolerance laboratory testing, whether roots are from seedlings or mature trees.

Climate-pathogen. A full examination of biotic factors including inoculations showed minimal involvement of fungi (Hennon et al., 1990c, 2016; Hennon & Shaw, 1997), indicating that this is primarily a tree stress disease. The *Phloeosinus* bark beetle could be favoured by warmer weather, but this insect is clearly of secondary importance to root freeze injury.

Management implications. Resource managers are now using a climate adaptation strategy to guide conservation and active management, including where to favour yellow-cedar by planting and thinning in climate and soil environments favourable to yellow-cedar but not to conditions driving mortality (Hennon et al., 2016).

Certainty of climate involvement: Confirmed.

The Fox (2020) causation criteria have been met, including consistency between climate and the disease, experimentation to replicate the cause and no plausible alternative hypothesis.

Information gaps/needed research. Quantifying the horizontal and vertical distribution of fine roots in mature trees has been a vexing problem but is needed to better understand shallow root freezing injury. This would help explain whether the 20–30 percent of yellow-cedar trees that typically survive in disease-affected stands (Hennon et al., 2012; Oakes et al., 2014) differ in their rooting habits or genetic traits. The most pressing information needs are now related to adapting management of yellow-cedar to climate change, including conservation monitoring of decline in young managed stands (FS-R10-FHP, 2020) and regeneration strategies in favourable climate and edaphic habitats.

3 | DISCUSSION

3.1 | Demonstrating climate-causality for tree diseases

The climate–disease framework of Hennon et al. (2020) facilitated the systematic evaluation of climate involvement in the tree disease examples presented. These examples from western North America include climate-pathogen diseases (climate modulates disease by directly influencing a pathogen, Type 1) and both types of climate-stress diseases (climate directly influences host trees to alter disease, with or without substantive involvement of secondary pathogens and insects, Types 2a and 2b). Example diseases of conifers and hardwoods, in both coastal and continental environments, were affected by climate; all are suitable for this climate causality framework but with varying levels of certainty. Disease increases and decreases were linked to key meteorological conditions at different times of year.

In the examples where climate modulates disease by its direct influence on the pathogen (Type 1), the causal agent was already known, but, initially, the reason for altered disease expression was not. Specific weather conditions (or climate trends of repeated weather patterns) enhanced various aspects of pathogen reproductive and infection biologies in the Dothistroma needle blight, Swiss needle cast and hard pine rust pathosystems. Weather conditions can alter fungal biology and thereby change the impact on the host from parasitic or endophytic, causing no apparent symptoms, to pathogenic, as occurs in Swiss needle cast in the PNW.

The example of hemlock dwarf mistletoe differs from the other examples in that there is no evidence of varying disease intensity within the pathogen's current range to compare with weather records, but range extensions are expected as climatic barriers are lifted by warming. Range expansions are likely to develop gradually, as spread rates are limited by the ability of the pathogen to disperse into new environments.

The other type of climatic influence on tree disease is by direct physiological stress or injury to the trees. In our three ‘Type 2, climate-stress disease’ examples, the cause of disease was not initially known. Preliminary investigations examined and eventually deduced that insects or pathogens were not the primary cause. Climate factors were then considered as part of the cause by exploring the relationship between disease expression and weather records. The onset, duration and remission of sudden aspen decline and pole blight of western white pine were found to be closely associated with droughts. The cause of yellow-cedar decline was determined to have two climate factors: short-term cold temperatures that kill fine roots and, as an essential predisposing condition, reduced insulating snowpack that historically protected against injury. For this long-lived species, sites which were previously adequately protected by snow have become unsuitable with the loss of snowpack.

Opportunistic secondary organisms are often present on dying trees, regardless of the primary cause of death. It is a challenge to distinguish between the Type 2a and 2b diseases; that is, do weather conditions stress the tree sufficiently for direct mortality (e.g., western white pine pole blight and yellow-cedar decline)? Or, do secondary insects or pathogens kill stressed trees that otherwise might recover (e.g., sudden aspen decline)? This distinction requires focused observation, knowledge of the behaviour of the secondary agents following other kinds of stress, and possibly experimentation with all three factors (climatic conditions, tree species, secondary organisms) to determine individual and combined effects. For instance, a shoot blight fungus *Diplodia sapinea*, (formerly *Sphaeropsis sapinea*)—not one of our examples—was found to occur as a latent organism until its host, red pine (*Pinus resinosa*), experienced water stress (Stanosz et al., 2001). When trees are under stress, endophytic fungi, such as members of the Botryosphaeriaceae, have been implicated in mortality of numerous woody hosts worldwide (Slippers & Wingfield, 2007). During early stages of mortality investigations, or in response to intense drought or other stressors, the large number of secondary and saprophytic agents recovered, possibly from multiple declining tree species, can complicate causality determinations.

It is also conceivable that climate factors may influence both the host tree and the primary pathogen to alter disease expression, thereby blurring our distinction between Type 1 and 2 diseases. None of our seven disease examples followed this scenario. However, for many stress-related Cytospora cankers, warming could increase the rate of growth and sporulation and extend the active season of the pathogen, while also increasing moisture stress of the host tree due to warmer conditions and extended growing season (Bloomberg, 1962; Butin, 1955). Similar dual effects of climate influence on the host and pathogen could be anticipated for many stress-related diseases (e.g. some Armillaria root diseases (Sturrock et al., 2011; Wargo & Harrington, 1991), sooty-bark disease of maple (*Cryptostroma corticale*, Ogris et al., 2021), pitch canker (*Fusarium circinatum*, Elvira-Recuenco et al., 2021; Swett et al., 2016), Hypoxylon canker of poplar, and bacterial leaf scorch, caused by *Xylella fastidiosa*. For insects, bark beetles are known to increase their populations and related damage during the combination of warm conditions that enhance overwintering success (in some cases, number of generations per year) and periods of increased vulnerability of trees facilitated by drought or other stress (Bentz et al., 2010). Also, changes in weather could affect tree and pathogen phenology differentially to alter disease infection or expression. Disease incidence may be reduced as the tree and pathogen react to different environmental cues, and the timing of pathogen sporulation and infection becomes unlinked to critical stages in host tree development.

3.2 | Predisposing factors and tree genetics

Predisposing site and stand factors, such as soil characteristics: texture, depth and saturation; location factors: elevation and aspect; and stand variables: structure, density, age and species composition, are considered in the climate–disease framework because of their effects on tree vulnerability to disease and microclimate. These factors have not yet been found to be the most significant factors in development of the Type 1 diseases (climate-pathogen) we evaluated; however, thinning treatments can reduce disease severity for Dothistroma (Bulman et al., 2016) and altering stand structure affects the response of Swiss needle cast to short-term directional climate changes (Mildrexler et al., 2019). For Type 2 (climate-stress) diseases, stand conditions are considered very important in the development of pole blight of western white pine, where a particular size-age class is vulnerable, and in yellow-cedar decline, where canopy cover alters microclimate to create conditions conducive to abiotic injury. Soil properties are also critical in the expression of both of these forest declines; soil moisture-holding capacity and limits on rooting depth (for pine and cedar, respectively) distinguished between areas with diseased versus healthy trees. The occurrence of sudden aspen decline was not strongly linked to soil factors despite investigation, but elevation, aspect, slope position, basal area, and tree slenderness were related to damage (Worrall et al., 2008, 2010).

Our approach has been to primarily consider climatic conditions, or climate zones, for the distribution of each tree species to evaluate climate effects on disease, but individual tree characteristics also modify disease development in various ways. Genetic resistance to pathogens plays a role in climate-pathogen diseases (Sniezko & Koch, 2017). Genetic variation in drought responses, for populations or for individual trees (Moran et al., 2017), influences outbreak patterns of climate stress diseases. Natural variation associated with climate of seed source and disease tolerance has been demonstrated using provenance tests, for the Swiss needle cast example (Montwé et al., 2021; Wilhelmi et al., 2017) and for other tree diseases (e.gMcDermott & Robinson, 1989; Morton & Zhu, 1986; Steiner et al., 2019). These data may be coupled with climate change models to identify populations at risk of climate maladaptation and associated disease (Rehfeldt, 2004; Rehfeldt et al., 1999; Rehfeldt et al., 2014; St. Clair & Howe, 2007).

3.3 | Links to climate may be difficult to document for some diseases

Some diseases are challenging to monitor through time, and therefore, it becomes problematic to make any links to climatic conditions. Changes in perennial, chronic diseases of roots and stems (including decays) are particularly difficult to monitor because they are hidden either below ground or within the tree bole. These locations are also somewhat buffered from short-term weather events due to the insulating properties of those niches.

For stem decays, such as those caused by *Phellinus tremulae*, *Porodaedalea pini* and *Ganoderma applanatum*, it is difficult to accurately measure the volume of decayed wood; however, both direct and indirect estimation methods have been developed (Soge et al., 2021). Stem decay rates vary depending on factors that include wood moisture content and temperature (Boddy, 2001), and growth temperature optima have been measured (Humphrey & Siggers, 1933). Assuming that mycelial growth rate is correlated with decay rate in live trees, it is logical to conclude that greater decay volume will develop in many cool temperate and boreal forests if growth temperature optima are met over extended periods of time, provided adequate moisture is also present. Excessive heat could reduce vegetative growth of stem decay fungi in some warmer pathosystems. Carbon dioxide (CO_2) and methane (CH_4) are released to the atmosphere during the decay process (Hietala et al., 2015); therefore, it is predicted that increased stem decay rates will lead to increased rates of emission of these greenhouse gases. The weather triggers for spore production are complex (Kadowaki et al., 2010). Additionally, under changing climatic conditions the rate and distribution of establishment for new infections could also be altered. All of these effects are likely to be related to climate affecting the fungus (Type 1) rather than by initiating tree stress (Type 2).

Likewise, variation in root disease activity, such as caused by *Armillaria* spp., is notoriously difficult to monitor through time. Challenges include attributing death to *Armillaria* species, which may act as a primary pathogen or as a secondary agent that infects hosts where immunity is impaired by drought, temperature extremes, other pathogens, insect or reductions in site quality (Goheen & Otrosina, 1998; Wargo & Harrington, 1991). These factors contribute to inoculum quantity and quality, which needs to be assessed to account for changes in disease behavior. However, Murray and Leslie (2021) showed that levels of Armillaria root disease intensity are associated with drought events where the disease is present in a plantation in southern British Columbia (i.e., Type 2 climate–disease). Some root diseases such as laminated root rot caused by *Coniferiporia weirii* (formerly *Phellinus weirii*) are not associated with host stress and any climate effects on disease behavior may be related to vegetative growth and sporulation similar to stem decay fungi (i.e., Type 1 climate–disease).

3.4 | Research and monitoring needs

Most of the information that contributed to our understanding of climate-tree disease interactions for the examples described was derived from a combination of monitoring surveys and research. To evaluate climate associations with tree disease expression, widely available weather data can be extrapolated with models at all spatial scales and may be used for back-casting (e.g., Welsh et al., 2009), retrospective studies (e.g., Woods et al., 2005) as well as forecasting using general circulation models (e.g., Desprez-Loustau et al., 2007); Hennon et al., 2016).

Incomplete monitoring records of spatial and temporal information on forest diseases and other biotic disturbance agents continues to represent a critical gap in efforts to better understand climate-induced forest disturbances (McDowell et al., 2015). Disease-specific aerial surveys documented the extent of sudden aspen decline, yellow-cedar decline, and Swiss needle cast, all of which can be identified from the air without the need for labour-intensive ground-checking and laboratory confirmation. When conducted annually, these surveys provide useful data to compare disease response with contemporaneous weather records. Many of the more diffusely distributed diseases (i.e., those without a unique aerial signature), such as pine rusts, some root diseases and hemlock dwarf mistletoe, require ground-based monitoring methods to determine increases or decreases in disease. Data from most ground-based forest inventory plots are often not disease specific and not analysed to determine the cause of damage or mortality.

Research findings are necessary to build hypotheses on climate–disease interactions that can lead to more refined model projections. Without more detailed information derived from focused mechanistic research, we assume that climate affects pathogen reproductive biology but cannot build risk projection models with relevant weather-climate inputs to capture the timing of key events such as sporulation or infection. Physiological investigations brought clarity to the specific mechanistic roles of weather and climate in disease development in the three tree-stress disease examples. Both tree and fungal physiological data either did, or could, help identify specific weather-climate variables needed for more refined disease risk factor models (as discussed further in Section 3.6).

3.5 | Modelling of climate and disease

Various forest ecological modelling approaches, including physiological, biotic interaction, species distribution, ecological niche, bioclimate niche and others, are used to project future forest conditions. All incorporate climate variables as inputs, but each model type has a specific goal—not all are appropriate for forest diseases or particular situations, so they need to be applied cautiously. Relevant to our disease examples, Watt et al. (2009) demonstrated in a global model that climatic stresses that commonly limit the occurrence of Dothistroma needle blight are more likely to constrain the distribution of the host before they affect the fungus. However, in British Columbia, the pathogen has not yet reached the northern range of lodgepole pine, which has wide climatic suitability.

Bioclimatic niche models offer the potential to predict both the future distribution of forest trees and their associated damaging biotic agents. These models are based on assumptions that the distribution of an organism is synchronous with the current climate, and as climate changes, so will the potential distribution of the organism. Using bioclimate niche modelling, significant potential range expansions for both western hemlock and hemlock dwarf mistletoe in Alaska have been forecast (Barrett et al., 2012). However, lags in migration for both the tree and pathogen seem to have created a disconnect between current distributions and current climate, and it is unlikely that either the tree or the pathogen will disperse to keep pace with the predicted expanding suitable climate space. A bioclimatic niche model prediction accurately identified locations where sudden aspen decline occurred (Rehfeldt et al., 2009) but would not have predicted yellow-cedar decline, which occurs in the heart of the yellow-cedar range (Buma et al., 2017; Hennon et al., 2016). Desprez-Loustau et al. (2007) cautioned that the use of the bioclimate models for pathogens like rusts, with their complex life cycles involving multiple spore types with differing responses to climatic variables, could be problematic.

3.6 | Applying climate–disease concepts to forest management through climate–disease risk factor models

For some disease outbreaks tied to weather or climate drivers, forest management strategies may be designed by using the type of information presented in the examples to develop climate–disease risk factor models. A climate–disease risk factor model predicts risk of disease occurrence or severity in a particular location based on disease presence and condition of the forest tree, key climate variables and relevant predisposing factors. Such a model will be only as robust as the supporting tree species distribution, and additionally for Type 1 diseases, the quality of the pathogen or disease distribution layer.

The steps needed to develop and use a management strategy that incorporates climate influences on tree diseases include recognizing the occurrence of disease increase or decrease, distinguishing between biotic and abiotic causes, considering climate inputs in creating and refining models that predict disease incidence and/or severity, and employing the resulting climate–disease risk models in conservation and management strategies (Table 2).

Climate–disease risk factor models have been partially or fully developed for a few of the disease examples presented. For yellow-cedar decline, the risk factor model required two major factors, the climate variable 'snow' and the predisposing factor 'hydrology impacting rooting depth' (Hennon et al., 2016). The climate variable that causes actual injury to yellow-cedar, short-term freezing events, was not included in the model because these conditions occur anywhere in the broad areas where the disease occurs including hypermaritime environments (Comeau et al., 2019). Two other climate tree-stress diseases, sudden aspen decline and western white pine pole blight were shown to be drought-driven, so drought models essentially serve as disease risk factor models. Stand age and soil moisture-holding capacity were important risk factors that could be added as input variables for the white pine pole blight risk model. For most of our other examples, the necessary components for constructing similar models are known. For example, risk factor models could be constructed to predict future activity for Swiss needle cast (Lee et al., 2017; Manter et al., 2005; Stone et al., 2008) and pine rusts based on the specific weather variables described as essential for those diseases to develop. A climate–disease risk model has been created for Swiss needle cast on Douglas-fir in North America (Manter et al., 2005) and New Zealand (Watt et al., 2010) where neither host nor pathogen is native.

3.7 | Conclusions and implications for conservation and management

Based on the examples presented above, several generalizations for disease management emerged to adapt to changing climate conditions. First, favour the desired tree species through active management in climate zones where that species is well adapted, and the future climate–disease risk is expected to be low. Unfortunately, the magnitude of forecast climatic changes, high levels of uncertainty particularly with precipitation trends, and the increased frequency of extreme events limit the opportunities to apply this approach. A second broad theme is to favour a greater number of alternative tree species in areas of high climate–disease risk. But, the limitations of this approach are illuminated by the sudden aspen decline example: there is no replacement for the aesthetic and biodiversity values of quaking aspen and, similarly, no mitigation for the loss of keystone species in other ecosystems.

Our understanding and ability to manage tree diseases is often limited by a lack of recurring tree disease monitoring data to track annual disease expression with weather records. Focused research is also needed to determine specific temperature and precipitation influences and physiological limits of the host and pathogen. Collaboration between pathologists, physiologists, ecologists, entomologists and others is needed to understand the causes of tree mortality or decline. Greater integration of the impacts of climate-driven tree diseases on forest dynamics is needed to manage and sustain forests under threat from numerous disturbance agents and processes.

To solve problems, one needs to understand their causes. This is true for forest health as it is in human and animal illness (Rizzo et al., 2021). Expanding on our climate–disease framework (Hennon et al., 2020), we used information from previous studies to form and test hypotheses for the strength of climate involvement for seven forest

TABLE 2 Steps and methods to develop a disease risk factor model with climate inputs. The model can be used to create tree conservation and disease management strategies

Step	Method
1. Recognize change in disease incidence	Detection of increased or decreased disease by survey and monitoring
2. Preliminary assessment of biotic or abiotic cause	Evaluate diseased trees to find primary biotic agents or their absence
3. Initial associations of climate and disease	Develop information on spatial and temporal disease expression, compare with weather station data and spatial climate layers
4. Climate controls in disease confirmed	Analyse consistency of biotic or abiotic disease with climate conditions at several spatial and temporal scales; research mechanistic links; develop climate hypothesis consistent with knowledge of tree or pathogen physiology
5. Check for predisposing factors	Observe and measure relationship between relevant site factors or stand characteristics that influence climate effects and disease expression
6. Develop climate–disease risk factor model	Analyse key aspects of climate involvement in disease; develop models with climate inputs to explain past, current and future disease outbreaks
7. Refine and validate model	Continually improve and validate model with new monitoring and research information
8. Conservation and management implications	Use climate–disease risk factor model to develop conservation/management strategy

tree diseases. Using the framework structure, we found key climatic and related factors that control disease development. These variables can be incorporated into climate–disease risk factor models to project favourable and unfavourable locations for forest trees across landscapes under a changing climate. Incorporating these concepts into strategies for forest management can lessen the negative effects of tree diseases and improve adaptation to climate change.

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Review Article

Tree-ring history of Swiss needle cast impact on douglas-fir growth in Western Oregon: correlations with climatic variables

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Abstract

The fungal pathogen, *Phaeocryptopus gaeumannii,* occurs wherever Douglas-fir is found but disease damage is believed to be limited to the Coast Range and is of no concern outside the coastal fog zone (Shaw et al., 2011). However, knowledge remains limited on the history and spatial distribution of Swiss Needle Cast (SNC) impacts in the Pacific Northwest (PNW). We reconstructed the history of SNC impacts on mature Douglas-fir trees based on tree ringwidth chronologies from the west slope of the Coast Range to the high Cascades of Oregon. Our findings show that SNC impacts on growth occur wherever Douglas-fir is found in western Oregon and is not limited to the coastal fog zone. The spatiotemporal patterns of growth impact from SNC disease were synchronous across the region, displayed periodicities of 25-30 years, strongly correlated with winter and summer temperatures and summer precipitation, and matched the patterns of enriched cellulosic stable carbon isotope indicative of physiological stress. While winter and summer temperature and summer precipitation influenced pathogen dynamics at all sites, the primary climatic factor of these three limiting factors varied spatially by location, topography, and elevation. In the 20th century, SNC impacts at low- to mid-elevations were least severe during the warm phase of the Pacific Decadal Oscillation (PDO, 1924-1945) and most severe in 1984-1986, following the cool phase of the PDO (1945-1977). At high elevations on the west slope of the Cascade Mountains, SNC impacts were the greatest in the 1990s and 2000s, a period of warmer winter temperatures associated with climate change. Warmer winters will likely continue to increase SNC severity at higher elevations, north along the coast from northern Oregon to British Columbia, and inland where low winter temperatures currently limit growth of the pathogen. Surprisingly, tree-ring records of ancient Douglas-fir logs dated ~53K radioactive years B.P. from Eddyville, OR displayed 7.5- and 20-year periodicities of low growth, similar to those found in modern day coastal Douglas-fir tree-ring records which we interpret as being due to cyclic fluctuations in SNC severity. Our findings indicate that SNC has persisted for as long as its host, and as a result of changing climate, may become a significant forest health problem in areas of the PNW beyond the coastal fog zone.

Introduction

Swiss needle cast (SNC) is an economically important disease of most forms of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco, *P. menziesii* var. *glauca* [Beissn.] Franco, and *Pseudotsuga macrocarpa (Vasey) Mayr*) [1,2]. SNC is caused by the fungus *Phaeocryptopus gaeumannii* (Rhode) Petrak and occurs wherever its host is found, but historically has been of minor importance in western North American forests [1,3]. Epidemic outbreaks of SNC have been reported in coastal Oregon, Washington, and British Columbia and have steadily increased in severity since ~1984 [3-6]. Disease is most severe in forests and plantations on the western slopes of the Oregon Coast range within the coastal fog zone [3]. The affected area with visible SNC symptoms — chlorosis and premature needle loss — seen from annual aerial surveys of coastal Oregon have set new record highs each of the last six years [7]. Evidence suggests that SNC is affected by climate [8,9], alone or in combination with forestry practices of the (later) 20th century. Possible causes for the current increase in SNC severity include: climate warming and the introduction of Christmas tree plantations in the mid-1970s interacting with high soil nitrogen [10,11], or genetic changes in the pathogen [12]. There is mounting concern that SNC is increasing in severity, frequency and range in association with rising winter temperatures (and spring precipitation) and will continue to intensify over the 21st century due to climate change [13,14].

While the epidemiology of SNC and mechanisms of pathogenicity of *P. gaeumannii* on Douglas-fir have been well studied in young plantations, knowledge remains limited on the history and spatial distribution of SNC impacts on mature and older tree growth in the Pacific Northwest (PNW). *P. gaeumannii* is indigenous in western North America and has long believed to have been pervasive but innocuous in Douglas-fir forests prior to 1950 [1,15,16]. Increased severity since ~1950 is thought to be at least in part, climate mediated because the causal fungus is sensitive to small differences in temperature and moisture [5,8,9]. A recent dendrochronological study indicates that SNC has affected Douglas-fir growth at least back to 1592, which was the earliest of the available tree-ring records [17]. Furthermore, the spatiotemporal patterns of decreased annual ringwidth associated with SNC are synchronous across six coastal sites in Oregon representing a latitudinal transect at varying elevations, display periodicities of 25-30 years, and are strongly correlated with winter and summer temperatures and summer precipitation. SNC impacts as measured by tree ring width in coastal Oregon peaked in 1984-1986 —thought to be a period when the fungal population reached epidemic levels following several decades of environmental conditions favorable to growth and reproduction of *P. gaeumannii* [17].

Growth reduction of Douglas-fir due to SNC in the PNW is symptomatic in the Coast Range of Oregon and Washington, primarily, and is of limited concern outside this region [6]. There has been no reported evidence of SNC impacts on growth of inland Douglas-fir although symptoms are often noted in plantations in Northern Idaho and Western Montana [18]. A broad scale study involving 59 young Douglas-fir stands (10-23 years) found no growth reductions in the Oregon Cascades during a SNC outbreak between 2001 and 2006 [19]. To date, there have been no dendrochronological studies to reconstruct the history of SNC impacts on Douglas-fir growth in mature forest stands outside of the Coast Range of Oregon and Washington.

Here, we extend the dendrochronological findings of Lee et al. [17] to examine the history and spatial extent of the cyclical pattern of SNC outbreaks in association with the seasonal climate factors and address the three questions in the panel titled, “Where? Why there? Why now?”,” We conducted a dendrochronological study to test the following hypotheses: (1) *P. gaeumannii* is an ancient tree pathogen that affects Douglas-fir growth as far back as its earliest known existence in the Pacific Northwest; (2) SNC is ubiquitous and affects Douglas-fir growth across western Oregon from the Coast Range to the Cascade Range; (3) SNC is sensitive to winter and summer temperature, and summer precipitation, and so, spatial variability in SNC severity can be attributed to variations in site conditions and location. We developed new master chronologies of ancient and modern Douglas-fir ringwidth from the west slopes of the Coast Range to the west slopes of the Cascade Range of Oregon. We examined the spatial distribution of SNC impacts on mature Douglas-fir trees using time series intervention analysis of intra-annual tree ringwidth chronologies to reconstruct the history of SNC impacts by site.

The disease cycle

The key growth pattern in tree-ring records of coastal Douglas-fir is a sinusoidal cycle of anomalously low growth having a primary periodicity of ~25-30 years and a harmonic periodicity of ~ 4 years associated with SNC [17]. The cyclical patterns of SNC impact on Douglas-fir growth occur throughout the life of the tree and because of the effects synoptic seasonal weather patterns on fungal growth, are synchronous across coastal Oregon. We combined our dendrochronological findings with the epidemiology of SNC to develop a conceptual model of the disease cycle driven by needle retention and fungal fruiting body abundance which have routinely been used as indices of disease severity [3,8,11,16]. SNC reduces assimilation of carbon and tree diameter by stomatal occlusion and early needle abscission [3,8]. Consequently, yearly changes in SNC impacts depend upon inoculum abundance, ascospore germination, and pathogen colonization in association with climatic conditions which affect the proportion of stomata occluded and needle retention. Douglas-fir trees on the coast typically retain up to four years of needles but may only have current and 1-year-old foliage due to premature needle abscission in severely affected plantations [3,13,20]. In our conceptual model, the disease cycle begins when pathogen abundance is at epidemic levels, resulting in loss of 2-year-old and older needles and a significant reduction in stem growth (Figure 1). The pathogen population will be reduced due to premature needle abscission resulting in fewer infected needles and a reduction in inoculum. Peak SNC outbreaks reduce tree growth for several consecutive years because photosynthetic capacity is restored to normal only after all needle classes have formed [21]. A delay of several years between inoculation and growth of the fungus and tree growth reduction is expected because the pathogen infects only the newly emerged needles [9,22]. This lagged growth response to SNC is represented by a 4-year periodicity in disease impacts (Figure 1). The slow buildup of pathogen abundance from endemic to epidemic levels over several generations is represented by a 20-year

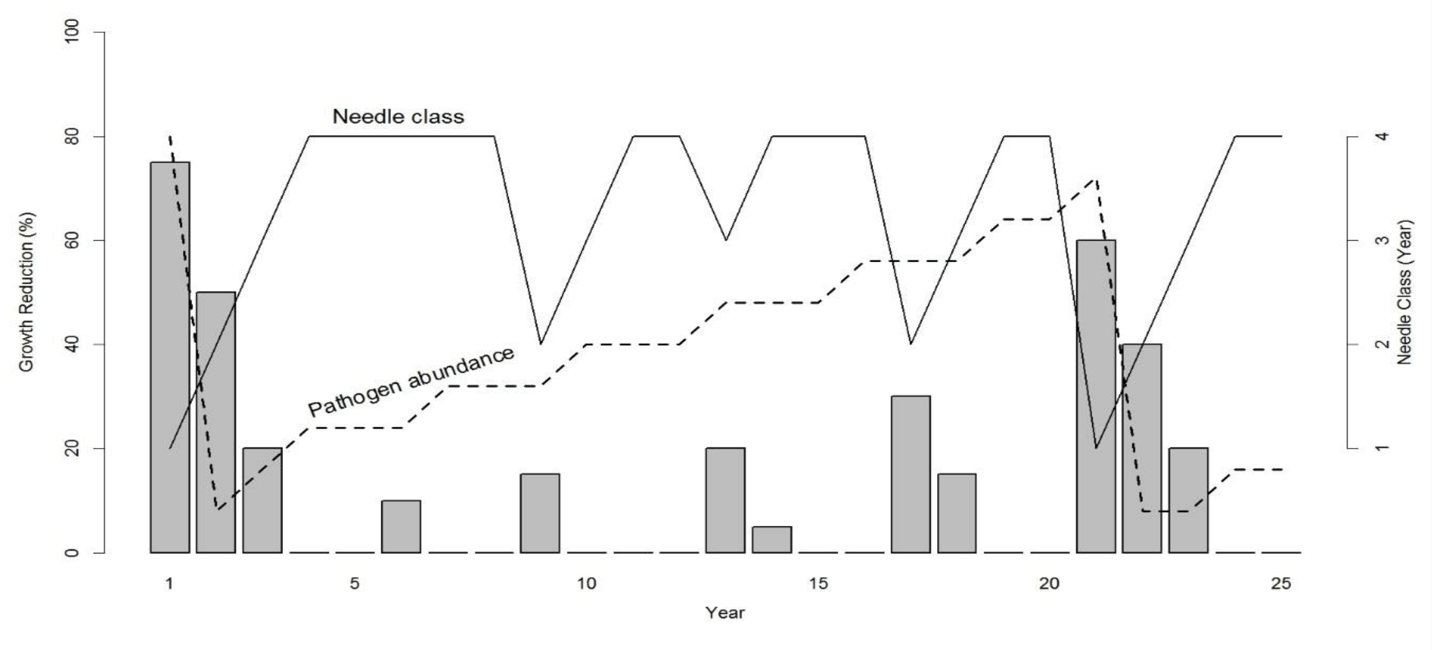

Figure 1: Conceptual model of Swiss needle cast (SNC) impact on tree growth in association with the abundance of Phaeocryptopus gaeumannii and number of needle classes retained *[17]*. The number of needle classes retained varies from one (when the tree is heavily infected) to four (least infected). Pathogen abundance increases from endemic (when two-year-old and older needles are abscised) to epidemic levels (when tree is heavily infected) over several decades. The disease cycle begins anew with a peak reduction in growth when pathogen abundance reaches epidemic levels and is then reset to endemic levels following the early abscission of two-year-old and older needles. Growth reductions display 4- and ~20-year periodicities because P. gaeumannii infects only the newly emerged needles at time of sporulation and has a four-year life cycle.

periodicity. The dominant periodicity of 20 years varies by site and is a low as 6 years at Tillamook where more favorable climatic conditions allow the fungus to develop faster [9,17]. Pseudothecia can be commonly found on 4 to7-year-old needles in the Cascade Range of Oregon and Washington, and on 1 to 2-year-old needles in some areas of the Coast Range where pathogen dynamics are enhanced by more favorable climatic conditions [9]. Pathogen abundance is not reset to endemic levels by abscission of 2-year-old and older needles in areas where disease is constantly severe as indicated by a <10-year disease cycle and the presence of pseudothecia on 1 to 2-year-old needles.

Epidemiology of SNC and climate relations

Three major phases of the infection cycle of *P. gaeumannii* are relevant to the climate-growth relation [8]: (1) the fungus reproduces only sexually and pseudothecia (i.e., fruiting bodies) develop in winter and can begin plugging stomata as early as December; (2) sporulation and initial infection of needles occur from May to July; and (3) needle colonization by internal hyphal growth occurs year round following initial infection (Figure 2). Wet needles in late spring and early summer are necessary for spore dispersal and initial infection via the stomata [9,23]. Mild winters, spring precipitation, and moderate summer temperatures at a coastal site on west slopes of the Coast Range are highly favorable conditions for *P. gaeumannii* (Figure 2A). While precipitation is steadily decreasing during sporulation in the summer, fog frequency is steadily increasing (Figure 2B). Needle wetness is maintained by coastal fog in late summer and is less a limiting factor of fungal development along the coast (Figure 3). SNC impacts on Douglas-fir growth are most severe along the coast where winter daily maximum temperatures are above 7 ºC [9], summer temperatures range between the temperature optima for germination (18 ºC) and growth (22 ºC) [23], and summer needle wetness is adequate for fungal colonization of needles.

Reconstruction of SNC impacts on douglas-fir growth in coastal Oregon

We analyzed tree-ring chronologies from six late-successional Douglas-fir stands in the western Oregon Coast Range using Time Series Intervention Analysis (TSIA) to address how climate relates to the impact of SNC on tree growth (Figure 4) [17]. Tree-ring chronologies of western hemlock (*Tsuga heterophylla*), a species not susceptible to the fungus *Phaeocryptopus gaeumannii*, and Douglas-fir at Soapgrass Mountain, a high Cascades site, were used as a climate proxy in the TSIA. We found that growth reductions associated with SNC dated back to the 1590s, the earliest record in our dendrochronological data (Figure 5). Growth reductions were synchronous across the six sites indicating that the disease severity was influenced by regional climatic conditions. SNC impact peaked in 1984-1986 at all six study sites, followed by unprecedented disease impacts of 100% in 1996 and 2004 at one site, while decreasing to previous levels at the other five sites. SNC impacts displayed cyclical patterns having periodicities of 6, 12, and 25-30 years which were coherent across the region and represented the disease cycle

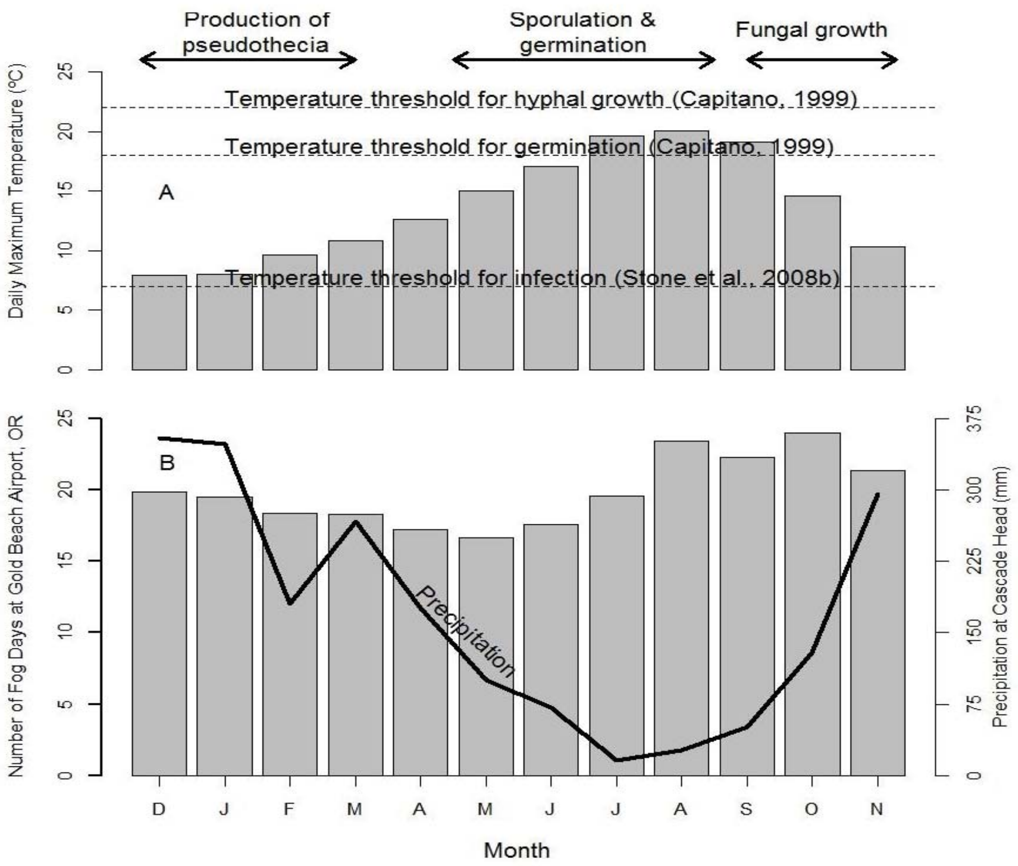

Figure 2: Seasonal pattern of (A) temperature, (B) precipitation and fog frequency at Cascade Head on west slopes of Coast Range of Oregon in relation to the three developmental stages of Phaeocryptopus gaeumannii. The climatic factors limiting pathogen dynamics are winter (November-February) and summer (June-July) temperatures and summer (June-July, primarily July) needle wetness.

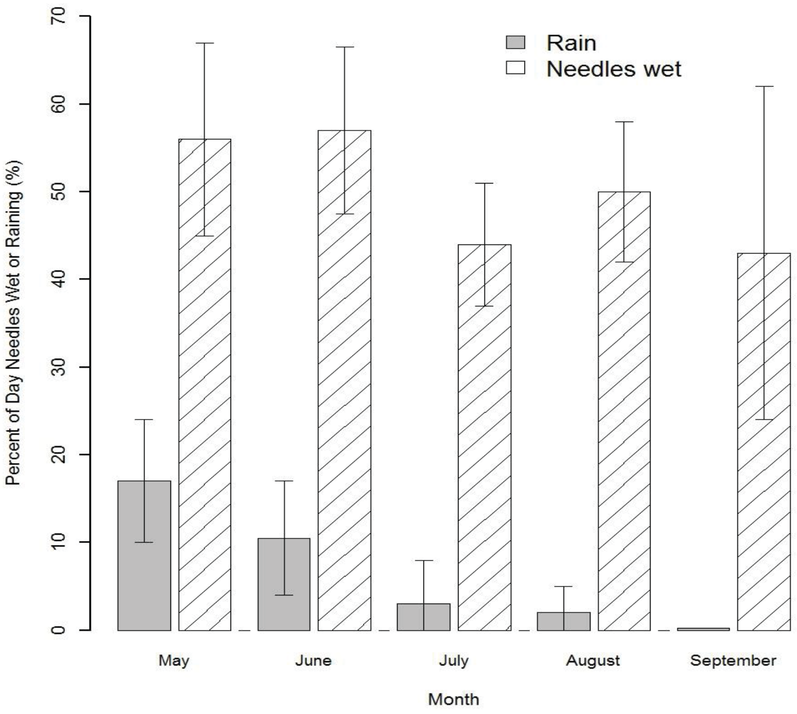

Figure 3: Percent of day when precipitation occurs versus when needles are wet in the summer of 2014 at Cascade Head. Needle wetness is maintained by coastal fog during the annual summer drought period.

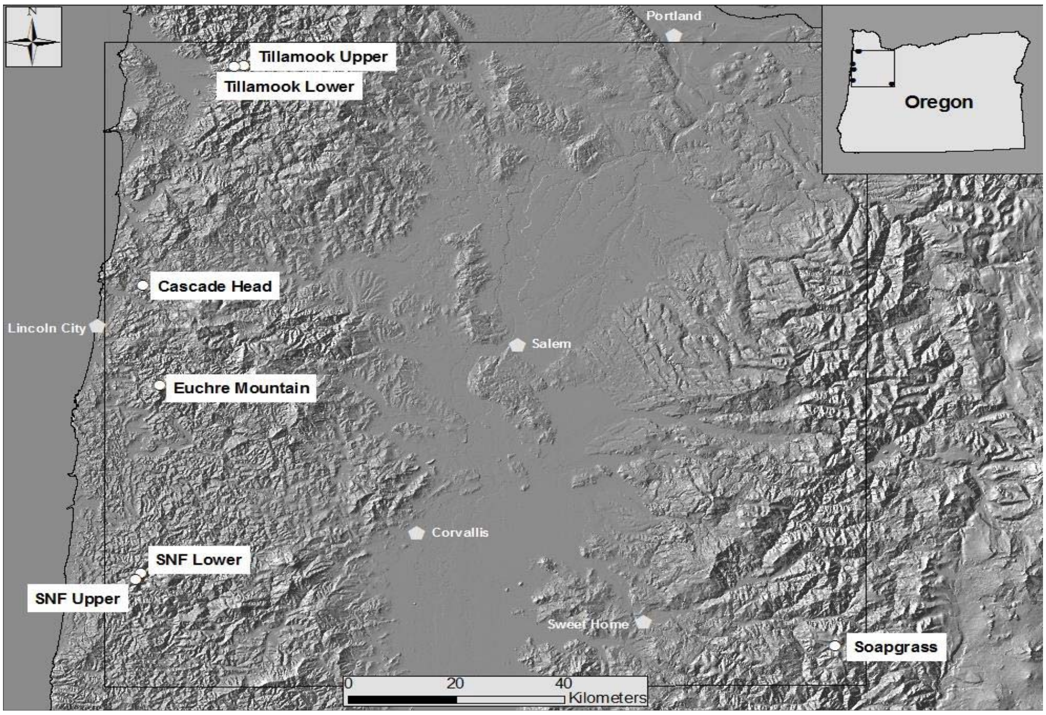

Figure 4: Locations of six study sites in Oregon Coast Range [17]. One reference Douglas-fir site, Soapgrass Mountain, is located at about 1200 m elevation on the western slope of the Cascade Range of Oregon.

unique to SNC (Figure 5). The synchronization of SNC impact on Douglas-fir across the landscape indicated that there were climate factors, which favored disease conditions at these sites in coastal Oregon.

SNC impacts on ancient douglas-fir

We analyzed tree-ring chronologies from two of 11 Douglas-fir logs that were unearthed in 2008-2010 by the Oregon Department of Transportation along the U.S. Highway 20 reconstruction site due east of Eddyville, OR (N44º39′, W123º47′). The logs, needles, and seed cones were encased in ancient landslide deposits at 26 m below the surface and were remarkably preserved. Radiocarbon dating estimates ages ~53K Before Present (BP) in the Marine Isotope Stage 3 (MIS3, ca. 60 to 27 K BP) period which was generally cold but with intermittent Dansgaard-Oeschger warm phases [24]. Stem diameters range from 64 cm for the 89 year-old log (351) to 128 cm for the 233 year-old log (355) and are comparable in size to contemporary coastal Douglas-fir trees of the same age. The similar growth rates indicate that the ancient Douglas-fir come from a temperate rainforest environment comparable to present day. Needles of the ancient Douglas-fir appear to have significant stomatal occlusion by structures resembling pseudothecia of *P. gaeumannii*, as seen under a scanning electron microscope (Figure 6). The two tree-ring series were successfully cross-dated but diverged and displayed periodicities of either 7.5 or 20 years (Figure 7), indicative of a non-climatic forest disturbance agent that affected one tree (351) more than the other (355). The chronology of tree 351 displays several 3-year periods of growth reduction approximately every 7.5 years. The 7.5-year disturbance cycle is similar to that of Tillamook Lower which has a periodicity of 6 years caused by SNC (Figure 8). The 20-year disturbance cycle of tree 355 is similar to the 25-year SNC cycle at Horse Creek Trail Lower in the Siuslaw National Forest (not shown). We attribute the 7.5 and 20 year disturbance cycles of the ancient Douglas-fir to SNC because the periodicities of low growth are similar to those of the SNC disease cycles of contemporary Douglas-fir and the stomata are possibly occluded. Furthermore, the anomalously low growth years of tree 351 are not synchronous with those of tree 355, indicating a non-climatic stress on individual trees rather than a climatic stress on all trees.

SNC impacts douglas-fir inland

We examined the spatial distribution of SNC impacts on mature Douglas-fir trees using TSIA of earlywood (EW) and latewood (LW) ringwidth chronologies from the west slope of the Coast Range to mid- and high-elevations on the west slope of the Cascade Mountains of Oregon (Figure 9). The EW and LW series represent a seasonal time series with a mean response function that contains components for climate and SNC outbreaks. The spatially-explicit predicted growth response to temperature and water was used as a climate proxy and was subtracted from the master chronology to isolate the disease signal. All sampled stands experienced significant radial growth reductions in Douglas-fir that could not be accounted for by current and previous-year seasonal climatic factors. The spatiotemporal patterns of growth reduction attributable to SNC were synchronous across the region, displayed periodicities of 25-30 years, and were

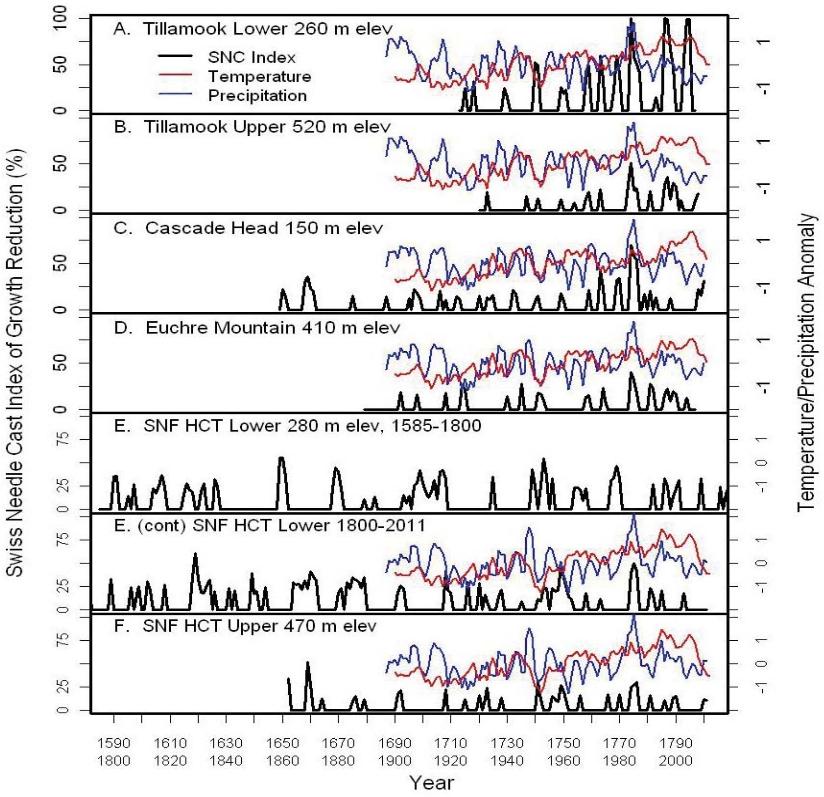

Figure 5: The percent reduction in annual tree-ring width increment of Douglas-fir adjusted for temperature and a climate proxy at six study sites in coastal Oregon [17]. Temperature and precipitation were normalized to a mean of 0 and a variance of 1. The red line is the 5-year running average of mean daily maximum temperature for January and February. The blue line is the 3-year running average of total precipitation for June and July.

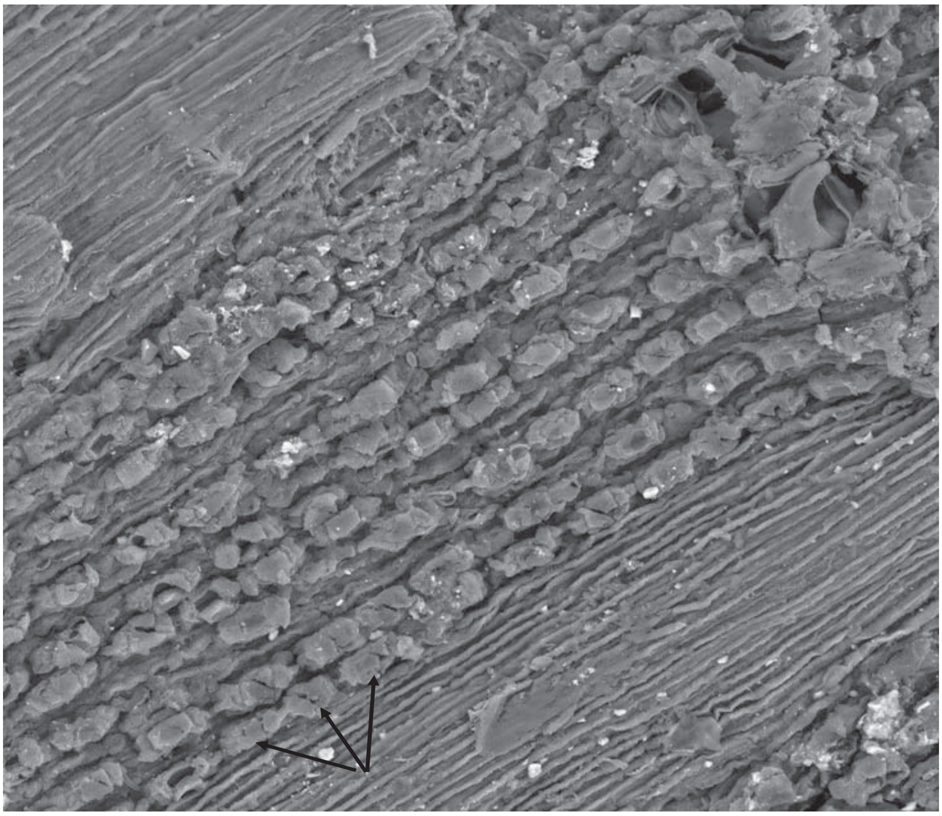

Figure 6: Scanning electron micrograph of pseudothecia primordia (see arrows) blocking the stomata of an ancient Douglas-fir needle found 29 m below the surface in landslide deposits near an Oregon Department of Transportation highway reconstruction project by Eddyville, Oregon. Image courtesy of William Rugh.

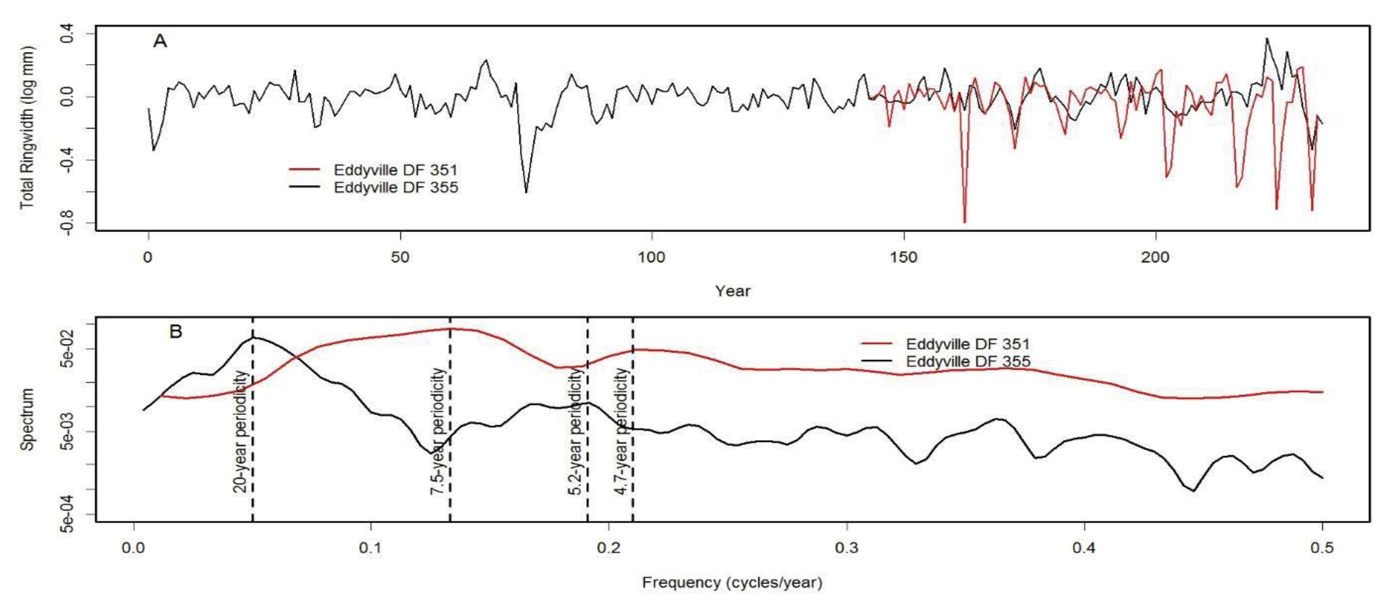

Figure 7: (A) Master chronologies of two ancient Douglas-fir trees from Eddyville, Oregon and (B) comparison of their spectrum. The chronology of tree 351 diverges from that of tree 355 and displays a cyclical pattern of anomalously low growth having a primary periodicity of 7.5 years and secondary periodicity of 4.7 years. Tree 355 displays a cyclical pattern having a primary periodicity of 20 years and a secondary periodicity of 5.2 years.

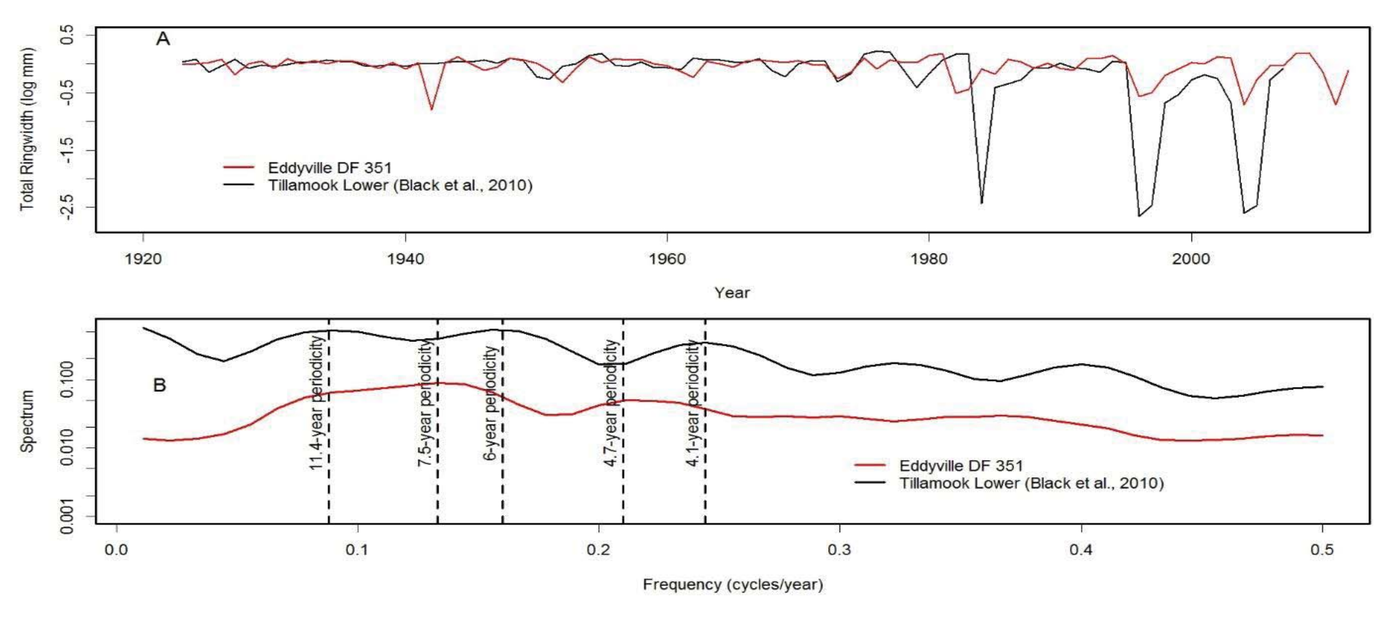

Figure 8: (A) The modern day analog of the ancient Douglas-fir tree 351 from Eddyville, Oregon is the master chronology of Douglas-fir at Tillamook Lower which displays cyclical patterns of anomalously low growth attributed to Swiss Needle Cast (Black et al., 2010). (B) The disease cycles at Tillamook and Eddyville have a similar primary periodicity of 6 and 7.5 years, respectively, and a secondary periodicity of 4.1 and 4.7 years, respectively. The disease cycle at Tillamook has another primary periodicity of 11.4 years which is less pronounced than at Eddyville.

strongly correlated with winter and summer temperatures and summer precipitation. Our findings indicate that detectable SNC impacts occur wherever Douglas-fir is found in western Oregon and is not limited to the coastal fog zone.

Climate relations with SNC

To infer the climate relations with SNC, we used TSIA to classify each year into one of three disease states, SNC growth suppression, no suppression, and release. The dominant pattern of Douglas-fir growth at each site was a disease cycle with a primary periodicity of 25-30 years and secondary periodicity of ~4 years (Figures 5, 7, 8, and 10) that is the interaction of climatic and non-climatic factors (Figure 1). We hypothesize that changes in pathogen abundance, amount of inoculum, needle class retention, stomatal occlusion, and climate over one or more decades cause the cycling of disease states throughout the life of the tree. To determine the climate relations with SNC, it was necessary to isolate the climate effects which were confounded with the biotic effects. The years classified as no SNC suppression or release have

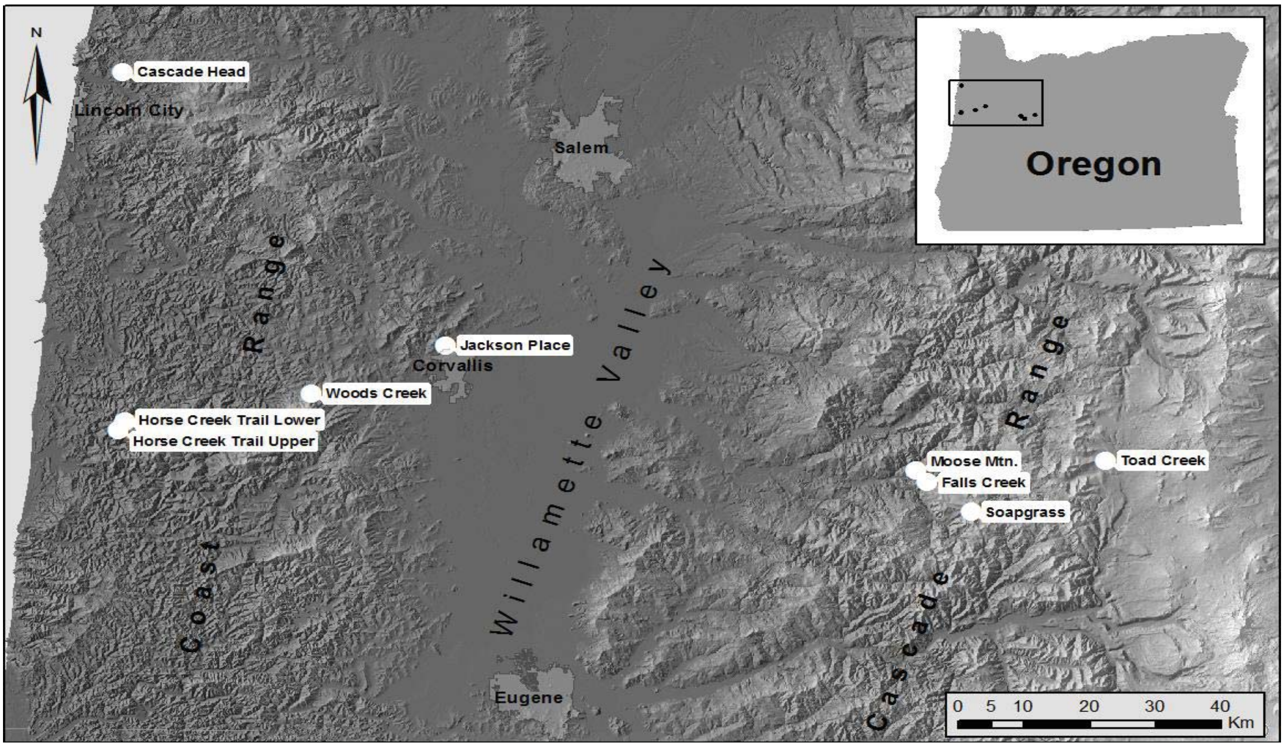

Figure 9: Tree core samples were collected from nine field sites located in mature Douglas-fir stands on the west and east sides of the Coast Range, in the Willamette Valley, and on the west side of the Cascade Mountains.

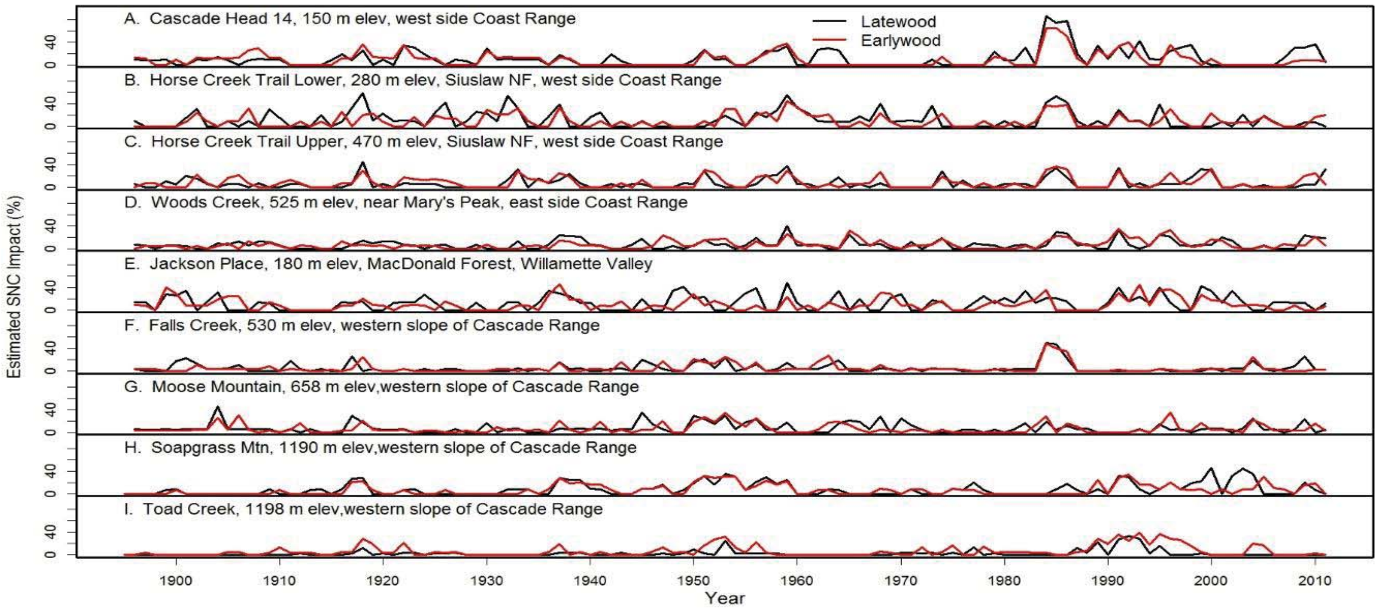

Figure 10: The percent reduction in earlywood and latewood ringwidth increment of Douglas-fir attributed to Swiss Needle Cast at nine study sites from the west slopes of the Coast Range to the west slopes of the Cascade Mountains of Oregon. The growth anomalies could not be explained by seasonal climate variables for temperature and water. Peak SNC impacts occurred in 1918, 1959, and 1984-1986 approximately 25-41 years apart and were synchronous across the region.

a SNC index value of 0% and do not correlate with climate. Consequently, the climate relations with SNC were determined using only the years classified as SNC suppression which have a negative pulse intervention resulting in a positive SNC index value. According to the conceptual disease cycle model, growth response to SNC was lagged and was the culmination of the interaction of climatic and biotic factors over multiple decades. Rather than correlating the nonzero SNC index with seasonal temperature and precipitation in the current and each previous year, we calculated the canonical correlations of SNC index with temperature and precipitation for the current and previous 30 years by site [17].

For Cascade Head, the SNC index of impact on latewood growth correlated best with the canonical variables for June-July temperature ($r_{can}=-0.98$) and June-July dewpoint deficit ($r_{can}=-0.98$) (Figure 11). The multiple regression equation of SNC impact on climate was

$$\text{SNC index} = 815 - 47.1\ \text{JJ\_Temp} + 4.3\ \text{DJF\_Temp} + 0.19{*}\text{JJ\_Prec}$$

and accounted for 96% of the variation where JJ_Temp= June-July mean daily maximum air temperature (ºC), DJF Temp= December-February mean daily maximum air temperature (ºC), and JJ_Prec= June-July total precipitation (mm). The key explanatory variable was June-July temperature based on Kruskal's measure of relative importance, indicating that high summer temperatures reduce the SNC impacts on Douglas-fir growth at this coastal site. While summer temperature and precipitation were correlated, identification of the key climatic factors associated with SNC was possible because the long history of SNC impacts represented a century that had high climatic variability as well as high variability in the tree-ring records.

For the high Cascades site, Soapgrass Mountain, the SNC index correlated best with the canonical variables for June-July precipitation ($r_{can}=-0.91$) and February-April temperature ($r_{can}=0.88$) (Figure 12). The multiple regression equation of SNC impact on climate was

$$\text{SNC index} = -30 - 9.2\ \text{JJ\_Temp} + 26\ \text{FMA\_Temp} + 2.5{*}\text{JJ\_Prec}$$

and accounted for 95% of the variation where JJ_Temp= June-July mean daily maximum air temperature (ºC), FMA_Temp= February-April mean daily maximum air temperature (ºC), and JJ_Prec= June-July total precipitation (mm). The key explanatory variable was February-April temperature based on Kruskal's measure of relative importance. The multiple regression results differed from the canonical correlation results because correlation considers one factor at a time whereas regression considers all factors simultaneously. Note also that the winter months of importance at Soapgrass were different than those at Cascade Head because temperatures in the two coldest months, December and January, were below the growth threshold in the high Cascades. Consequently, pseudothecia of *P. gaeumannii* likely formed one to two months later due to the colder environment.

Winter temperature, summer temperature and precipitation are the key limiting factors of pathogen abundance at all sites but, of these three climate factors, the primary limiting factor varies by site conditions and location (Figure 13). Summer precipitation is most limiting in warm, dry environments in the Willamette Valley and in some coastal sites in southern Oregon where summer needle wetness is less maintained by coastal fog. Winter temperature is most limiting in cool environments on the east slopes of the Coast Range and above the snowline on the west slopes of the Cascade Mountains. Summer temperature is most limiting at one coast site that lies more within the coastal fog zone.

SNC is influenced by the Pacific Decadal Oscillation (PDO)

In the 20th century, the PNW has experienced high climatic

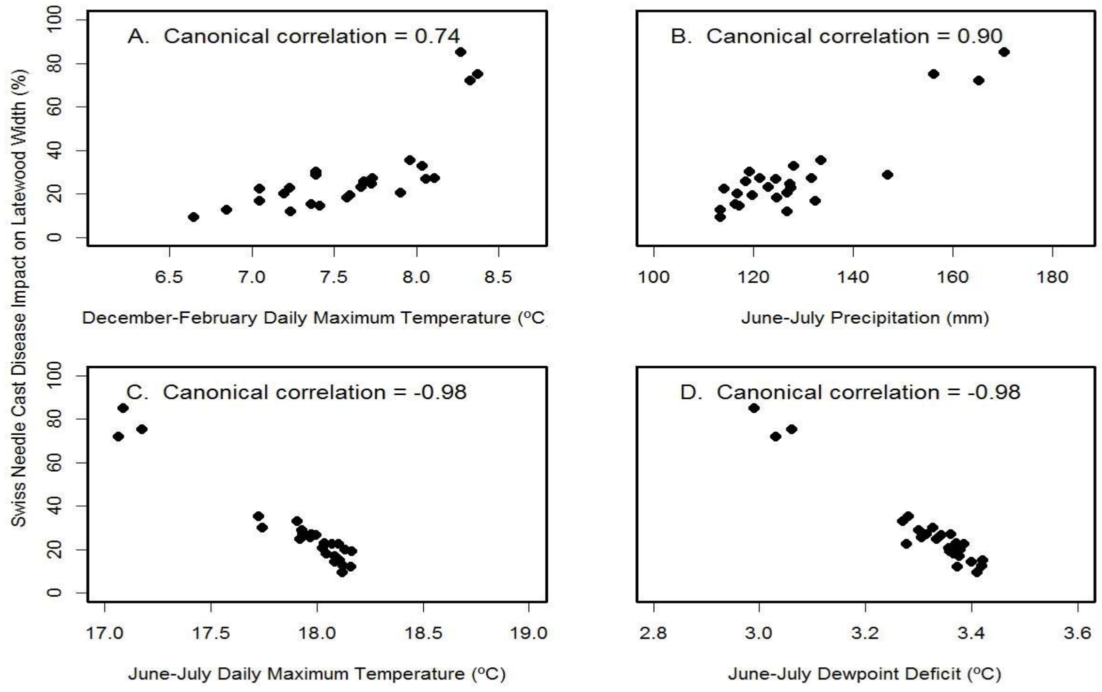

Figure 11: Canonical correlation of SNC index of impact on latewood growth with (A) winter temperature, (B) summer precipitation, (C) summer temperature, and (D) summer dewpoint deficit at Cascade Head. Temperature and precipitation were summarized on a seasonal basis so as to maximize the canonical correlations with the SNC index.

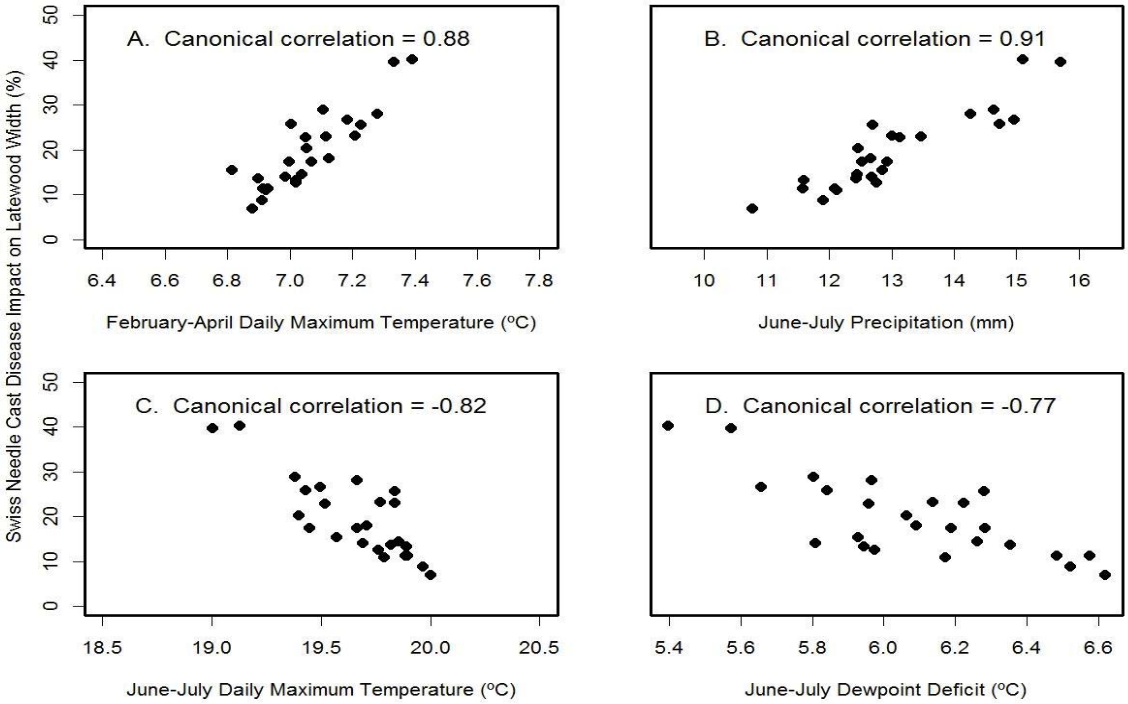

Figure 12: Canonical correlation of SNC index of impact on latewood growth with (A) winter temperature, (B) summer precipitation, (C) summer temperature, and (D) summer dewpoint deficit at Soapgrass Mountain. Temperature and precipitation were summarized on a seasonal basis so as to maximize the canonical correlations with the SNC index.

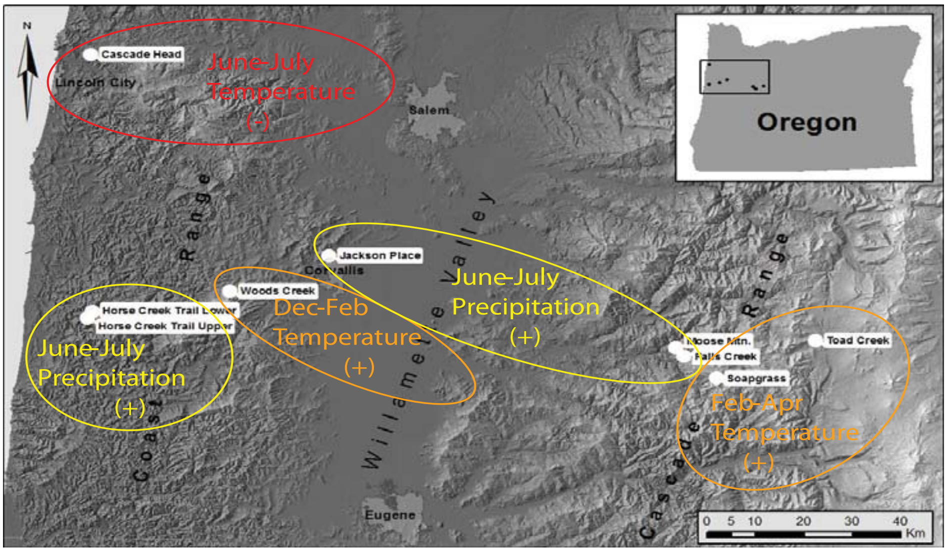

Figure 13: Map of study sites indicating the primary climatic factor that is most limiting to fungal development at each site based on time series intervention analysis of dendrochronological data.

variability including a strong warm phase of the PDO (1925-1946), followed by a strong cool phase (1947-1978). We found an inverse relation between PDO and SNC effects on tree-ring width, i.e., reduced effects during the warm phase and increased effects during the cool phase (Figure 14).

The period from 1917 to 1940 was exceptionally warm and dry and the drought of the 1930s was the second most severe drought of the last 250 years [25], likely resulting in less SNC impact on tree growth (Figure 14). This was followed by several wet periods from 1941 to 1955 and from 1968 to 1984, likely resulting in greater SNC impact and culminating with the 30-year peak impact in 1984-1986. The linkage between cool PDO phases and increased SNC impact continued after 1984 as evidenced by the intensification of SNC impacts on the east side of the Coast Range and in the high Cascades in recent decades during a mostly cool PDO phase (1998-2014) (Figure 14). However, the positive trend in SNC impacts at two sites (Woods Creek, Soapgrass Mountain) was more influenced by increasing winter temperatures due to climate warming than

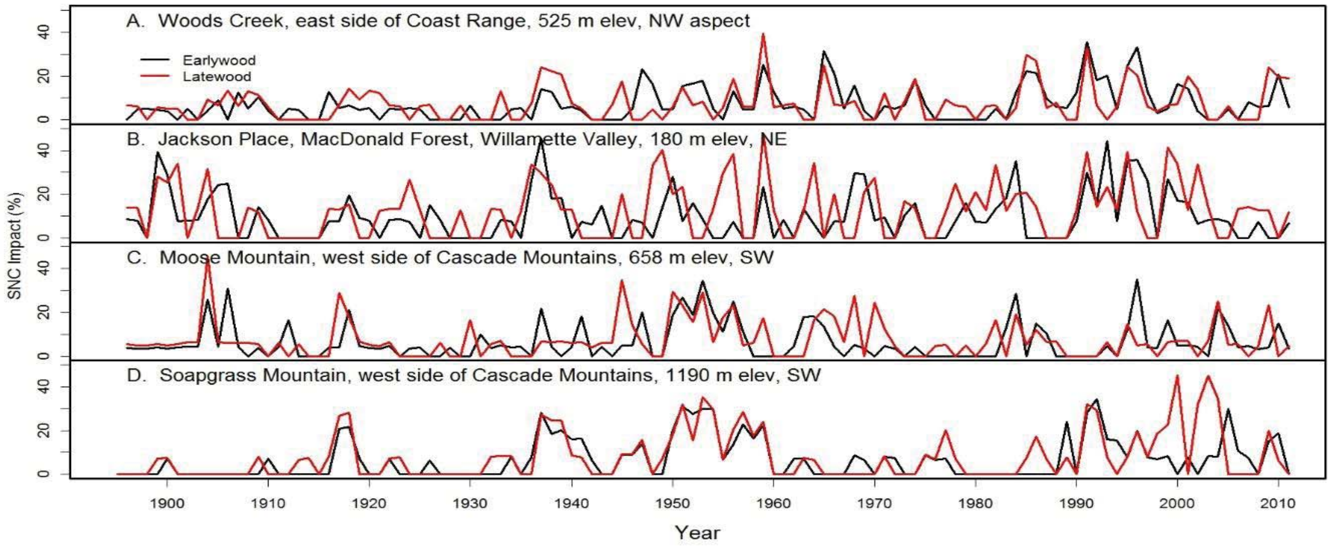

Figure 14: Swiss needle cast (SNC) index of impact at four inland sites display disease cycles having a 25-30 year periodicity, a relationship with the Pacific Decadal Oscillation (PDO), as well as an increasing trend at two sites, Woods Creek and Soapgrass Mountain. SNC impacts were less frequent and severe between 1925 and 1946 during a strong warm phase of the PDO than between 1947 and 1978 during a strong cold PDO phase.

by summer conditions which were more favorable to fungal develop in part due to the cool PDO phase.

Conclusion

SNC impacts occur wherever Douglas-fir is found and are synchronous across western Oregon, indicating that SNC is influenced by regional climate. SNC impacts in the PNW date back to ~53K radioactive years BP as evidenced by the cyclical patterns of low growth in the master chronologies of ancient Douglas-fir that match the modern SNC disease cycles at coastal sites, and supported by the presence in the ancient needles of putative pseudothecia of *P. gaeumannii.* This long history of SNC predates forest management practices and improves our understanding of the climate factors affecting the causal fungus. SNC impacts on Douglas-fir growth as seen in tree-rings display 6 to 30 year periodicities throughout the life of the tree. The higher frequencies in the disease cycle represent a lagged growth response to SNC caused by the infection of only the newly emerged needles at time of sporulation, followed by colonization of the needle over several years which is unique to *P. gaeumannii.* With warmer winters, SNC impacts are increasing in mature closed-canopy Douglas-fir stands on the east slopes of the Coast Range and in the high Cascades. Temperatures will likely continue to increase due to climate change, and consequently, SNC is expected to intensify in frequency and magnitude at higher elevations, north along the coast from northern Oregon to British Columbia, and inland where current winter temperatures limit fungal growth.

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Research paper

Physiological responses of Douglas-fir to climate and forest disturbances as detected by cellulosic carbon and oxygen isotope ratios

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Swiss needle cast (SNC), caused by a fungal pathogen, *Nothophaeocryptopus gaeumannii*, is a major forest disease of Douglas-fir (*Pseudotsuga menziesii*) stands of the Pacific Northwest (PNW). There is mounting concern that the current SNC epidemic occurring in Oregon and Washington will continue to increase in severity, frequency and spatial extent with future warming. *Nothophaeocryptopus gaeumannii* occurs wherever its host is found, but very little is known about the history and spatial distribution of SNC and its effects on growth and physiological processes of mature and old-growth forests within the Douglas-fir region of the PNW. Our findings show that stem growth and physiological responses of infected Douglas-fir to climate and SNC were different between sites, growth periods and disease severity based on cellulosic stable carbon and oxygen isotope ratios and ring width data in tree rings. At a coastal Oregon site within the SNC impact zone, variations in stem growth and Δ^{13}C were primarily influenced by disproportional reductions in stomatal conductance (g_s) and assimilation (A) caused by a loss of functioning stomates through early needle abscission and stomatal occlusion by pseudothecia of *N. gaeumannii*. At the less severely infected inland sites on the west slopes of Oregon's Cascade Range, stem growth correlated negatively with δ^{18}O and positively with Δ^{13}C, indicating that g_s decreased in response to high evaporative demand with a concomitant reduction in A. Current- and previous-years summer vapor pressure deficit was the principal seasonal climatic variable affecting radial stem growth and the dual stable isotope ratios at all sites. Our results indicate that rising temperatures since the mid-1970s has strongly affected Douglas-fir growth in the PNW directly by a physiological response to higher evaporative demand during the annual summer drought and indirectly by a major SNC epidemic that is expanding regionally to higher latitudes and higher elevations.

Keywords: Douglas-fir, Douglas-fir, forest disturbances, Pacific Northwest, stable isotopes, stomatal conductance, Swiss needle cast, time series, tree rings.

Introduction

Climate change is affecting sensitive forested ecosystems, making them more vulnerable to tree pathogens, phytophagous insects and fires (Dalton et al. 2013). Western North American forests are experiencing climate-mediated disturbances at large spatial scales (Raffa et al. 2008). Since the mid-1970s, forests in Oregon, USA have experienced increased severity and frequency of forest diseases and insects, increased mortality rates, and decreased growth rates (Wickman 1992, Van Mantgem et al. 2009, Beedlow et al. 2013, Lee et al. 2013, 2016, 2017*a*). With a predicted increase of pests, diseases and fire frequency (Halofsky et al. 2020), understanding the interactions between climate and these disturbances is central

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to predicting climate change impacts on forest structure and functioning at local and regional scales.

Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) is a dominant tree species in the Pacific Northwest (PNW), USA, and is important for timber production, carbon sequestration and wildlife habitat (Kline et al. 2016). Douglas-fir is host to many forest pathogens (e.g., *Nothophaeocryptopus gaeumannii*, *Arceuthobium* spp., *Armillaria*, *Phaseolus schweinitzii*) and pests (e.g., *Dendroctonus ponderosae*, *Dendroctonus pseudotsugae*, *Choristoneura occidentalis* Freeman, *Orgyia pseudotsugata* McDunnough), but the cumulative and interacting effects of climate, forest diseases and pests on tree growth and mortality are unclear. Douglas-fir responses to climate and disturbances have been extensively studied (Agne et al. 2018, Cohen et al. 2002, Healey et al. 2008, Lee et al. 2013, 2016, 2017*a*, Shaw et al. 2011, Wimberly and Spies 2001), but there is still considerable debate regarding the growth and physiological responses to climate in light of disturbance by biotic agents within the Douglas-fir region.

Douglas-fir growth responses to abiotic factors have been well described and depend on location and site conditions (Brubaker 1980, Case and Peterson 2005, Lee et al. 2016, 2017*a*, Watson and Luckman 2002). In warm, dry sites at low- to mid-elevations, growth correlates positively with growing season soil moisture and precipitation, and negatively with summer temperatures in both current and prior years (Brubaker 1980, Case and Peterson 2005, Watson and Luckman 2002). At high elevations, growth correlates positively with summer and annual temperatures, winter snowpack and growing season length (Littell et al. 2008, Nakawatase and Peterson 2006). Typical Mediterranean climate conditions in the PNW—high vapor pressure deficit (VPD) in combination with high temperature and low soil moisture—impacts trees by either stressing the hydraulic conductivity mechanism and/or by inducing stomatal closure, resulting in growth reduction and subsequently mortality (Breshears et al. 2013, McDowell et al. 2008). Prolonged periods of high summer VPD and low soil moisture can lower assimilation (A) and cause reductions in carbohydrate reserves from the continued demand of carbohydrates for respiration and other metabolic processes (McDowell et al. 2011). Ultimately, this reduction in carbohydrate reserves may impair the plant's ability to defend against pest attacks and have carryover effects on primary and secondary growth processes for several years. However, these climate growth relationships likely include interactions with biotic factors mentioned above that need to be more explicitly examined.

For PNW Douglas-fir stands, the growth responses to climate are complex, interact with Swiss needle cast (SNC) and vary by site (Lee et al. 2016, 2017*b*). Swiss needle cast is a foliage disease associated with a ubiquitous native endophytic fungus, *Nothophaeocryptopus gaeumannii*, which is currently defoliating and decreasing growth of Douglas-fir in the Coast Range of the PNW (Shaw et al. 2021, Ritóková et al. 2016). Disease is caused when the fruiting bodies (pseudothecia) of *N. gaeumannii* emerge from and occlude the stomates, which causes reduced gas exchange and carbon starvation (Manter et al. 2000). Epidemiological studies suggest needle retention drives the episodic SNC-induced growth impacts on Douglas-fir, with foliage retention of 2 years causing a reduction in growth of about 30% (Maguire et al. 2002, 2011, Shaw et al. 2021). Coastal Douglas-fir plantations typically retain up to 4 years of needles but may have only current and 1-year-old foliage in some years (Hansen et al. 2000, Maguire et al. 2002, Zhao et al. 2011) due to early needle abscission when between 25–50% of the stomates are occluded (Hansen et al. 2000, Manter et al. 2003, Stone et al. 2008). In severely infected plantations, stomatal occlusion reduces stomatal conductance (g_s) by about 83% and carbon assimilation rate (A) by about 72% in the following year (Manter et al. 2000), and, in combination with early needle abscission, reduces stored non-structural carbohydrates (NSC) by 60% and ensuing growth by about 80% over a longer period of time (Saffell et al. 2014*b*). Tree growth can be reduced by a reduction in carbohydrate reserves due to either SNC or environmental conditions during the annual summer drought but the physiological basis for these responses is unclear (Klein et al. 2014).

Stable isotope analyses of tree-rings have been shown to provide a better understanding of the growth and physiological responses of Douglas-fir to climate and SNC (Saffell et al. 2014*a*). In a severely infected Douglas-fir plantation in coastal Oregon, a fungicide treatment resulted in increased growth, and greater carbon isotope discrimination (Δ^{13}C), but no change in δ^{18}O in tree rings (Saffell et al. 2014*a*). In addition, untreated trees decreased Δ^{13}C with higher relative humidity (RH), indicating greater disease severity under higher humidity and the effect of stomatal occlusion. In mature Douglas-fir stands located on the western slopes of the Cascade Range of Oregon where SNC severity was low, the cellulosic δ^{13}C and δ^{18}O in tree rings were positively correlated and responded uniformly to RH, indicating a negative g_s response to high evaporative demand (Barnard et al. 2012). The physiological responses of growth for PNW Douglas-fir are more highly influenced by SNC than climate for sites on the west side of the Coast Range of Oregon and Washington and vice versa for inland sites east of the Coast Range (Barnard et al. 2012, Black et al. 2010, Lee et al. 2017*a*).

Recent epidemiological evidence suggests that disease severity and history, as recorded by growth and Δ^{13}C in tree-rings of young severely infected Douglas-fir trees, may not be generalizable to less severely infected mature trees due to tree age differences in pseudothecia dynamics and foliage retention (Lan et al. 2019). The percentage of pseudothecia present is greatest in 2-year-old needles for young trees and 3-to 5-year-old needles for older trees, resulting in greater health and needle retention for mature trees (Lan et al. 2019). The reason for this difference is unknown and is not explained by foliar nitrogen and leaf wetness. While there is considerable evidence of disease severity for young Douglas-fir plantations in coastal Oregon and Washington (Ritóková et al. 2016, 2021), the data and knowledge gaps of disease severity for mature Douglas-fir are large due primarily to comparably few epidemiological and dendro-isotopic studies on mature Douglas-fir and scaling issues from young to older stands. The isotope climate relations remain unknown for mature Douglas-fir stands in western Oregon where SNC severity is moderate to high, but likely vary by site and interact with disturbance.

Swiss needle cast and climate impacts on Douglas-fir growth in western Oregon have increased throughout the region since 1980 (Lee et al. 2016, 2017*a*, Ritóková et al. 2016), while regional temperatures rose at an accelerated rate of 0.3 °C per decade (Abatzoglou et al. 2014). Swiss needle cast impacts in western Oregon display regional sinusoidal cycles with periodicities ranging from 12 to 40 years and a peak in 1984–86 based on dendrochronological reconstructions of disease history (Lee et al. 2013, 2017*a*). The cause of the synchronous cyclical patterns of SNC growth impacts is attributed to defoliation due to SNC following the initial infection of newly emerged needles by ascospores of *N. gaeumannii* and blockage of stomates in older needles (Lee et al. 2013). Since 1986, disease severity has increased in magnitude and frequency with increasing winter temperatures for Douglas-fir stands within the SNC impact zone ($<$40 miles distance from coast) (Ritóková et al. 2016), but decreased in magnitude and frequency with increasing summer temperatures and decreasing summer precipitation for inland stands $<$1000 m elevation (Lee et al. 2017*a*). Disease severity in Oregon and Washington is greatest at low elevation sites, on south-facing aspects, and close proximity to the coast (Coop and Stone 2007, Rosso and Hansen 2003). The current warming and SNC epidemic occurring in western Oregon provide an opportunity to examine the growth and physiological responses of mature Douglas-fir stands to climate and forest diseases across a climate and disease gradient.

Several lines of evidence from empirical and modeling studies suggest that tree growth and physiological processes are influenced by current and antecedent climate conditions lagged one or more years depending upon tree species and their ability to store and use carbohydrate reserves for current-year wood formation (Anderegg et al. 2015, Ogle et al. 2015, Zweifel and Sterck 2018). However, few dendro-isotopic studies have examined the cellulosic stable isotope responses to current and antecedent conditions more than 1 year in the past in disturbed and undisturbed stands (e.g., Saffell et al. 2014*a*, Szejner et al. 2020). Notably, no cellulosic stable isotope data exist from moderately infected Douglas-fir stands outside of the SNC impact zone to infer physiological responses of mature trees to changing environmental conditions and biological disturbance agents.

This paper extends our previous dendrochronological studies to examine the physiological responses of mature Douglas-fir trees to climate and forest disturbances based on stable carbon and oxygen isotope ratios in tree rings for the same sites as reported in Lee et al. (2016, 2017*a*). The general objective of this study was to quantify the isotope climate disturbance relations of SNC-infected Douglas-fir in western Oregon to determine the key biotic and abiotic factors influencing physiological processes of growth and reconstruct the history of SNC impacts using a time series intervention model (Lee et al. 2017*b*). Our specific objectives were: (i) to separate and compare the climate and disease signals in the stable carbon and oxygen isotope ratios in the earlywood (EW) and latewood (LW) of tree rings for mature Douglas-fir stands having a range of SNC severities from low to moderate; (ii) to evaluate the ability of the Δ^{13}C and δ^{18}O time series to record the influence of climate and *N. gaeumannii* on changes in physiology in terms of the rates of g_s and A; (iii) to determine whether stem growth and the stable isotope ratios in tree rings respond uniformly to the same key climatic drivers or are influenced by different climatic drivers depending on disease severity and site conditions; and (iv) to determine whether the regional SNC signals in the Δ^{13}C time series are concurrent with the cyclical SNC impacts on tree growth or asynchronous and aperiodic. It is hypothesized that stem growth decreases with decreasing g_s under high summer evaporative demand for less diseased inland stands (Barnard et al. 2012), and with decreasing g_s and A due to stomatal occlusion and loss of foliage associated with SNC for more severely diseased coastal stands (Saffell et al. 2014*a*).

Materials and methods

Research sites

The five study sites were established in mature, closed-canopy Douglas-fir stands in western Oregon, USA in the late 1990s as part of a long-term ecological monitoring network of field sites by the US Environmental Protection Agency Pacific Ecological Systems Division laboratory in Corvallis, Oregon, USA (Figure 1). The sites represent a range of climatic and edaphic conditions at varying elevations above and below the snowline of ~1,000 m and proximal distances to the coast along a precipitation and disease gradient (Table 1 and Figure 2). The study plots range in area from 0.4 to 1.0 ha and have been instrumented with meteorological stations at ground level and in tree-tops to provide a continuous record of local conditions since 1998 (Lee et al. 2007). Measurements of soil available water and soil temperature, and above-ground ambient air temperature, precipitation, VPD, photosynthetically active radiation, wind speed and direction were continuously recorded within 100 m

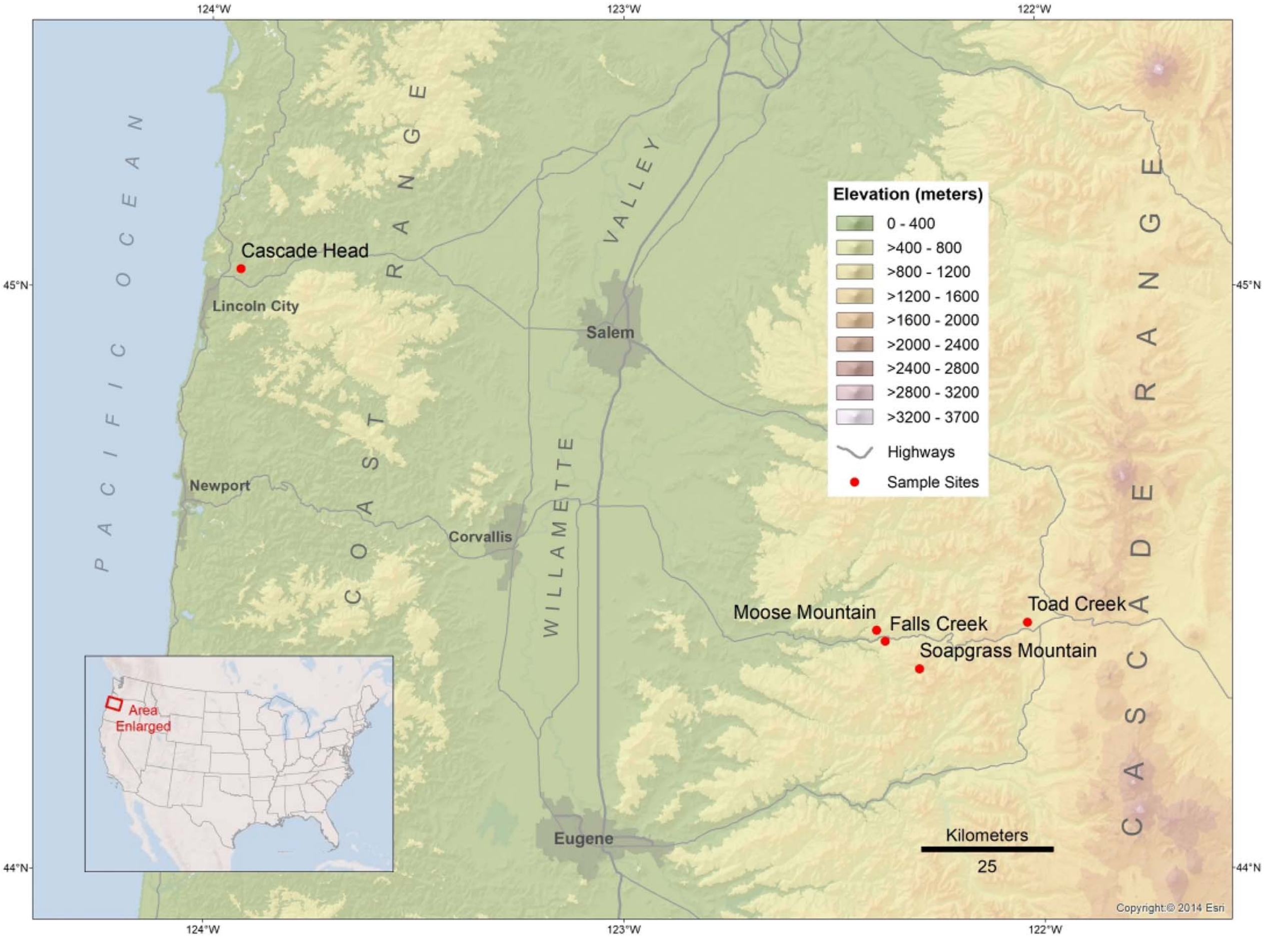

Figure 1. Map showing location of the five study sites along a precipitation and disease gradient in western Oregon.

of the trees sampled for cellulosic dual stable isotope analysis at each site (Beedlow et al. 2017).

The Cascade Head (CH) site is a mixed conifer stand comprised of ~150-year-old dominant Douglas-fir and younger western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and is located within the SNC impact zone (Shaw et al. 2011). The CH study site is one of the permanent sample plots established in the Cascade Head Experimental Forest, Oregon by the US Department of Agriculture Forest Service (Smith et al. 1984). The lower-elevation montane sites, Falls Creek (FC) and Moose Mountain (MM), are predominantly covered by 110-to 125-year-old Douglas-fir whereas the higher-elevation sites, Soapgrass Mountain (SM) and Toad Creek (TC), are mixed conifer stands dominated by 200+-year-old Douglas-fir with smaller components of western hemlock and true firs (*Abies* spp.). These sites have been used in previous studies to examine the growth-climate relations and reconstruct the regional history of forest disturbances for Douglas-fir, (Beedlow et al. 2013, Lee et al. 2016, 2017*a*). At the SM site with 470-year-old Douglas-fir that was previously sampled for dendrochronology (Lee et al. 2016), we chose a nearby stand of 128-year-old Douglas-fir in close proximity to a meteorological station to collect 12 mm tree core samples that had wider rings suitable for stable isotope measurement. Swiss needle cast was present but varied in severity from very low (TC, SM) to low-to-moderate (FC, MM) to high (CH) based on the SNC infection index from needle samples collected in 2015 that were infected by the causal fungus, *N. gaeumannii* (Lan et al. 2019). See Beedlow et al. (2013) and Lee et al. (2007, 2013, 2016) for a complete description of the sites.

Tree-ring sampling

At each field site, we selected three or four healthy dominant Douglas-fir trees that were free of visible signs of disturbance other than SNC and had suitably wide rings >0.6 mm from 1980 to present. For each tree, we measured the diameter at breast height (DBH) and collected three or four 12-mm core samples from different cardinal directions near DBH in 2012–13. High SNC infection from 1984 to 1986 produced anomalously narrow (<0.3 mm) ring widths at CH and FC (Lee et al. 2013, 2016, 2017*a*). Consequently, it was not always possible to find trees with suitably wide rings in all years at

Table 1. Site information for tree core sampling in western Oregon (Lee et al. 2016, 2017*a*).

Name	Latitude, longitude	Elevation (m)	Distance to coast (km)	Aspect	Slope (%)	Basal area density (m^2 ha^{-1})	Mean daily minimum plant available soil moisture (mm) and percent of maximum in parentheses[1]	Stem diameter at breast height (m)	Tree height (m)	Climate and edaphic grading
Cascade Head	N45°02′ W123°54′	150	8.7	80° (E)	19	88[2]	93.9 (39%)	1.0–1.5	55–58	Temperate rainforest
Falls Creek	N44°24′ W122°22′	530	136.6	45° (NE)	8	60[2]	33.7 (23%)	0.6–1.1	48–63	Warm, dry montane
Moose Mountain	N44°25′ W122°24′	658	134.8	250° (SW)	17	61[2]	13.2 (17%)	0.6–0.9	44–58	Warm, drier montane
Soapgrass Mountain, young	N44°21′ W122°18′	1,170	144.0	97° (E)	13	67[3]	36.0 (21%)	0.7–0.8	39–43	Cool, wet montane
Toad Creek	N44°26′ W122°02′	1,198	163.1	100° (E)	12	85[2]	26.8 (32%)	0.8–1.3	48–63	Cool, dry montane

[1] Mean values for the years 1998–2009 from Beedlow et al. (2013).

[2] Basal area density is based on a complete plot survey of individual trees at these permanent field sites.

[3] Basal area density is based on multiple stand measurements using a wedge prism that has a basal area factor of either 20 or 30.

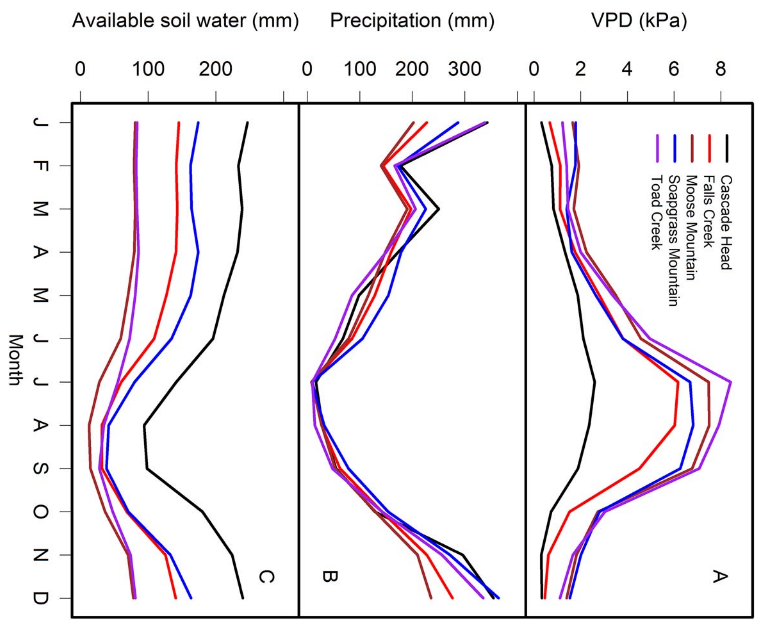

Figure 2. Study sites represent a range of environmental and edaphic conditions as indicated by the monthly mean of (A) vapor pressure deficit (VPD), (B) total precipitation and (C) total available soil water in the top 80 cm of soil based on instrumental data from local meteorological stations for the period 2000–11.

all sites. Each tree was cored to a depth to cover the period from 1980 to present for stable isotope analysis. This period was chosen because: (i) temperature increased linearly at an accelerated rate of ~0.3 °C per decade in the 1980–2012 period (Abatzoglou et al. 2014); (ii) climate-induced growth rates of Douglas-fir declined steadily beginning ~1990 at the mid-elevation sites (FC, MM) (Lee et al. 2016); (iii) SNC-induced impacts on Douglas-fir growth were unprecedented at mid- to low-elevations in 1984–86 and were increasing at higher elevations in the 1990s (Lee et al. 2013, 2017*a*); and (iv) concurrent supplemental tree-ring width and local climate data and field observations on forest health and condition, phenology and disturbances were available for some or all of this period. Furthermore, the first 75+ years of growth were discarded to minimize the 'juvenile effect' indicated by an increasing trend in the δ^{13}C series (Schleser and Jayasekera 1985).

Sample processing

Tree cores were air-dried, sanded, and scanned using an Epson Expression 10000XL flatbed scanner to generate a digital image of the cellular structure for dendrochronological study and also used for stable isotope analyses. We measured EW and LW ring widths to the nearest 0.01 mm using the WinDENDRO

2008 g tree-ring measuring system (Regent Instruments Inc., Quebec, Canada). The EW and LW ring widths allow examination of the growth response to primary climatic factors at a seasonal time-scale (Meko and Baisan 2001, Watson and Luckman 2002). Following measurement, the tree-ring data were cross-dated by matching patterns of narrow and wide rings between cores from the same tree or from different trees within and between sites. We used the master Douglas-fir chronologies from these same sites for cross-dating and time series statistical analysis (Lee et al. 2016), and only the tree-ring width data for the younger SM stand were used to develop a new master chronology for that site. The University of Arizona Laboratory of Tree-Ring Research software program COFECHA Version 6.06P (Holmes 1983) was used to confirm assignment of the correct calendar year to each growth increment. After the cores were cross-dated, each core was color-coded with a permanent marker pen to ensure that the ring for a given calendar year from each of the cores from the same tree were matched and pooled correctly.

Several lines of evidence indicate that EW in tree rings is partially formed using stored photosynthates from the previous year, while LW is formed almost exclusively from current photosynthates (Helle and Schleser 2004, Kagawa et al. 2006, McCarroll and Loader 2004, Tepley et al. 2020). Consequently, the EW and LW sections for each year were separated and milled to a fine powder using a hand rotary tool with a drum sander attachment. The powder from multiple core samples from the same tree were combined prior to α-cellulose extraction (Leavitt and Danzer 1993, Sternberg 1989) and were analyzed for stable carbon and oxygen isotope ratios. The EW and LW samples of one or more consecutive years having narrow rings were combined for isotopic analysis for several trees and two sites, CH and FC (Table S1 available as Supplementary data at *Tree Physiology* Online).

About 1–2 mg of α-cellulose was either decomposed under high temperature in an elemental analyzer (ECS 4010; Costech, Valencia, CA, USA) to produce CO_2 for $\delta^{13}C$ or in a conversion elemental analyzer (TC/EW ThermoQuest Finnigan, Bremen, Germany) to produce CO for $\delta^{18}O$. The product gases were analyzed on a Finnigan MAT deltaPlus XL or XP isotope ratio mass spectrometer located at the Environmental Protection Agency's Integrated Stable Isotope Research Facility laboratory in Corvallis, Oregon, USA. The $\delta^{13}C$ and $\delta^{18}O$ values are expressed in ‰ relative to the standard Peedee belemnite (PDB) and Vienna Standard Mean Ocean Water (V-SMOW), respectively. The precision of α-cellulose standards was 0.1‰ for $\delta^{13}C$ and 0.25‰ for $\delta^{18}O$ based on sample replicates.

Statistical analysis

The tree-ring width data were log-transformed, detrended and deseasonalized using a cubic spline with a 50% frequency response of 32 years separately for earlywood and latewood. The tree-ring series for each core from the same tree were averaged and the median across trees was then used to produce the master chronologies of EW and LW widths for the young SM site. The master chronologies for the other four sites were developed in a previous study using 5-mm cores that spanned the lifetime of the tree (Lee et al. 2016, 2017*a*).

The consumption of fossil fuels has resulted in a lowering of the $\delta^{13}C$ value of air ($\delta^{13}C_{air}$) by about 1.5‰ since 1950, which is reflected in the $\delta^{13}C$ values in tree rings ($\delta^{13}C_{cell}$) (McCarroll and Loader 2004). To remove this source of variation from $\delta^{13}C_{cell}$, the discrimination against ^{13}C, denoted $\Delta^{13}C$, was calculated using the following equation (Farquhar et al. 1982):

$$\Delta^{13}C = \frac{\delta^{13}C_{air} - \delta^{13}C_{cell}}{1 + \delta^{13}C_{cell}/1000} \qquad (1)$$

where $\delta^{13}C_{air}$ values from the Mauna Loa Observatory, Hawaii for the period 1958 to present were downloaded from the Scripps CO2 program website (https://scrippsco2.ucsd.edu/data/atmospheric_co2/mLo.html). Plant $\Delta^{13}C$ responds linearly to changes in the ratio of internal $[CO_2]$ (c_i) to atmospheric $[CO_2]$ (c_a) according to the following equation (Farquhar et al. 1989)

$$\Delta^{13}C = a + (b - a)\left(\frac{c_i}{c_a}\right) \qquad (2)$$

where a is fractionation associated with diffusion (4.4‰) and b is fractionation associated with carboxylation by Rubisco (∼27‰). The $\Delta^{13}C$ and $\delta^{18}O$ time series were deseasonalized by centering the EW and LW values about their respective means.

Plant $\Delta^{13}C$ is related to intrinsic water-use efficiency (iWUE) which is estimated from c_i and c_a as follows

$$\text{iWUE} = \frac{A}{g_s} = \frac{c_a - c_i}{1.6} \qquad (3)$$

where 1.6 is the ratio of diffusivities of water and CO_2 in air, A is the rate of photosynthesis and g_s is the rate of stomatal conductance. Combining Eqs 2 and 3, the inter- and intra-annual variations in $\Delta^{13}C$ in tree rings are related to changes in A and g_s in response to seasonal climatic factors. Monthly atmospheric $[CO_2]$ data for the period 1958–2019 for Mauna Loa Observatory from http://scrippsco2.ucsd.edu/data/atmospheric_co2/primary_mlo_co2_record were summarized on an annual basis for the calculation of iWUE in terms of c_a and $\Delta^{13}C$.

Cross correlation analysis

We interpret the dual stable isotope ratios in terms of the two limiting rates for iWUE with guidance from the dendrochronological reconstruction of forest disease history. A negative correlation between $\Delta^{13}C$ and $\delta^{18}O$ results from an increase in $\delta^{18}O$ with decreasing g_s in response to increasing VPD and a concurrent decrease in $\Delta^{13}C$ with increasing A/g_s. In infected Douglas-fir, a negative correlation between Δ^{13}C and δ^{18}O is not expected to be consistent for all years because of possible asynchronous and disproportional changes in g_s and A due to early needle abscission associated with SNC. A departure from the negative correlation in the dual stable isotope space is hypothesized to represent a SNC outbreak event but, unfortunately, the periods of SNC outbreaks are seldom known. Because SNC causes a concurrent reduction in stem growth and A due to a loss of foliage (Maguire et al. 2002), the tree-ring width chronologies for Douglas-fir were used to reconstruct the history of forest disturbances (Figure 3) and provide supplemental information to separate the interacting effects of climate and disturbance on the dual stable isotope ratios (Lee et al. 2017*a*). Divergences from an isotopic response to climate were examined by comparing the co-variations of Δ^{13}C and δ^{18}O for years with and without low growth anomalies associated with SNC at each site. Isotopic divergences from climate were also examined by time series regression and correlation analyses of the tree ring-width and dual stable isotope series for each site. Coherence in stem growth and isotopic ratio chronologies is indicated by stem growth displaying a positive correlation with Δ^{13}C and a negative correlation with δ^{18}O. Further, the climate and disease signals in the isotope chronologies were inferred using time series regression analysis following Lee et al. (2017*a*).

Time series intervention model

Tree growth has been described conceptually by Cook (1987) as a structural time series model with components for age trend (A_t), climate (C_t) and disturbance (D_t), i.e., $E(Y_t) = A_t + C_t + D_t$, where $E(Y_t)$ is the mean response function for the tree-ring width chronology (Y_t). The same model applies for Δ^{13}C and δ^{18}O with the exception of an age trend. The climate component, C_t, represents the interactions of temperature, precipitation, soil moisture and evapotranspiration demand on tree growth and stable isotope ratios, and is assumed to be the same for all trees within a stand (Fritts 1976), as well as a climate trend. The δ^{13}C and δ^{18}O ratios in conifers are correlated with RH (Barnard et al. 2012, Roden and Ehleringer 1999), precipitation (Anderson et al. 1998, Burk and Stuiver 1981), temperature and soil moisture status. The disturbance component, D_t, has been described by Lee et al. (2016, 2017*a*, 2017*b*) as a set of pulse functions to detect outliers representing the outbreak events of one or more forest disturbance agents (e.g., SNC). In addition to an isotopic and growth response to climate and disturbance, the intra-annual radial stem growth, δ^{13}C and δ^{18}O in tree-rings of Douglas-fir and other tree species showed significant regular and seasonal autocorrelations (Monserud and Marshall 2001, Lee et al. 2017*b*; Szejner et al. 2018). In the Box-Jenkins modeling framework, the earlywood and latewood stable isotope ratios (e.g., Δ^{13}C or δ^{18}O) can be viewed as a seasonal time series with two measurements per year that display a non-constant mean, $\mu_t = C_t + D_t = \sum_{i=1}^{p} \beta_i X_{it}$, and a seasonal autoregressive, moving average (SARMA) autocorrelation structure (Lee et al. 2017*a*). The predictor variables are either monthly or seasonal means of temperature, precipitation, vapor pressure deficit and the Palmer Drought Severity Index (PDSI) for the current and previous years or 0–1 indicator variables for a disturbance event. For a first-order seasonal and regular ARMA, denoted SARMA $(1,0)_2 \times (1,0)$, with a non-constant mean μ_t, the model is:

$$\begin{aligned}(Y_t - \mu_t) &= \rho_1 (Y_{t-1} - \mu_{t-1}) + \theta_1 (Y_{t-2} - \mu_{t-2}) \\ &\quad - \rho_1 \theta_1 (Y_{t-3} - \mu_{t-3}) + e_t \end{aligned} \tag{4}$$

where $e_t \sim \mathrm{NID}(0,\sigma^2)$, ρ_1 and θ_1 are <1 in absolute value. The mean response function and autoregressive model parameters in Eq 4 were assumed to differ seasonally by growth period because the EW and LW ring widths and isotope ratios reflect seasonal climate conditions during cell formation (Meko and Baisan 2001, Watson and Luckman 2002, Griffin et al. 2011). Douglas-fir trees in western Oregon transition from EW to LW in mid-to late-July (Beedlow et al. 2013).

The time series intervention model was used to assess the presence of regional climate and SNC signals in the stable carbon and oxygen series in EW and LW of tree rings, using the climate and SNC signals in radial stem growth series of mature Douglas-fir reported in Lee et al. (2016, 2017*a*) as guides to interpretation. We hypothesized that the years with anomalously low growth which could not be attributed to climate were either concurrent or delayed by one or more years with anomalously low Δ^{13}C and/or anomalously high δ^{18}O in either the EW or LW time series. Given the explicit characterization of the isotope-climate relation (C_t) of the host species, the disturbance events are unknown and must be inferred by comparing Y_t and C_t to detect isotopic ratio divergences, which cannot be attributed to the measured climate variables. To test for a departure from the climate signal in the stable isotope series, we included a 0–1 indicator variable for each year sequentially in the mean response function equation following Lee et al. (2017*b*).

Outlier detection tests are performed using the Wald test statistic, i.e., $W = \hat{\beta}_i / \sqrt[2]{\hat{\mathrm{Var}}\left(\hat{\beta}_i\right)}$ where β_i is the model parameter for the pulse disturbance event at time $t = t_i$ for $i = 1,2,\ldots r$. In general, the disturbance events $t* = (t_1, t_2, \ldots, t_r)$ are unknown and must be inferred. Some multiple testing adjustment like Bonferroni or Tukey and/or specification of a critical value A is appropriate for detection of multiple outliers because every point is a potential outlier. Chang and Tiao (1983) suggest values of A between 3 and 4. The forest disturbance events were detected as outliers based on the Wald test statistic using a critical value A of 4 for the reconstruction of SNC impacts by site (Lee et al. 2017*a*). See Lee et al. (2017*b*) for a more complete description of the Box-Jenkins time series intervention methodology. Maximum likelihood for a Gaussian time series

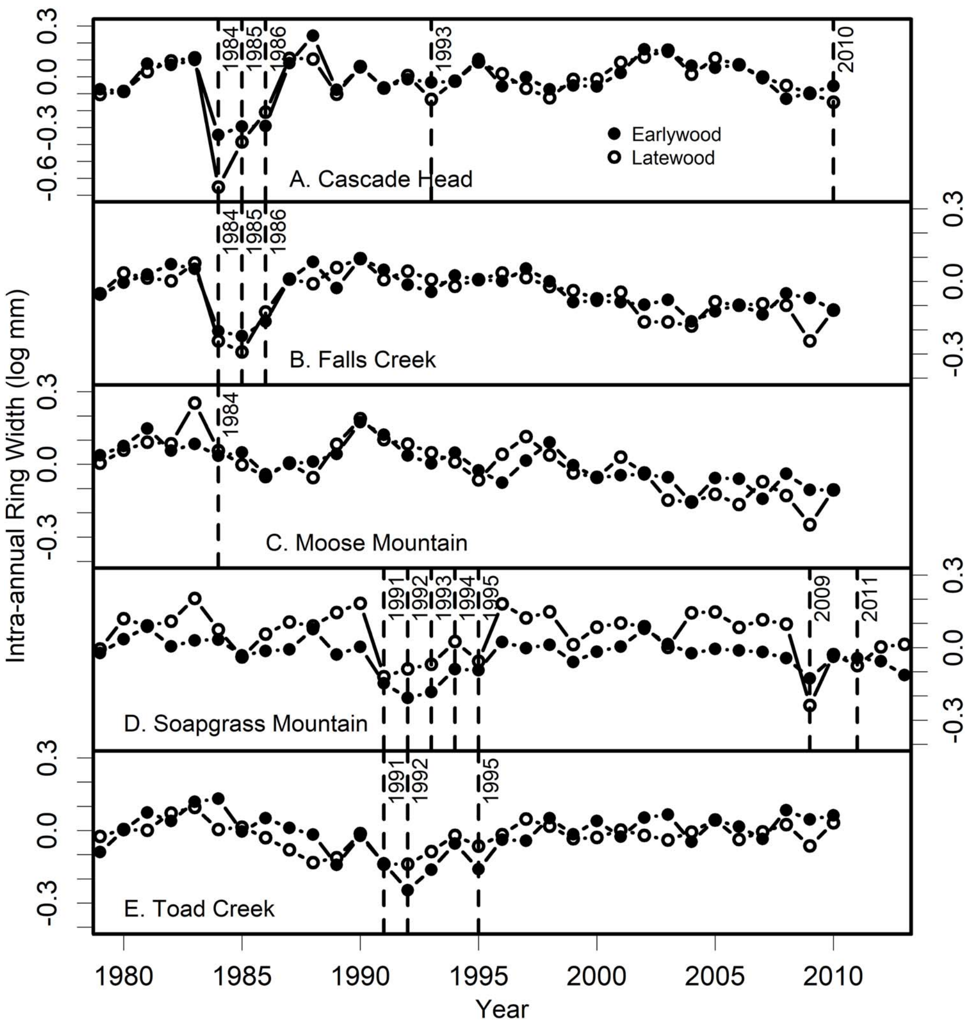

Figure 3. Time series plot of earlywood and latewood ring width chronologies for (A) Cascade head, (B) Falls Creek, (C) Moose Mountain, (D) Soapgrass Mountain and (E) Toad Creek. Diseased years were detected as low growth anomalies that could not be attributed to climate based on time series intervention analysis (Lee et al. 2017*a*). Diseased years are indicated by dashed vertical lines.

with a SARMA $(1,0)_2 \times (1,0)$ autocorrelation structure was used for parameter estimation and hypothesis testing to reconstruct the forest disturbance history of SNC outbreaks by site.

Climate data

Monthly mean maximum, minimum, and dewpoint temperatures, VPD and total precipitation data for the period 1895–2012 were obtained from the PRISM Climate Group at Oregon State University at http://prism.oregonstate.edu. Variables were obtained for the specific study site locations when spatially-interpolated climate data were available and for the nearest location or division otherwise (Lee et al. 2016). The divisional monthly Palmer Drought Severity Index data for the period 1895–2012 were obtained from the NOAA's National Climate Data Center (NCDC) at http://www.ncdc.noaa.gov. The PRISM climate and PDSI data correlated well with our local instrumental records for temperature, VPD, precipitation and total available soil moisture for the period 1998–2012 at each site (Lee et al. 2016). Because the local monitoring data do not capture the full period of the isotope and tree-ring width values, the PRISM and PDSI data were used as explanatory variables in our regression analysis. The climate variables used in the time series model were daily maximum air temperature, total precipitation, VPD and PDSI, which were summarized as seasonal averages that corresponded best with intra-annual growth and the dual stable isotopic ratios.

Results

Dendrochronological reconstruction of history of SNC impacts

The EW and LW tree-ring width chronologies for each sampling site were highly variable and responded synchronously to changes in VPD, temperature, precipitation and PDSI, and differentially to SNC depending on site conditions and elevation as indicated by low growth anomalies in some years (Figure 3). The site-specific time series models with pulse interventions to infer the growth–climate–disturbance relations and reconstruct the history of forest disturbance explained between 63% and 85% of the total variation in EW and LW ring widths (Table S2 available as Supplementary data at *Tree Physiology* Online). In general, both EW and LW radial stem growth increased with increasing precipitation, PDSI, and cool season (October to June) temperature and VPD, and decreased with increasing summer (July to September) temperature and VPD. The seasonal means for each climatic variable were calculated across one or multiple months and chosen for use as predictor variables in the time series regression model based on optimization of statistical fit and parsimony. Interannual variations in stem growth were related to current and antecedent seasonal climatic variables lagged one to four years rather than a 1-year lag as previously reported (Lee et al. 2017*a*). The EW and LW ring width chronologies for lower elevation Cascade sites (FC and MM) displayed a climate-induced multi-decadal declining growth trend since ~1990 during a period that included the two warmest decades on record (Figure 3B and C). In contrast, the LW ring width chronology for one high elevation Cascade site (SM) displayed an increasing growth trend since ~1978, indicating a positive growth response associated with a longer growing season due to increasing temperatures (Table S2 available as Supplementary data at *Tree Physiology* Online and Figure 3D). The tree-ring width chronologies for all sites displayed periodic low growth anomalies that could not be explained by climate based on time series intervention analysis. Anomalous growth reductions were synchronous at low- to mid-elevations across the region as evidenced by extremely narrow rings in the period 1984–86. which corresponded to growth reductions of 34% to 72% for the coastal site (CH) and 34% to 52% for FC. Similar low growth anomalies occurred in the years 1991–95 at the higher-elevation montane sites (SM and TC, Figure 3). These low-growth anomalies (i.e., disease signals) were the dominant pattern in the EW stem growth series for all sites except MM based on Kruskal's measure of relative importance (Table S4 available as Supplementary data at *Tree Physiology* Online). For MM, the interannual variations in EW stem growth series were largely explained by a climate-induced declining growth trend and only one disease signal (Table S4 available as Supplementary data at *Tree Physiology* Online). The years were classified as either healthy or diseased based on the dendrochronological reconstruction of forest disturbance history for each site (Figure 3 and Table S2 available as Supplementary data at *Tree Physiology* Online).

Isotope–climate–disturbance relations

Both Δ^{13}C and δ^{18}O in tree rings of mature Douglas-fir in western Oregon displayed high- and lower-frequency variations in response to VPD, temperature, precipitation and non-climatic anomalies for all five study sites (Figures 4 and 5). In general, the responses of stem growth, Δ^{13}C and δ^{18}O to the seasonal climatic variables were similar across sites, indicating that all three time series were the byproduct of the same physiological mechanisms. Climate and disease affected the mean and variance of the cellulosic stable isotope series, most notably for the coast site (CH) where the interannual variations in the Δ^{13}C and δ^{18}O series were substantially lower than the inland sites (Figures 4 and 5). For the rest of the results section, we focused on the results for Δ^{13}C and δ^{18}O time series in LW because the LW chronologies were more strongly influenced by current-year growing conditions than the EW chronologies. However, the growth–climate and isotope–climate models for Δ^{13}C and δ^{18}O in EW and LW were developed simultaneously because the EW and LW isotope ratio chronologies were modeled as a seasonal autoregressive time series (i.e., LW response considered the previous EW signal). Consequently, a growth or isotopic anomaly was sometimes detected in the EW series by a pulse intervention term but modeled as autocorrelation in the LW series and vice versa (Tables S2 available as Supplementary data at *Tree Physiology* Online and S3). The time series intervention model fit the LW stable isotope data well and explained 89% to 99% of the total variation in Δ^{13}C and 94% to 97% of the total variation in δ^{18}O (Table 2). The interannual variability in LW Δ^{13}C and δ^{18}O was primarily explained by warm and cool season climate variables for the current-year and previous 3 years (Table 3). Also, fewer isotope anomalies were identified, indicating that the disease signal in the dual stable isotope series was less pronounced than the climate signal based on Kruskal's measure of relative importance, most notably for CH, FC and SM (Table 3). For CH and FC where SNC severity was relatively modest to high, climate divergences were detected in the LW ring-width and δ^{18}O series but not in LW Δ^{13}C series based on the time series regression models (Table 3).

Consistent with the growth-climate relations, cellulosic Δ^{13}C increased with increasing precipitation, PDSI, and cool season temperature and VPD, and decreased with increasing summer evaporative demand (Table 2). Cellulosic δ^{18}O decreased with increasing precipitation, PDSI, and cool season temperature and VPD and increased with increasing summer evaporative demand. Apart from the expected change in signs of the model parameters, the isotope-climate relations differed in notable ways between the two isotopes, sites and intra-annual period (EW versus LW). In general, current- and previous-years VPD and temperature were the principal seasonal climatic variables affecting cellulosic LW Δ^{13}C for all sites based on Kruskal's importance values (Tables 2 and 3). High summer evaporative demand in the current year reduced LW Δ^{13}C for all sites, in particular for CH, MM and TC (Table 3). In contrast, cellulosic LW δ^{18}O was also strongly influenced by hydrological variables as well as temperature and VPD to varying degrees depending

Table 2. Cellulosic stable isotope responses of infected Douglas-fir to seasonal climatic variables based on time series intervention model of latewood δ^{18}O and Δ^{13}C chronologies 1980–2011 for Cascade Head (CH), Falls Creek (FC), Moose Mountain (MM), Soapgrass Mountain (SM) and Toad Creek (TC). Maximum likelihood estimates and the associated standard errors of the slopes (in brackets) for the measured climate variables are reported. Maximum likelihood estimates for the standard deviation of model error (σ) and autoregressive model parameters (θ_1 and ρ_1) for a first-order seasonal and regular autoregressive time series model are also reported. Divergences between the isotope values and climate are indicated by either a positive or negative pulse intervention term (e.g., I1984 = 0–1 indicator variable for 1984). The seasonal climatic variables are averaged across one or more months for either the previous years (e.g., SO_Prec$_{t-1}$ = total precipitation for previous-year September–October) or the current year (e.g., JJ_VPD$_t$ = average VPD for current-year June–July).

Site	Variable	Time series intervention model	ρ_1	θ_1	σ	R^2
CH	$\Delta\ ^{13}C_t$	21.7 + 0.075 JF_Tmax$_{t-3}$ + 0.00071 Feb_Prec$_{t-3}$ + 0.00137 Aug_Prec$_{t-3}$ (0.8) (0.013) (0.00011) (0.00044)—0.144 SO_Tmax$_{t-3}$ + 0.082 Apr_Tmax$_{t-2}$—0.122 Jul_Tmax$_{t-2}$ (0.028) (0.016) (0.019)—0.114 SO_Tmax$_{t-2}$ + 0.070 FM_Tmax$_{t-1}$—0.392 SO_VPD$_t$ (0.025) (0.017) (0.031)		0.87	0.18	0.89
CH	$\delta^{18}O_t$	33.0–0.00251 May_Prec$_{t-3}$—0.131 Jun_Tmax$_{t-3}$—0.067 Nov_Tmax$_{t-3}$ (0.6) (0.029) (0.021) (0.019)—0.116 Feb_Tmax$_{t-2}$—0.00056 MA_Prec$_{t-2}$—0.00189 Aug_Prec$_{t-2}$ (0.019) (0.00020) (0.00065)—0.112 MJ_VPD$_{t-1}$—0.00060 Feb_Prec$_t$—0.00221 Jun_Prec$_t$ + 0.424 JASO_VPD$_t$ (0.035) (0.00018) (0.00049) (0.058)—0.00418 AS_Prec$_t$ + 0.28 I1986$_t$ + 0.88 I1996$_t$ (0.00035) (0.13) (0.15)	0.39		0.09	0.97
FC	$\Delta\ ^{13}C_t$	13.2 + 0.121 FM_Tmax$_{t-3}$ + 0.052 Jan_Tmax$_{t-2}$ + 0.062 ND_Tmax$_{t-2}$ (0.4) (0.025) (0.021) (0.019) + 0.00020 pNDJF_Prec$_{t-1}$ + 0.00131 Mar_Prec$_t$ + 0.273 Apr_VPD$_t$ (0.00012) (0.00034) (0.034)—0.067 Jul_VPD$_t$ + 0.048 Oct_PDSI$_t$ (0.013) (0.020)	0.89	0.36	0.14	0.91
FC	$\delta^{18}O_t$	27.5–0.099 May_VPD$_{t-3}$—0.087 Nov_Tmax$_{t-3}$—0.149 Dec_PDSI$_{t-3}$—0.055 Nov_Tmax$_{t-2}$ (0.7) (0.025) (0.017) (0.025) (0.017)—0.00088 Dec_Prec$_{t-2}$—0.00130 Jun_Prec$_{t-1}$ + 0.080 Jul_Tmax$_{t-1}$—0.046 pDJ_Tmax$_t$ (0.00028) (0.00058) (0.018) (0.024)—0.126 JJ_PDSI$_t$—0.170 Jun_VPD$_t$ + 0.375 JAS_VPD$_t$ + 1.32 I1986$_t$ (0.022) (0.028) (0.027) (0.19)	0.28	0.89	0.30	0.97
MM	$\Delta\ ^{13}C_t$	21.0 + 0.054 FM_Tmax$_{t-3}$ + 0.038 Jun_VPD$_{t-3}$—0.067 AS_Tmax$_{t-3}$ (0.9) (0.016) (0.013) (0.019) + 0.00051 Nov_Prec$_{t-3}$—0.041 JJA_Tmax$_{t-1}$ + 0.050 Nov_Tmax$_{t-1}$ (0.00018) (0.019) (0.010)—0.390 JJASO_VPD$_t$ + 0.91 J I1987$_t$ (0.026) (0.13)	0.98	0.25	0.09	0.94
MM	$\delta^{18}O_t$	25.2 + 0.080 Aug_Tmax$_{t-3}$—0.104 pNDJ_Tmax$_{t-1}$—0.00160 FM_Prec$_{t-1}$ (1.1) (0.027) (0.023) (0.00035)—0.00520 Jun_Prec$_{t-1}$ + 0.113 JA_VPD$_{t-1}$—0.00261 Sep_Prec$_{t-1}$—0.091 pDJ_Tmax$_t$ (0.00076) (0.00045) (0.00053) (0.028)—0.00198 MJJAS_Prec$_t$—0.095 Jun_VPD$_t$ + 0.214 JAS_VPD$_t$ + 0.198 Aug_VPD$_t$ (0.00040) (0.022) (0.029) (0.025) + 1.28 I1985$_t$ (0.17)	0.45	0.97	0.48	0.97
SM	$\Delta\ ^{13}C_t$	17.2 + 0.022 May_VPD$_{t-3}$ + 0.00235 Jun_Prec$_{t-3}$—0.018 Jul_Tmax$_{t-3}$ (0.2) (0.005) (0.00019) (0.003) + 0.077 Feb_VPD$_{t-2}$ + 0.00100 FMA_Prec$_{t-2}$ + 0.00108 Jun_Prec$_{t-2}$ + 0.046 Apr_Tmax$_{t-1}$ (0.012) (0.00007) (0.00018) (0.004) + 0.00074 MJJ_Prec$_{t-1}$—0.072 JA_Tmax$_{t-1}$ + 0.064 Nov_Tmax$_{t-1}$—0.108 JA_VPD$_t$ (0.00010) (0.006) (0.003) (0.004) + 0.00111 AS_Prec$_t$—0.47 I1993$_t$ (0.00014) (0.05)		0.85	0.06	0.99
SM	$\delta^{18}O_t$	26.3–0.063 max(0,Year$_t$-1987)—0.205 Apr_VPD$_{t-2}$—0.00103 MJJA_Prec$_{t-2}$ (0.7) (0.016) (0.034) (0.00037) + 0.378 JASO_VPD$_{t-1}$—0.00268 Aug_Prec$_{t-1}$—0.072 Mar_Tmax$_t$—0.124 Jun_VPD$_t$ (0.035) (0.00107) (0.018) (0.024) + 0.220 AS_VPD$_t$—0.163 ASO_PDSI$_t$ (0.034) (0.033)	0.55	0.72	0.25	0.94
TC	$\Delta\ ^{13}C_t$	16.7 + 0.101 Apr_VPD$_{t-2}$—0.052 JA_VPD$_{t-2}$ + 0.000787 Feb_Prec$_{t-1}$ + 0.00184 JAS_Prec$_{t-1}$ (0.3) (0.017) (0.011) (0.000203) (0.00040) + 0.00365 JA_Prec$_t$—0.025 JA_Tmax$_t$—0.118 Oct_VPD$_t$—0.32 I2006$_t$ + 1.06 I2010$_t$ (0.00065) (0.013) (0.011) (0.11) (0.11)	0.67		0.08	0.95
TC	$\delta^{18}O_t$	36.0–0.113 max(0,Year$_t$-2003)—0.00140 Feb_Prec$_{t-2}$—0.00468 AM_Prec$_{t-2}$ (1.2) (0.022) (0.00038) (0.00066)—0.096 Jun_VPD$_{t-2}$ + 0.085 Jul_VPD$_{t-2}$—0.124 ND_Tmax$_{t-2}$—0.00296 FM_Prec$_{t-1}$ (0.025) (0.022) (0.036) (0.00040)—0.00931 Jun_Prec$_{t-1}$—0.126 Jun_Tmax$_{t-1}$ + 0.068 JA_Tmax$_{t-1}$—0.327 pNDJ_Tmax$_t$ (0.00137) (0.028) (0.026) (0.036)—0.00240 MA_Prec$_t$—0.184 Jun_VPD$_t$—0.00846 JJ_Prec$_t$ + 0.208 AS_VPD$_t$ (0.00042) (0.024) (0.00117) (0.035)	0.22		0.13	0.97

Table 3. Kruskal value of importance for the structural time series model for latewood ring width, stable carbon and oxygen isotope ratios. The Kruskal method (Kruskal 1987) estimates the relative importance of each variable to the fit of the regression model. Each Kruskal value is the average of the squared partial correlation coefficients over all possible orderings of the predictor variables. Higher Kruskal values indicate greater relative importance within a site and growth period. Kruskal values ≥0.20 are in bold. Anomalies in tree-ring width and stable isotope ratios are modeled as pulse interventions calculated as the difference between the observed value and the climate-based prediction.

Site		Cascade Head			Falls Creek			Moose Mountain			Soapgrass Mountain			Toad Creek		
Component/variable	Time period[1]	$\Delta^{13}C$	$\delta^{18}O$	LW[2]	$\Delta^{13}C$	$\delta^{18}O$	LW[2]	$\Delta^{13}C$	$\delta^{18}O$	LW[2]	$\Delta^{13}C$	$\delta^{18}O$	LW[2]	$\Delta^{13}C$	$\delta^{18}O$	LW[2]
R^2		0.89	0.97	0.79	0.91	0.97	0.85	0.94	0.97	0.77	0.99	0.94	0.70	0.95	0.97	0.63
AR x SAR[3]		**0.25**	0.16	**0.34**	**0.29**	**0.34**	0.01	**0.21**	**0.38**	**0.29**	**0.27**	**0.30**	0.14	**0.22**	0.09	**0.32**
Precipitation/PDSI[4]	4	0.19	**0.29**		0.09	**0.26**	0.04	0.08	**0.22**	0.08	**0.42**	0.09		0.15	**0.38**	0.12
	3					0.10	0.06		**0.31**	0.09	**0.21**	0.10	0.05	0.07	**0.24**	0.15
	2		0.16												**0.22**	0.03
	1		**0.61**		0.18	**0.25**	0.11		0.17	0.16	**0.22**	**0.30**		**0.31**	**0.36**	
Temperature/VPD[5]	4	**0.43**	**0.43**	0.12	**0.44**	**0.34**	0.09	**0.34**	**0.20**	0.09	**0.45**	**0.20**	0.18	**0.32**	0.18	0.03
	3		0.02	0.03		0.18	0.05	0.05	0.16	0.05	**0.36**	**0.40**			**0.21**	**0.20**
	2			0.10	**0.38**	0.06	0.12	0.19	0.09	0.10	**0.36**	0.11	0.14		**0.29**	0.06
	1	**0.46**	**0.43**		**0.31**	**0.63**	**0.23**	**0.73**	**0.64**	**0.20**	**0.45**	**0.37**	0.10	**0.52**	**0.44**	0.05
Trend							**0.33**			0.17		**0.25**	0.18		**0.25**	
Pulses[6]			**0.23**	**0.57**		0.15	**0.49**	**0.22**	**0.21**	0.16	0.15		**0.27**	**0.41**		

[1] Seasonal climate variables for current- and previous-years were calculated as the mean (or total for precipitation) for one or more months within a growing season (GS = June–October) or dormant period (DP = November–May). The four time periods correspond to: (1) current-year June–October; (2) previous-year November to current-year May; (3) previous-year June–October; and (4) prior to previous-year June.

[2] Latewood ring width.

[3] Regular and seasonal autoregressive model component.

[4] Palmer drought severity index.

[5] Vapor pressure deficit.

[6] Pulse intervention terms to account for variation that cannot be attributed to climate.

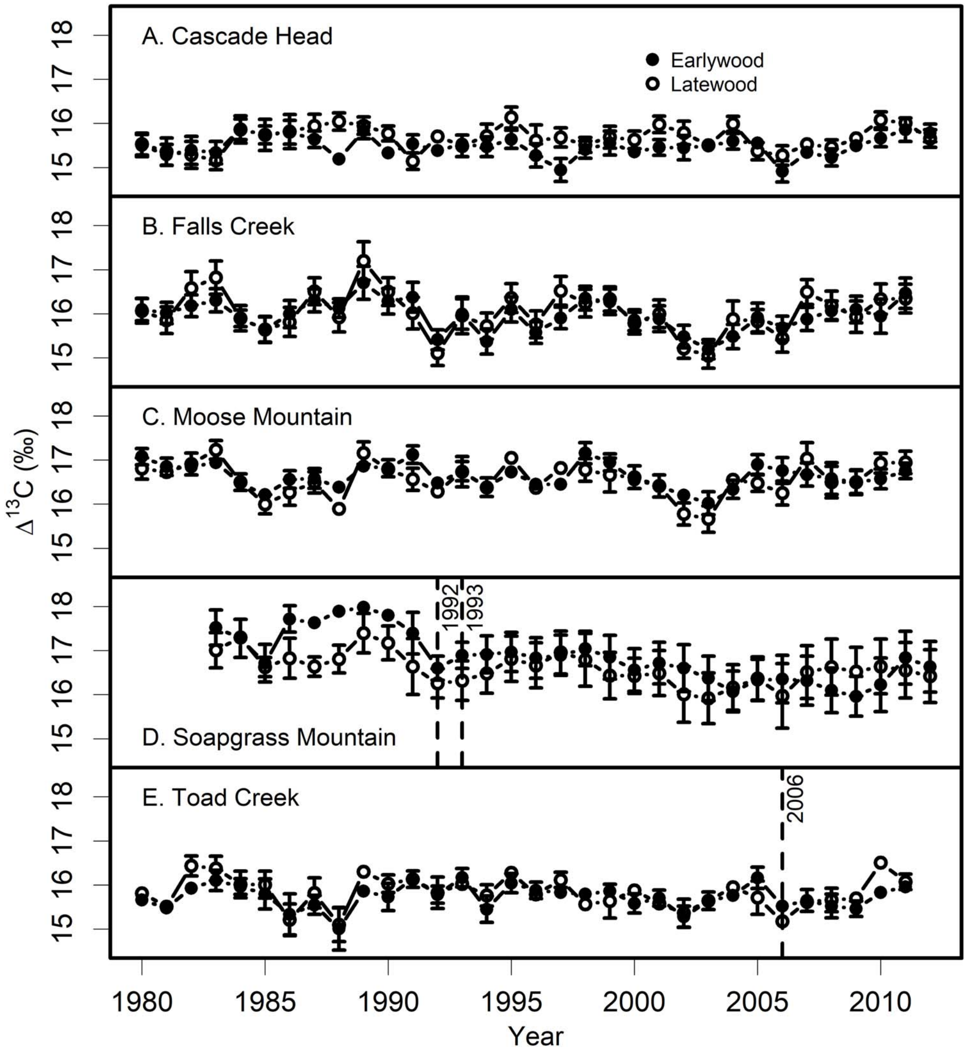

Figure 4. Time series plot of cellulosic $\Delta^{13}C$ in earlywood and latewood rings for (A) Cascade Head, (B) Falls Creek, (C) Moose Mountain, (D) Soapgrass Mountain and (E) Toad Creek. Error bars represent the standard error of the means. Diseased years were detected as low growth and $\Delta^{13}C$ anomalies that could not be attributed to climate based on time series intervention analysis. Diseased years are indicated by dashed vertical lines.

upon site conditions. For all sites, current-year summer evaporative demand and precipitation were the most important predictor variables for LW $\delta^{18}O$ based on Kruskal's measure of relative importance (Table 3).

Coherence of stem growth, $\Delta^{13}C$ and $\delta^{18}O$

Prior to examining the associations in dual stable isotope space, the tree-ring width, $\Delta^{13}C$ and $\delta^{18}O$ time series were detrended using spline regression to isolate the year-to-year variations associated with climate. The LW $\Delta^{13}C$ and $\delta^{18}O$ series for the two mid-elevation montane sites (FC, MM) responded uniformly and coherently to climate and disturbance as indicated by high inter-site correlations of 0.83 for $\Delta^{13}C$ and 0.94 for $\delta^{18}O$, in particular to the extreme summer droughts in 2002–2003 (Figures 4B, C and 5B, C). Similarly, for the two higher-elevation montane sites (SM, TC), the LW $\Delta^{13}C$ and $\delta^{18}O$ time series also responded uniformly and coherently to climate and disturbance as indicated by high correlations of 0.43 for $\Delta^{13}C$ and 0.40 for $\delta^{18}O$. The high inter-site correlations for both stable isotope ratio chronologies indicated that the interannual variability in $\Delta^{13}C$ and $\delta^{18}O$ were influenced primarily by a common climatic forcing regionally for inland sites where SNC severity was low. In contrast, LW $\delta^{18}O$ for CH was positively correlated with that of the four inland sites (0.29 to 0.50), but LW $\Delta^{13}C$ for CH did not correlate well with the four inland sites (−0.06 to 0.23), indicating a local divergence from climate in the $\Delta^{13}C$ time series for CH due to increased SNC severity. The positive inter-site correlations for LW $\delta^{18}O$ suggested that the interannual variability in LW $\delta^{18}O$ was likely influenced by regional environmental conditions rather than a local disturbance.

The LW $\Delta^{13}C$ time series for CH also did not correlate well with the LW $\delta^{18}O$ for CH, indicating a local divergence from climate in the carbon-isotope discrimination but not $\delta^{18}O$ in the

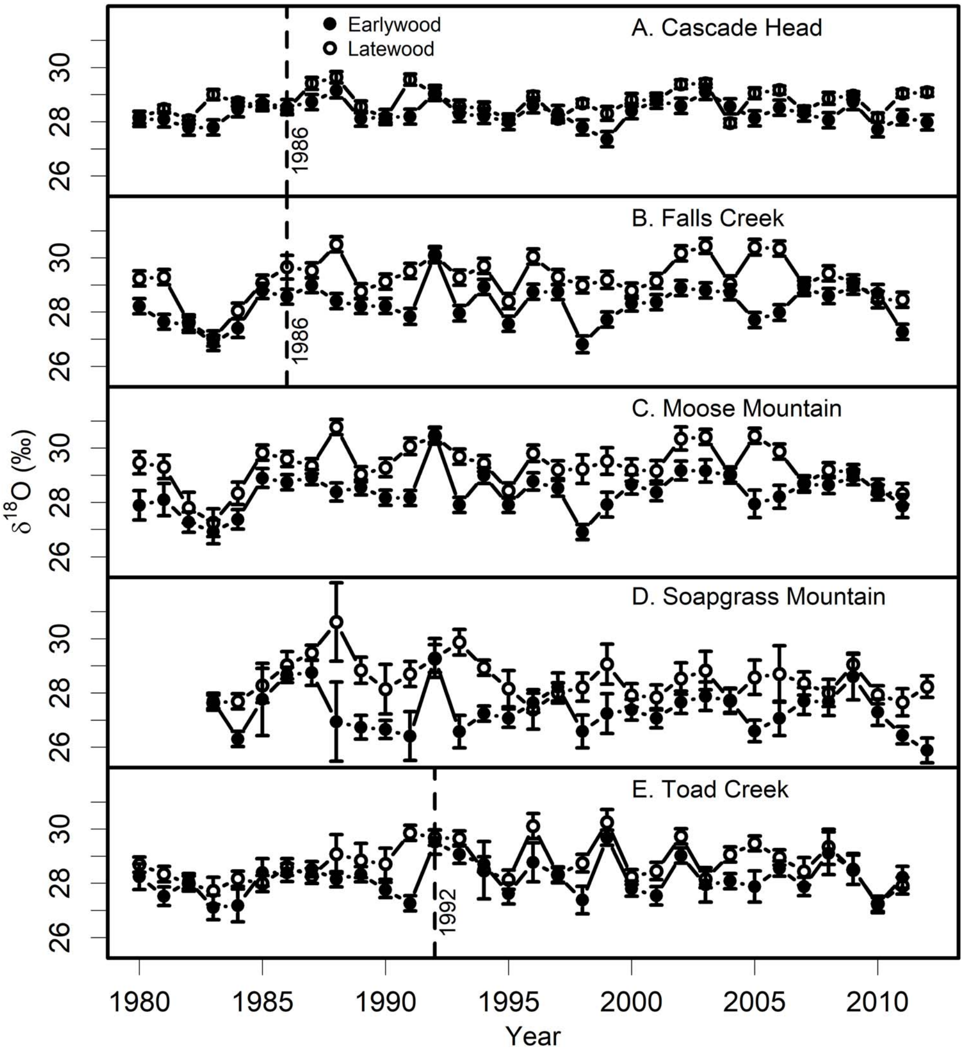

Figure 5. Time series plot of cellulosic $\delta^{18}O$ in earlywood and latewood rings for (A) Cascade Head, (B) Falls Creek, (C) Moose Mountain, (D) Soapgrass Mountain, and (E) Toad Creek. Error bars represent the standard error of the means. Diseased years were detected as low growth and high $\delta^{18}O$ anomalies that could not be attributed to climate based on time series intervention analysis. Diseased years are indicated by dashed vertical lines.

presence of high SNC severity (Figure 6A). In contrast, the LW $\Delta^{13}C$ and $\delta^{18}O$ for inland sites displayed substantial negative correlations (Figures 6B–E), indicating that the coherence in the dual stable isotope ratios were explained by a regional climate forcing in the presence of low SNC severity. In general, the $\Delta^{13}C$ and $\delta^{18}O$ chronologies in LW were more highly correlated than the EW values, and the LW $\Delta^{13}C$ chronologies were more negatively correlated with the LW $\delta^{18}O$ values for the mid-elevation sites (MM, FC) than the higher-elevation sites (SM, TC) (Table 4). For CH where temperature and water conditions were at or near the optimum range for tree growth and fungal development of *N. gaeumannii*, the $\Delta^{13}C$ and $\delta^{18}O$ values varied in a relatively narrow range, correlated poorly and displayed a weak seasonal pattern (Figures 4A and 5A).

Many of the EW and LW ring width series displayed substantial cross correlation with the dual stable isotopes and iWUE series for the four inland sites but not for CH (Table 4). The tree-ring width chronologies were generally positively correlated with $\Delta^{13}C$ values and negatively correlated with $\delta^{18}O$ and iWUE values for most sites with several exceptions, notably for CH and FC (Table 4). For CH, LW ring width correlated poorly with LW $\Delta^{13}C$, $\delta^{18}O$ and iWUE, particularly in diseased years 1984–86, when LW growth was reduced by 42% to 78%, whereas $\Delta^{13}C$ and $\delta^{18}O$ values fluctuated close to their respective means (Table 4 and Figure 7A and B). For FC and SM, LW ring width correlated positively with LW $\Delta^{13}C$ and negatively with LW $\delta^{18}O$ in healthy years, but, similar to CH, correlated differently to the dual stable isotopes in diseased years (Figure 7C–F). Results were similar for MM and TC (not shown). For FC and MM, LW stem growth was negatively correlated with iWUE in healthy years, indicating that the negative growth trend and concomitant rise in iWUE were attributed to decreasing g_s with increasing atmospheric evaporative demand in non-anomalous growth years (Figure 8). Non-climatic stress was indicated by

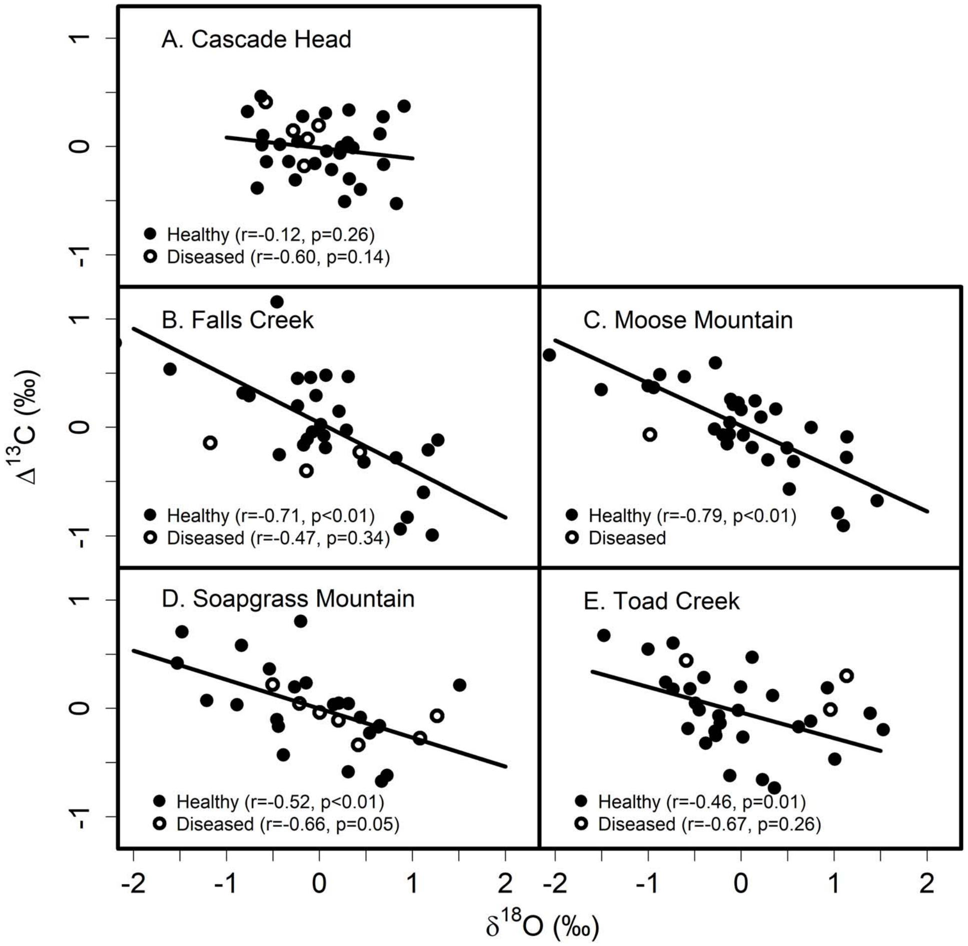

Figure 6. The relation between Δ^{13}C and δ^{18}O in latewood for (A) Cascade Head, (B) Falls Creek, (C) Moose Mountain, (D) Soapgrass Mountain, and (E) Toad Creek varied between healthy and diseased years. The dual stable isotope ratios were expressed as anomalies from their respective means and detrended to remove any climate-mediated trends (when present) in order to isolate the higher-frequency variability associated with climate.

Table 4. Pearson correlation coefficients of the cellulosic stable carbon and oxygen isotopes, intrinsic water-use efficiency (iWUE) and tree-ring width for five sites and two growth periods. Correlations in bold are significantly different from zero based on a one-sided *t*-test at 0.05 level of significance.

	Earlywood				Latewood			
Site	Δ^{13}C, δ^{18}O	Δ^{13}C, EW[a]	δ^{18}O, EW[a]	iWUE, EW[a]	Δ^{13}C, δ^{18}O	Δ^{13}C, LW[a]	δ^{18}O, LW[a]	iWUE, LW[a]
Cascade Head	−0.13	−0.48	0.12	0.30	−0.18	−0.16	0.23	0.28
Falls Creek	**−0.58**	**0.38**	−0.18	**−0.45**	**−0.66**	**0.46**	−0.09	**−0.55**
Moose Mountain	**−0.67**	**0.48**	**−0.38**	**−0.80**	**−0.77**	**0.41**	−0.29	**−0.77**
Soapgrass Mountain	−0.17, **−0.45**[b]	0.21, **0.34**[b]	−0.12, −0.12[b]	−0.15, −0.15[b]	−0.17, **−0.54**[b]	0.28, **0.42**[b]	**−0.31**, **−0.52**[b]	−0.27, **−0.52**[b]
Toad Creek	−0.25	−0.27	**−0.35**	0.20	**−0.39**	0.23	**−0.44**	−0.09

[a] Earlywood (EW) and latewood (LW) ring width.

[b] The EW ring width and Δ^{13}C, and LW ring width and δ^{18}O time series were detrended using spline regression to examine the correlations in the high-frequency interannual variations between the tree-ring width and dual stable isotope time series.

low growth anomalies that diverged significantly from climate, and by decreased variability in Δ^{13}C and δ^{18}O values. Climate stress was indicated by growth reductions < 25% and greater variability in dual stable isotope values and iWUE for all sites.

Discussion

Radial stem growth, Δ^{13}C and δ^{18}O in tree rings of mature Douglas-fir in western Oregon responds to a mixture of climate and disturbance signals that vary by location, elevation, site

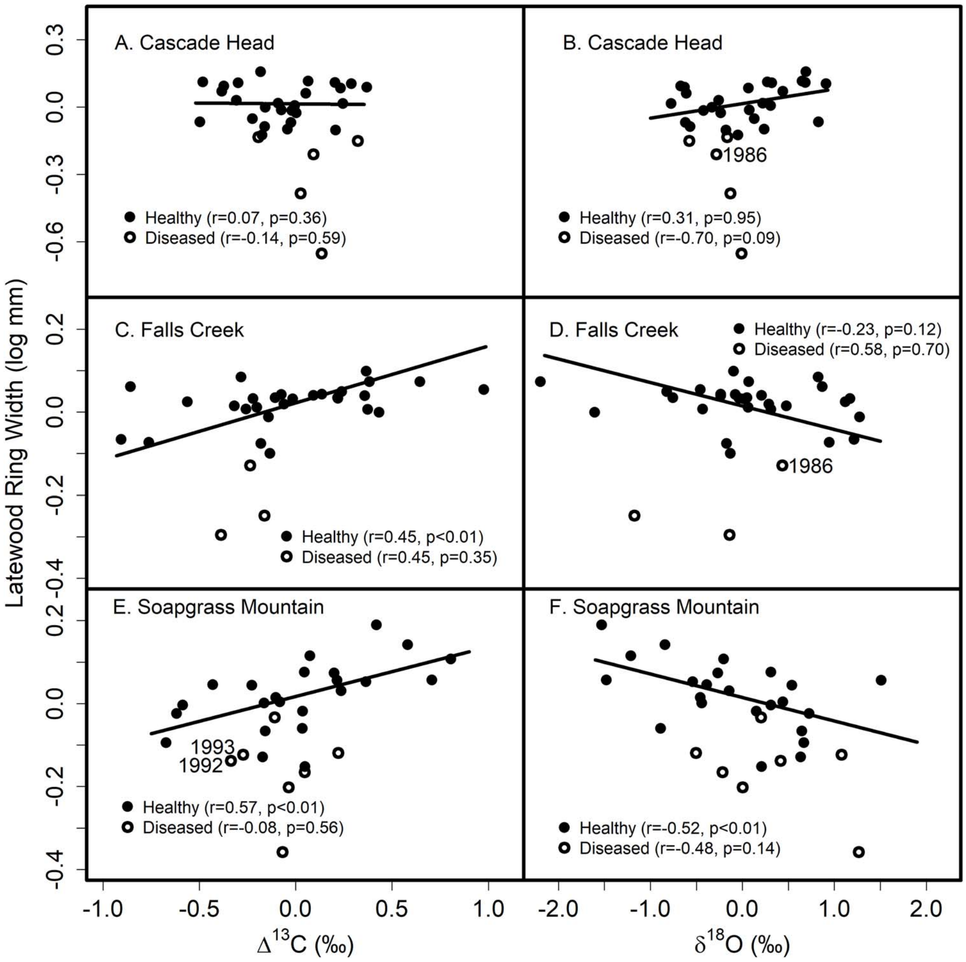

Figure 7. Latewood ring width of infected Douglas-fir was positively correlated with $\Delta^{13}C$ and negatively correlated with $\delta^{18}O$ at Cascade Head (A, B), Falls Creek (C, D) and Soapgrass Mountain (E, F). Several diseased years having reduced growth associated with Swiss needle cast were corroborated by either an anomalously low $\Delta^{13}C$ or high $\delta^{18}O$ value in the earlywood and/or latewood ring. These diseased years are annotated for the corroborating isotope value. The dual stable isotope ratios were expressed as anomalies from their respective means.

conditions and disease severity. Tree-ring width and the dual stable isotopes in tree-rings of Douglas-fir have been found to be good proxies of climate and disturbance, but the relation between tree growth and dual stable isotopes is complex in the presence of disturbance (Saffell et al. 2014*a*). The ambiguity in the dual stable isotope ratios and tree-ring width chronologies can be reduced by considering a multi-proxy approach to understand the inter- and intra-annual variations in growth and stable isotope chronologies in response to climate and biological disturbance agents across a climate and disease gradient. However, the growth, isotopic and physiological responses to climate are difficult to infer under natural changing environments (e.g., Savard and Daux 2020, Seibt et al. 2008) or in the presence of forest disturbance agents (i.e., pests, diseases, fire) (Saffell et al. 2014*a*). Any unexplained biotic and abiotic sources of variability influencing A and g_S will reduce the ability to interpret the physiological meaning of stable isotope discrimination (Werner et al. 2012). Consequently, it is important to separate the confounding effects of climate and disturbance on the dual stable isotope ratios in infected Douglas-fir tree-rings to interpret their physiological meaning in terms of the two limiting rates.

Variations in $\Delta^{13}C$ are related to iWUE which varies with changes to A and g_S (Farquhar et al. 1989), while variations in $\delta^{18}O$ reflect changes in VPD, which influences g_S and the $\delta^{18}O$ of source water (Kahmen et al. 2011, Roden and Ehleringer 2007). Tree-ring $\Delta^{13}C$ varied from 15 to 18‰ across our five study sites in western Oregon and decreased with decreasing water availability, consistent with soil moisture trends in tree-ring $\delta^{13}C$ in this region (Roden et al. 2005). Tree-ring $\delta^{18}O$ varied from 26 to 30‰ across the five sites due in part to differences in source water across the sites and variation in leaf water enrichment. Increasing VPD associated with increasing temperature or decreasing precipitation increased $\delta^{18}O$ in Douglas-fir tree rings, consistent with other studies that showed a strong $\delta^{18}O$ response to evaporative demand under low RH (Roden and Ehleringer 2007) and to precipitation $\delta^{18}O$ under high RH (Miller et al. 2006). Strong correlations between

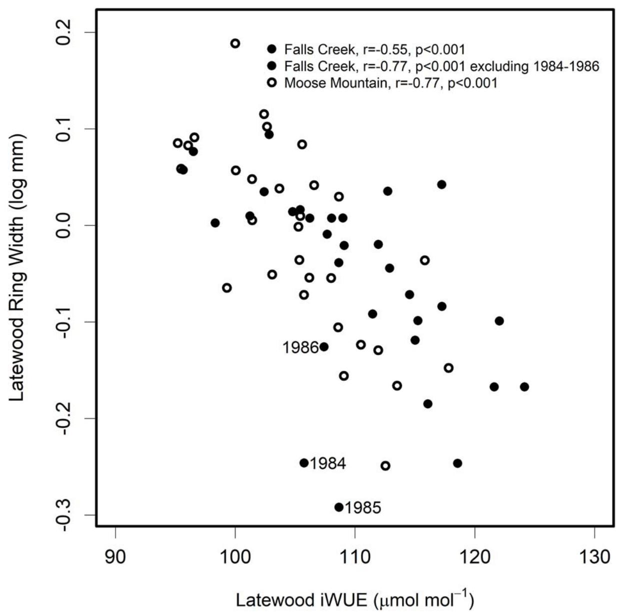

Figure 8. Relationship between latewood intrinsic water-use efficiency (iWUE) and latewood ring width for Falls Creek and Moose Mountain. Stem growth was negatively correlated with iWUE, indicating that growth was reduced by decreasing g_s with increasing evaporative demand. Several diseased years in 1984–86 for Falls Creek were divergent from the healthy years, indicating growth was reduced by decreasing a associated with stomatal occlusion and early needle abscission due to Swiss needle cast.

δ^{13}C and summer temperature have been reported in coastal California redwoods (*Sequoia sempervirens*) (Johnstone et al. 2013) and Scots pine (*Pinus sylvestris* L.) in Finland (Hilasvuori et al. 2009), but the δ^{13}C linkage to temperature is indirect because stomatal conductance and photosynthesis are more directly influenced by VPD and sunlight, which are correlated with temperature (Berninger et al. 2000). Similarly, δ^{18}O in tree rings is correlated with RH (Barnard et al. 2012) and δ^{18}O of precipitation (Anderson et al. 1998, Burk and Stuiver 1981). These findings in Oregon and Washington state in the USA indicate that tree-ring δ^{18}O is influenced by the δ^{18}O in meteoric water and atmospheric vapor, atmospheric humidity and VPD (Roden et al. 2000). The δ^{18}O-precipitation relation primarily reflects variability in δ^{18}O of source water during different periods of the growing season throughout the Pacific coast region (Johnstone et al. 2013).

In Mediterranean environments with an annual summer drought, high evaporative demand in the summer decreases g_s, Δ^{13}C and tree growth, and increases δ^{18}O and iWUE. Growing season humidity deficit is the primary factor limiting g_s of Douglas-fir along a climatic gradient in Oregon based on variations in δ^{13}C in foliage (Panek and Waring 1997). Trees growing at drier sites had lower growth rates and higher iWUE than trees at wetter sites (Panek and Waring 1997, Roden et al. 2005). For inland sites where SNC severity was low-to-moderate and intermittent, interannual variations in stem growth, Δ^{13}C and δ^{18}O in tree rings were primarily attributed to summer VPD, and to a lesser degree, winter temperature for the current- and previous-years based on statistical fit. Changes in Δ^{13}C values were concurrent with changing δ^{18}O and stem growth for the inland sites (Figure 6), indicating that variations in the growth and isotopic chronologies reflected changes in g_s in response to high summer evaporative demand, consistent with Barnard et al. (2012), who found a strong correlation between cellulosic δ^{18}O and RH, as well as between Δ^{13}C and δ^{18}O, and related it to temporal variation in g_s. Annual variations in tree growth and the dual stable isotopes in tree rings are best explained by VPD and temperature as studies have shown that stomata in mature Douglas-fir trees are responsive to VPD (Bond and Kavanagh 1999). Growth decline of healthy Douglas-fir are attributed to a reduction in g_s based on the relations between δ^{18}O and δ^{13}C in tree rings (Barnard et al. 2012, Jansen et al. 2013). The isotopic responses to VPD are consistent with other studies that have found that the spatial variability in carbon and oxygen isotopic composition is associated with changes in VPD across a precipitation gradient in western Oregon (Bowling et al. 2002) and the southwestern USA (Szejner et al. 2018). Prolonged periods of high VPD conditions during the summer drought reduce g_s and leads to reduced A and ultimately reduced annual stem growth regionally.

Annual stem growth is also reduced periodically by SNC in Douglas-fir stands throughout the region (Black et al. 2010, Lee et al. 2013, 2017*a*) with or without a synchronous change in the cellulosic dual stable isotope chronologies (Barnard et al. 2012, Saffell et al. 2014*a*). Swiss needle cast impacts on growth of mature Douglas-fir are evident throughout western Oregon and are most severe and frequent within the coastal fog zone and least severe at warmer, drier sites inland (Lee et al. 2017*a*). In contrast to inland sites, changes in Δ^{13}C values for CH were not concurrent with changing δ^{18}O and stem growth and were also asynchronous with Δ^{13}C values for the inland sites, and the range of isotopic variation at CH was much smaller than inland sites. Three possible causes for a lack of coherency and limited range of Δ^{13}C and δ^{18}O series for CH are: (i) SNC impact on functioning stomata reduced g_s and A (Manter et al. 2000) reducing temporal variance in tree-ring Δ^{13}C and disconnecting physiological responses to climate; (ii) SNC has a substantial effect on tree-ring Δ^{13}C but has no effect on δ^{18}O of severely infected Douglas-fir (Saffell et al. 2014*a*); and (iii) CH has much higher RH than the inland sites reducing any sensitivity to g_s, and variation in annual precipitation δ^{18}O inputs is small (mean annual Newport OR precipitation $\delta^{18}O = -7.1 \pm 0.6$ SD, J.R. Brooks, unpublished data), both of which would reduce variation in cellulosic δ^{18}O. The lack of coherency of stem growth and dual stable isotope series can occur in SNC-infected Douglas-fir trees because cellulosic Δ^{13}C records the average needle function with stomatal occlusion due to SNC but stem growth responses to total leaf area which can be more dynamic. Decreased growth in coastal Douglas-fir with heavy SNC infection is primarily attributed to a reduction in A through the loss of foliage (Maguire et al. 2002) rather than the average needle A recorded in cellulosic Δ^{13}C. In Douglas-fir trees severely impacted by SNC within the coastal fog zone of Oregon, only current and 1-year-old needles are retained (Hansen et al. 2000) resulting in a reduction in tree volume growth >23% (Maguire et al. 2002). Needle abscission generally occurs once pseudothecia density exceeds a threshold of 25–50% (Hansen et al. 2000, Manter et al. 2003). Prior to early needle abscission, g_s in 1- and 2-year needles decreases linearly with increasing pseudothecia density whereas photosynthesis in infected current-year needles is uninhibited (Manter et al. 2003, Manter and Kavanagh 2003). The decreased variability in Δ^{13}C in tree-rings for CH is consistent with a blockage of stomates by pseudothecia of *N. gaeumannii* which reduces g_s by about 83% and A by about 72% (Manter et al. 2000), and a decline in g_s (Day et al. 2001) and A at high VPD (Yoder et al. 1994) as trees mature. In contrast, the greater variability in Δ^{13}C for the inland sites is consistent with decreased pseudothecia incidence and disease severity due to less favorable environmental conditions for fungal dynamics (Lan et al. 2019). For CH, at high RH when SNC infections tend to be high, the oxygen isotope exchange with atmospheric vapor is substantially higher and dominates the δ^{18}O signal in tree-rings, minimizing any potential impact of g_s on δ^{18}O (Brooks and Mitchell 2011, Roden and Ehleringer 1999). Swiss needle cast is mediated by climate and affects the physiological processes of infected Douglas-fir needles in most years with or without an apparent immediate reduction in tree growth, which responds more to total leaf area.

Our findings suggest that there is clear potential in using tree-ring width and Δ^{13}C chronologies for paleoclimatic reconstruction of disturbance history in SNC-infected mature Douglas-fir stands provided data from Douglas-fir or co-occurring species are sampled along a disease gradient, consistent with Saffell et al. (2014*a*). In a fungicide trial, basal area increment and Δ^{13}C in treated, young, plantation-grown Douglas-fir responded positively and immediately to the treatment with no change in δ^{18}O (Saffell et al. 2014*a*). The disease signal in the tree-ring width series was synchronous across the region at low and higher elevations and expressed as periodic low growth anomalies, which were detected as climate divergences based on the time series regression model (Lee et al. 2013, 2017*a*). In contrast, the disease signal in the Δ^{13}C series was local and most evident within the SNC impact zone and was expressed as low variability and a lack of coherence in the Δ^{13}C series for CH with other proxy series. The time series regression model detected few climate divergences in the Δ^{13}C series for CH because high SNC severity suppressed the variability in the Δ^{13}C series to fluctuate in a narrow range about its mean during years with or without a change in growth. The lack of a positive correlation between stem growth and Δ^{13}C for CH indicated that the growth response to SNC was from total leaf area dynamics, whereas climate impacts on growth are responding to the average needle function which would be recorded in Δ^{13}C. Stem growth, isotopic and physiological responses to SNC are more evident and coherent in young than the less-severely diseased mature Douglas-fir in coastal Oregon (Saffell et al. 2014*a*). These age differences in growth and stable isotopes in tree-rings may be due to differences in specific leaf area, branch elongation, needle thickness, ontogeny or disease severity (Grulke and Miller 1994, Lan et al. 2019, Woodruff et al. 2004). A more pronounced Δ^{13}C response to SNC for young Douglas-fir trees is consistent with lower foliage retention and higher incidence of disease for 2-year-old needles of young Douglas-fir trees than mature trees throughout western Oregon (Lan et al. 2019). The incidence of disease is highest for 2-year-old needles of young trees and 3–to 5-year-old needles of mature trees, indicating fungal development and needle colonization are enhanced in young stands relative to mature stands due possibly to age differences in morphology and needle function (Lan et al. 2019).

While SNC affected Douglas-fir growth and physiological processes at local and regional scales, the tree-ring width, Δ^{13}C and δ^{18}O series were affected by common climate forcings associated with large-scale maritime oscillations such as the El Niño-Southern Oscillation (ENSO), the Pacific North American pattern, and the Pacific Decadal Oscillation (PDO) (Abatzoglou et al. 2014, Dalton et al. 2013), consistent with known mechanistic processes and prior studies (Barnard et al. 2012, Lee et al. 2013, 2016, 2017*a*). For less-infected inland Douglas-fir, stem growth, cellulosic Δ^{13}C and δ^{18}O responded similarly and synchronously to seasonal climatic factors for the current- and previous-years for lags up to 4 years for ring width and 3 years for the dual stable isotope ratios. The LW series of Δ^{13}C and δ^{18}O series for Douglas-fir were more strongly influenced by high summer evaporative demand in the current growing season than the EW series, consistent with other studies (Barnard et al. 2012, Johnstone et al. 2013, Saffell et al. 2014*a*). In contrast, interannual variations of EW and LW ring width were more strongly influenced by antecedent conditions, consistent with other studies that report only 20–40% of the annual variation in stem growth is explained by current-year conditions (Anderegg et al. 2015, Ogle et al. 2015). Empirical and modeling studies indicate that the impact of antecedent environmental conditions is species specific and is controlled by organ (i.e., buds, leaves, sapwood) and reserve lifetimes (Zweifel and Sterck 2018). Conceptually, mature Douglas-fir trees having up to 11 needle age classes in western Oregon are considered to have a strong legacy effect via the contribution of each needle cohort to current assimilation and transpiration and ensuing growth. Recent studies have shown that environmental conditions over years and decades affect the amount and availability of stored carbon serving the current physiological performance of a tree (Martínez-Vilalta et al. 2016). Evidence suggests that SNC can also affect the amount and availability of stored NSC reserves for use in formation of current-year wood in coastal Douglas-fir (Saffell et al. 2014*b*). According to the carbon-starvation hypothesis, stomatal closure during periods of high evaporative demand to maintain plant water status and decrease risk of hydraulic failure comes at a cost of reduced CO_2 uptake and carbon assimilation (Meinzer et al. 2016). Several consecutive years of hot dry summers can lower A and cause reductions in carbohydrate reserves from the continued demand of carbohydrates for respiration and other metabolic processes (McDowell et al. 2011). Alternatively, SNC can also decrease A and g_s and the buildup of carbohydrate reserves in Douglas-fir with heavy SNC infection through the loss of foliage (Maguire et al. 2002). These reductions in stored NSC may impair the plant's ability to defend against pest attacks and have carryover effects on primary and secondary growth processes for several years. The decoupling of stem growth and current climate due to remobilization of stored carbon is consistent with several dendroisotopic studies that showed a complacent stem growth response to current environmental conditions with changing Δ^{13}C and/or δ^{18}O (Barnard et al. 2012, Ratcliff et al. 2018).

The carry-over effect in stable isotope ratios of Douglas-fir trees is consistent with several studies that show both EW and LW contained information from starch δ^{13}C formed in previous years (Kagawa et al. 2006). Remobilization of starches from one year to the next or intra-annually can alter the cellulosic stable isotopic ratio values in any given year (Farquhar et al. 2007, Gessler et al. 2014, Helle and Schleser 2004, Offermann et al. 2011, Ogée et al. 2009, Tepley et al. 2020). The LW ring width, Δ^{13}C and δ^{18}O chronologies are better proxies of current-year climate than the EW chronologies, because EW production uses stored photosynthates from the previous year while LW is formed more from current photosynthate (Helle and Schleser 2004, Kagawa et al. 2006, McCarroll and Loader 2004). The intra-annual sampling of EW, LW and/or middlewood series of ring width and cellulosic stable isotopes has been shown to enhance the ability to infer the regional climate and disturbance signals (Barnard et al. 2012, Johnstone et al. 2013, Lee et al. 2016, Saffell et al. 2014*a*), which could have otherwise been masked (Tepley et al. 2020). Similarly, the dual stable isotope series in tree-rings combined with concurrent growth data from live and dead trees have been used to examine whether hydraulic failure or carbon starvation are stronger predispositions to drought-induced tree mortality, which cannot be proven based on dendrochronological data alone (Gessler et al. 2018).

Rising temperatures in recent decades have strongly affected Douglas-fir growth in the PNW directly by a physiological response to higher evaporative demand during the annual summer drought and indirectly by a major SNC epidemic that is expanding regionally to cooler environments at higher latitudes or higher elevations (Lee et al. 2013, 2016, 2017*a*, Ritóková et al. 2016). Regional differences in growth and physiological responses to changing climate and SNC severity are expected. Temperature stress will likely continue to increase in PNW terrestrial ecosystems as summer temperatures are predicted to continue rising. The current SNC epidemic is also expected to continue and expand regionally to cooler environments at higher latitudes and/or higher elevations in the PNW as winter temperatures become less limiting for fungal development.

Conclusion

Annual growth and physiological responses of mature Douglas-fir to climate and low-growth anomalies attributed to SNC were strongly synchronized across western Oregon, but the role of climate and SNC varied between coastal and inland sites. Summer VPD was the principal seasonal climatic variable affecting radial stem growth and the dual stable isotope ratios at all inland sites. At a coastal Oregon site within the SNC impact zone, interannual variations in stem growth was primarily influenced by SNC-driven leaf-area dynamics, while Δ^{13}C values were low with low variability reflecting continually impaired needle function due to SNC. A mild climate with higher RH resulted in complacent cellulosic δ^{18}O unrelated to growth or Δ^{13}C values. At sites on the west slopes of the Cascade Range of Oregon, stem growth decreased primarily due to decreasing g_s in response to high evaporative demand and a concomitant reduction in A. The synchronous multi-decadal decline in annual growth rates and rise in iWUE at mid- to lower-elevations inland were indicative of a downward trend in g_s that is expected to continue with increasing temperature. The dual stable isotope values in tree-rings of mature Douglas-fir were not as sensitive as stem growth for detecting low-growth anomalies such as those resulting from SNC outbreaks, but better at indicating climate responses. A multi-proxy approach that includes stem growth and cellulosic stable carbon and oxygen isotopic ratios in tree-rings separated by growth period is recommended for understanding the coherent growth and physiological responses to climate in the presence of forest disturbances.

Authors' contributions

E.H.L., P.A.B., and J.R.B. conceived of and designed the study. E.H.L. and P.A.B. collected the field data and tree core samples, and E.H.L., W.R. and J.R.B. processed the tree core samples in the laboratory. E.H.L. and C.W. analyzed the time series data with input and guidance from J.R.B.. E.H.L. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

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Conflicts of interest

None declared.

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Distribution of a Foliage Disease Fungus Within Canopies of Mature Douglas-Fir in Western Oregon

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Nothophaeocryptopus gaeumannii is a common native, endophytic fungus of Douglas-fir foliage, which causes Swiss needle cast, an important foliage disease that is considered a threat to Douglas-fir plantations in Oregon. Disease expression is influenced by fungal fruiting bodies (pseudothecia), which plug the stomata and inhibit gas exchange. Trees are impacted when pseudothecia plug stomates on 1-year-old and older needles resulting in early needle abscission. Mature (100 years+) trees appear to be less impacted from disease, and we hypothesize this is due to the greater emergence of pseudothecia on older than younger needles, which allows for more needle retention. We measured the density of pseudothecia occluding stomates across 2- to 5-year-old needles from upper, middle, and lower canopy positions of mature trees at three sites in the Oregon Coast Range and two sites in the western Oregon Cascade Mountains. Binomial generalized linear mixed model (GLMM) was used to test for the effects of canopy position (upper, middle, and lower), sites, needle age (2–5 years old), and years (2016 and 2017), and their interactions on the pseudothecia density. Pseudothecia density varied annually depending on sites, needle age and canopy positions. Pseudothecia density peaked on 3-, and 4-year-old needles, however, needles emerging from the same year, like 2-year-old needles in 2016 and 3-year-old needles in 2017 both emerged in 2014, had consistently similar patterns of pseudothecia density for both years, across site and canopy positions. Canopy position was important for 3-, and 4-year-old needles, showing less pseudothecia in the lower canopy. This research confirms that *N. gaeumannii* pseudothecia density is greatest in 3- and 4-year old needles in mature trees in contrast to plantations where pseudothecia density usually peaks on 2-year-old needles, and that pseudothecia density (disease severity) is generally lower in mature trees. Something about mature forest canopies and foliage appears to increase the time it takes for pseudothecia to emerge from the needles, in contrast to younger plantations, thus allowing the mature trees to have greater needle retention.

Keywords: Douglas-fir, fungal disease, foliar pathogen, *Nothophaeocryptopus gaeumannii*, Swiss needle cast, tree canopy

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INTRODUCTION

Nothophaeocryptopus gaeumannii is a common native, endophytic fungus which occurs only in Douglas-fir (*Pseudotsuga menziesii*) foliage (Hansen et al., 2000). The fungus can cause a foliage disease known as Swiss needle cast, which is currently defoliating and decreasing growth of Douglas-fir along the Pacific Coast in Oregon, Washington, and SW British Columbia (Ritóková et al., 2016; Shaw et al., 2021). Disease is caused when the fruiting bodies of the fungus, known as pseudothecia (**Figure 1**), emerge from and plug the stomates which causes reduced gas exchange and carbon starvation (Manter et al., 2000). This fungus may be unusual for a pathogen in that newly emerged needles are the predominant substrate for new infection by ascospores (Rohde, 1937; Chastagner and Byther, 1983) and colonization within needles is exclusively intercellular and non-lethal to cells (Stone et al., 2008a). Swiss needle cast induced reductions in tree growth of coastal Douglas-fir stands vary in space and time depending upon elevation, aspect, proximity to the coast, and site conditions and primary environmental factors influencing the degree of pathogen dynamics (Rosso and Hansen, 2003; Coop and Stone, 2007). Evidence from dendrochronological studies indicate that Swiss needle cast impacts in Oregon were least severe in the first half of the 20th century and increased in frequency, severity and range after ∼1980 due to increasing winter temperature associated with climate change (Black et al., 2010; Lee et al., 2013, 2017). The Swiss needle cast epidemic in the most recent decades is a primary economic and ecological concern to the timber industry in the Pacific Northwest because disease severity is greater in young coastal Douglas-fir plantations than in mature stands but reasons for this remains elusive (Lan et al., 2019; Mildrexler et al., 2019). Coastal young Douglas-fir trees typically retain up to 4 years of needles but may have only current and 1-year-old foliage in severely infected plantations (Hansen et al., 2000; Maguire et al., 2002; Zhao et al., 2011) due to early needle abscission when between 25 and 50% of the stomates are occluded (Hansen et al., 2000; Manter et al., 2003; Stone et al., 2008a). Anecdotal evidence from epidemiological studies suggest needle retention appears to drive the growth impacts on the tree, with foliage retention of only 2 years causing a reduction in growth of about 30% (Maguire et al., 2002, 2011; Shaw et al., 2021). Needle retention and fungal fruiting body presence and abundance on 1- and 2-year-old foliage have routinely been used as indices of disease severity in Douglas-fir plantations (Hood, 1982; Michaels and Chastagner, 1984; Hansen et al., 2000). However, disease severity on 2-year-old needles may be misleading for mature Douglas-fir trees which typically have greater needle retention of more than 5 years (Lan et al., 2019) and lesser frequency and magnitude of growth losses (Lee et al., 2017).

Recent epidemiological evidence suggests that disease severity, as measured by incidence times the percentage of pseudothecia occluding stomates (Mulvey et al., 2013), is greatest in 2-year-old needles for young trees, and 3–5 year-old needles for older trees (Lan et al., 2019). The reason for this difference remains elusive, as foliar nitrogen and leaf wetness did not explain the difference. The reason mature trees have greater foliage retention, and are healthier, may be influenced by the timing of pseudothecia emergence. While there is considerable epidemiological evidence of disease severity for young Douglas-fir plantations in coastal Oregon and Washington (Ritóková et al., 2016, 2021), the data and knowledge gaps of disease severity for mature Douglas-fir are large due primarily to comparably few epidemiological studies on mature Douglas-fir and scaling issues from sampling only 2-year-old needles for measuring incidence.

This manuscript extends our previous epidemiological study (Lan et al., 2019) to examine the differences in disease severity between needle age classes and canopy position of mature Douglas-fir trees based on within-leaf measurements of the density of pseudothecia occluding stomates. There is no published data on pseudothecia density of multiple needle age classes in mature trees. Lan et al. (2019) found a greater percentage of 3–5 year-old needles of mature Douglas-fir were infected by the presence of pseudothecia than younger needles, but the amount of stomata occluded by pseudothecia on infected needles (i.e., pseudothecia density) was not measured. Consequently, the pathogenicity of *N. gaeumannii* and epidemiology of mature trees are still not very clear. Because the physiological effects of SNC (impaired CO_2 uptake and photosynthesis) are associated with the physical blockage of stomata, the density of pseudothecia occluding stomates is a relevant response variable for assessing disease severity across needle age classes and canopy positions of mature trees. We hypothesized that disease severity is less in mature trees because the time since initial infection to the emergence of pseudothecia is longer for mature than young trees. Within the mature tree crowns, we also explored whether pseudothecia density varied with needle age, canopy position, and site. We believe that this analysis provides important insight into spatial and temporal dynamics of Swiss needle cast disease progression in mature tree canopies. Also, filling a data gap of the differences in mature and young trees can lead to a better understanding of the ecology and epidemiology of this important foliage disease.

MATERIALS AND METHODS

Study Sites

We sampled the same mature trees from five of the seven sites in western Oregon that were included in the study by Lan et al. (2019); three sites were in the long-term ecological monitoring plot (LTEM) system established by the United States Environmental Protection Agency (hereafter EPA; Lee et al., 2007; Beedlow et al., 2013) and two sites were not part of the LTEM system. Moose Mountain and Falls Creek are located on the west slope of the Cascade Range in the Willamette National Forest, and Cascade Head, Woods Creek, and Klickitat Mountain are in the Siuslaw National Forest in the Coast Range (**Figure 2**). The forests were unmanaged mature stands of Douglas-fir that were 120–150 years old and ranged in height from 55 to 70 m. Elevation of sites varied from 140 to 670 m. Annual precipitation varied from 1700–2500 mm. Associated tree species included western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*), in Cascade Head Sitka spruce (*Picea sitchensis*)

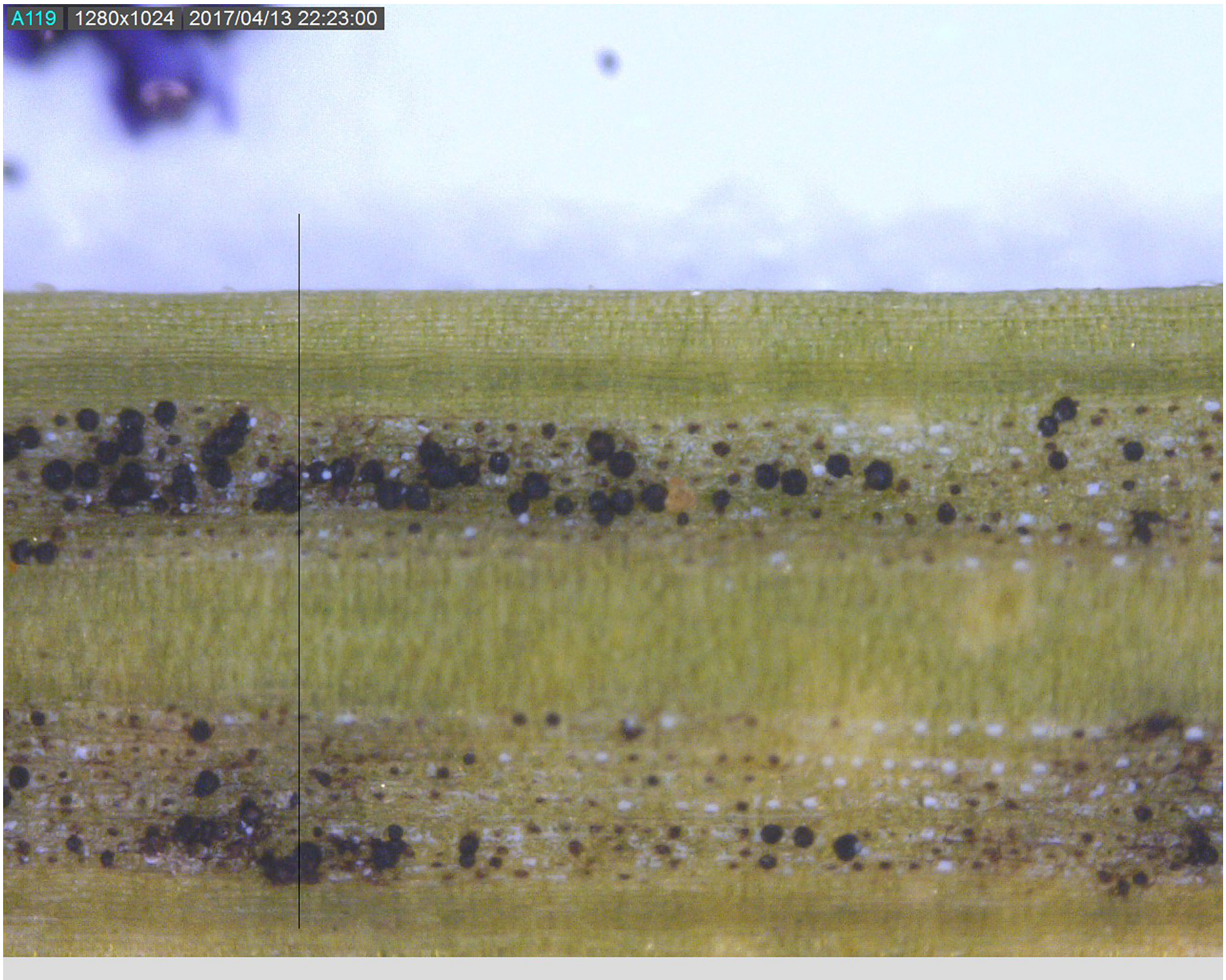

FIGURE 1 | Photo of pseudothecia blocking stomates on the underside of a Douglas-fir needle.

is also associated. Monthly precipitation and mean temperature data from 2010 to 2017 at all sites were downloaded from PRISM at Oregon State University[1] by providing GPS coordinates. We use average winter mean temperature (December, January, and February) and average summer precipitation (May, June and July), the climatological variables that are associated with Swiss needle cast severity (Manter et al., 2005), to compare the weather conditions across the sites (**Figure 3**).

Field Sampling

Branch samples were collected on the south side of each tree in late May through early June in 2016 and 2017, after bud-break and before new branchlets were elongated. The May–June period is also optimal for sampling because *N. gaeumannii* asci mature during April–June in western Oregon and sporulation occurs mid-May to July (Rohde, 1937; Chastagner and Byther, 1983; Michaels and Chastagner, 1984). We collected 1–3 branches from three canopy positions (lower, middle, and upper crown) in each of three trees at each site (total number of trees = 15). At least one branch > 1 m in length was selected to ensure sufficient needle material for measurements. Several shorter branches were chosen if there were no branches greater than 1 m in length. Branches were transported to the lab and stored in a 5°C cold room. Three young trees (20 – 30 years old) next to the mature trees at each site were sampled at the same time by Lan et al. (2019) and data are used here for comparison to older stands.

Lab Analysis

For each canopy position of 15 mature trees, 50 individual needles were randomly selected from the cohort of each foliar age class and needles were taped on an index card and stored at −20°C. All needle age classes from 2 to 6 years old were examined for *N. gaeumannii* pseudothecia incidence and density. The pseudothecia incidence is defined as the percentage of the 50 needles with pseudothecia present. Pseudothecia density was determined by selecting the first 10 needles with pseudothecia present beginning at the top of the card and working down,

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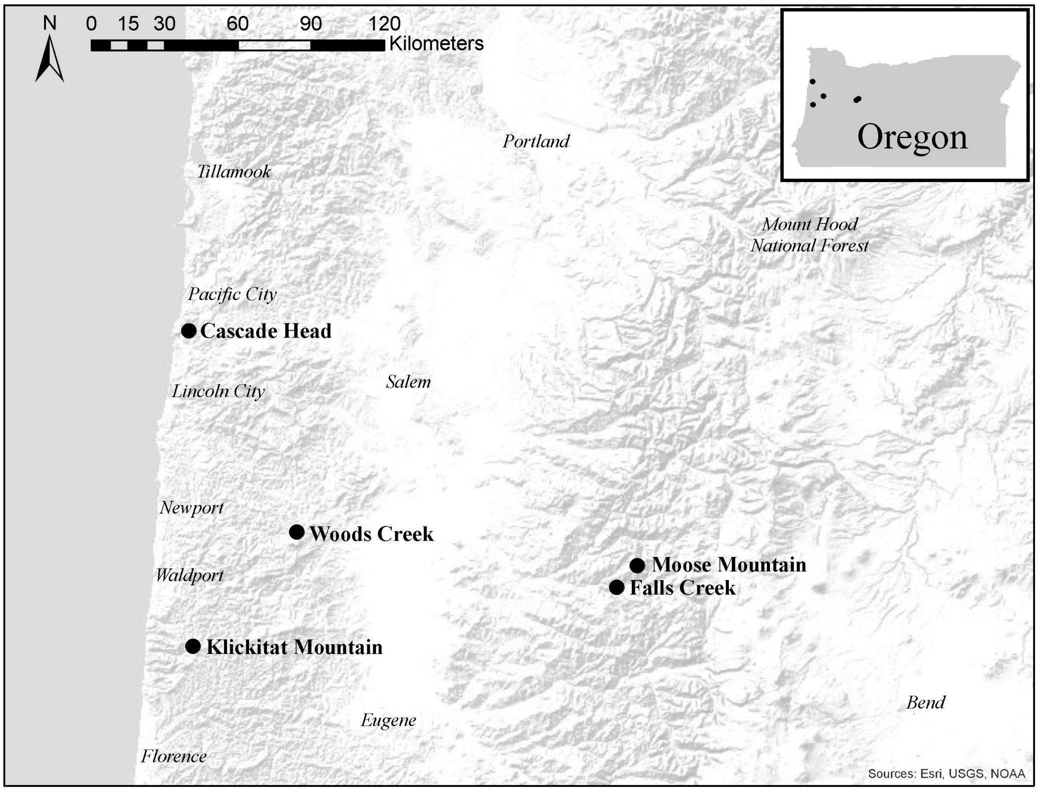
[1] http://www.prism.oregonstate.edu/explorer/, accessed 11 April 2021.



Sources: Esri, USGS, NOAA

FIGURE 2 | Map of study sites in the Oregon Coast Range and western Cascade Mountains of western Oregon, United States. Cascade Head, Falls Creek, and Moose Mountain are in the long-term ecological monitoring plot (LTEM) system, and Klickitat Mountain and Woods Creek are not part of the LTEM system. Cascade Head, Klickitat Mountain, and Woods Creek are in the Siuslaw National Forest. Falls Creek and Moose Mountain are in the Willamette National Forest.

and then counting the percent of stomates occluded in three regions (base, middle, and tip) of the needle (Mulvey et al., 2013). The entire length of the needle was evenly divided into three regions, for each region we picked a starting point using a random number table, and examined 100 contiguous stomates from the starting point to determine the number that were occluded by pseudothecia. Pseudothecial occlusion in the three regions was then averaged for each needle and then averaged for 10 needles per canopy position per tree.

Disease severity is typically determined by multiplying the incidence times the density of stomates blocked by pseudothecia for 2-year-old needles (Mulvey et al., 2013; Ritóková et al., 2021; Shaw et al., 2021). Disease severity is an important metric used to compare disease importance in forest stands (Shaw et al., 2021), while density alone is most important in casting of individual needles (Hansen et al., 2000; Manter et al., 2003; Stone et al., 2008a). The 2-year-old foliage is the key age class in coastal forests but foliage retention of severely diseased trees can be less than 2 years (Ritóková et al., 2016). Where disease severity is lower, pseudothecia can take as long as 4 years to mature when environmental conditions are less favorable for fungal growth (Stone et al., 2008a). In this study, we measured density of stomates plugged with pseudothecia for needles aged 2–5 years and included incidence data from Lan et al. (2019). We used the pseudothecia occlusion density rather than incidence as the primary measure of disease expression because there were many incidence values at or near zero.

Statistical Analysis

Binomial generalized linear mixed model (GLMM) was used to test for effects of canopy positions (upper, middle, and lower), sites, needle ages (2–5 years old), years (2016 and 2017), and their interactions on the pseudothecia density at the 0.05 level of significance. In the GLMM, canopy position, site, and needle age were treated as fixed effects with interaction terms in the GLMM whereas year was treated as an additive fixed effect, the individual trees on the same site were treated as random effects. We first ran the GLMM by using only 2-year-old needles of mature and young trees, to confirm the statistical differences of pseudothecia incidence and density between mature and young trees. We analyzed pseudothecia incidence and density ratios (0–1) using binomial GLMM assuming a logit-linear model with four fixed factors and one random factor for individual trees.

To understand more deeply about pseudothecia density on mature trees, we first ran the GLMM by using the complete dataset. In the preliminary results, there were interactions involving canopy positions, sites, and needle age, so we also ran the GLMM by year and by needle age, to test for differences in pseudothecia density on canopy position and site separately. We conducted a Bonferroni mean separation test to

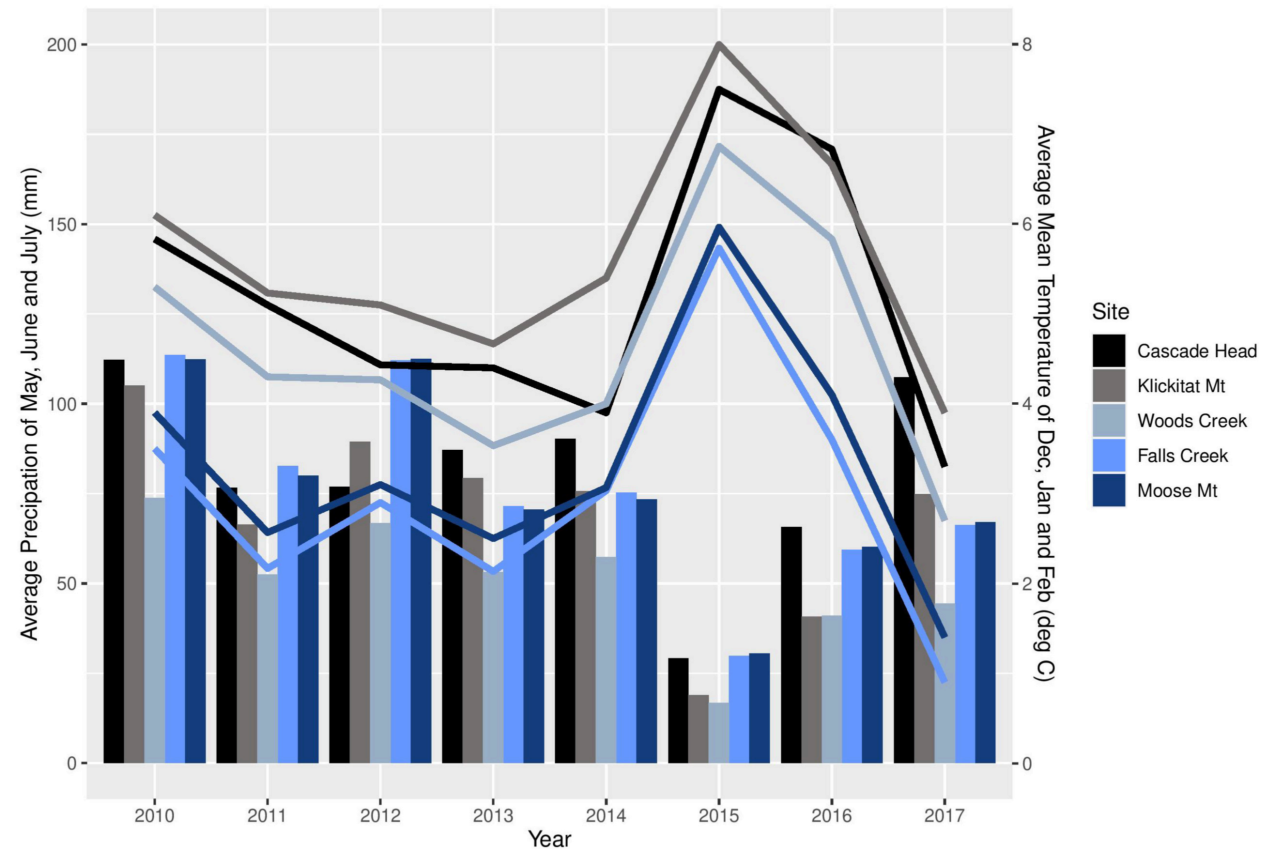


FIGURE 3 | Average winter (December, January, and February) mean temperature (lines) and average summer (May, June, and July) precipitation (bars) of each study site from 2010 to 2017.

infer which treatment means were different. GLMM tests were performed using R (v. 4.0.2, R Core Team, 2020) and package dplyr (Wickham et al., 2017), emmeans (Lenth, 2018), ggplot2 (Wickham, 2009), nlme (Pinheiro et al., 2017), glmmTMB (Brooks et al., 2017), and multcomp (Hothorn et al., 2008).

RESULTS

Mature Douglas-fir trees were less severely infected by *N. gaeumannii* than nearby young Douglas-fir trees (10–20 years old) based on examination of pseudothecia incidence and density for 2-year-old needles (**Table 1**). The mean percentage of 2-year-old needles with pseudothecia present, or incidence, ranged from 1.3 to 98% across sites and years for mature Douglas-fir trees, compared with 44 to 100% for the young plantations (**Table 2**). Tree age differences (i.e., mature vs. young trees) in pseudothecia incidence and density for 2-year-old needles were highly significant at the 0.05 level of significance (p = 0.02 and $p < 0.001$ respectively, **Table 1**). To a lesser extent, site and canopy position effects and their interactions on incidence and density for 2-year-old needles were also significant at the 0.05 level of significance based on the binomial GLMM, however, year effect was significant only in pseudothecia incidence but not density (**Table 1**).

Pseudothecia incidence was uniformly high for all needle classes of mature trees at Cascade Head where disease severity was greatest. For less severely diseased stands of mature trees, incidence varied by needle age class and peaked for 3- and 4-year old needles rather than for 2-year-old needles. The mean percentage of occluded stomates on 2-year-old needles with pseudothecia present, or pseudothecia density, ranged from 0.1 to 6.5% for mature trees in comparison to a range of 2–21% for young plantations. The highest pseudothecia density recorded for mature trees were: Cascade Head 9.3% for 6-year-old needles, Klickitat Mountain 4.0% for 5-year, Woods Creek 8.4% for 4-year, Moose Mountain 8.8% for 4-year, and Falls Creek 8.6% for 3-year old needles (**Table 2**). Because of the limited sample size in this study, the variation of pseudothecia density and incidence between tree to tree could be large (**Table 2**).

Disease severity (incidence times density) was consistently greater for 2-year-old needles of young plantation trees than for 2–5 years old needles of mature trees (**Figure 4**). Disease severity was greatest for 3- and 4-year old needles of mature trees, although 5-year-old needles were similar to 4-year old needles at Cascade Head and Moose Mountain.

TABLE 1 | Summary of GLMM of pseudothecia incidence and density, across five study sites (15 trees) in western Oregon, tree age (mature or young trees), year, canopy positions and their interactions.

	Density					Incidence				
	Estimates	**SE**	**z value**	**p value**		**Estimates**	**SE**	**z value**	**p value**	
(Intercept)	−2.49	0.24	−10.56	<0.001	***	2.18	0.48	4.51	<0.001	***
treeageYoung	1.02	0.29	3.49	<0.001	***	2.22	0.95	2.33	0.020	*
canopyMiddle	−0.67	0.36	−1.86	0.063	.	1.87	0.64	2.91	0.004	**
canopyLower	−1.59	0.49	−3.20	0.001	**	0.00	0.37	0.00	1.000	
siteKlickitat Mt	−0.80	0.40	−2.00	0.046	*	−2.95	0.66	−4.50	<0.001	***
siteWoods Creek	−1.00	0.42	−2.37	0.018	*	−6.55	0.95	−6.89	<0.001	***
siteFalls Creek	−2.48	0.74	−3.37	0.001	***	−5.47	0.76	−7.22	<0.001	***
siteMoose Mt	−1.89	0.58	−3.28	0.001	**	−3.88	0.67	−5.81	<0.001	***
year2017	0.19	0.29	0.64	0.523		1.15	0.49	2.32	0.021	*
treeageYoung:canopyMiddle	0.25	0.43	0.58	0.559		−1.57	1.26	−1.25	0.213	
treeageYoung:canopyLower	0.34	0.57	0.60	0.550		0.29	1.15	0.25	0.800	
treeageYoung:siteKlickitat Mt	0.04	0.49	0.08	0.939		1.99	1.21	1.64	0.101	
treeageYoung:siteWoods Creek	0.87	0.49	1.76	0.078	.	4.01	1.34	2.99	0.003	**
treeageYoung:siteFalls Creek	1.50	0.79	1.90	0.057	.	4.90	1.31	3.75	<0.001	***
treeageYoung:siteMoose Mt	0.85	0.65	1.32	0.186		2.58	1.18	2.18	0.029	*
canopyMiddle:siteKlickitat Mt	−0.53	0.72	−0.73	0.465		−2.44	0.70	−3.49	<0.001	***
canopyLower:siteKlickitat Mt	−0.05	0.89	−0.06	0.952		−0.88	0.47	−1.87	0.061	.
canopyMiddle:siteWoods Creek	−2.65	1.80	−1.47	0.141		−1.45	1.12	−1.29	0.196	
canopyLower:siteWoods Creek	1.62	0.69	2.37	0.018	*	1.29	0.89	1.45	0.148	
canopyMiddle:siteFalls Creek	0.36	1.12	0.32	0.749		−1.32	0.83	−1.59	0.113	
canopyLower:siteFalls Creek	1.85	1.04	1.77	0.077	.	1.27	0.61	2.07	0.038	*
canopyMiddle:siteMoose Mt	0.25	0.90	0.28	0.778		−1.35	0.71	−1.91	0.057	.
canopyLower:siteMoose Mt	0.49	1.14	0.43	0.665		0.48	0.48	1.01	0.312	
treeageYoung:year2017	0.33	0.35	0.93	0.351		−0.85	1.20	−0.71	0.475	
canopyMiddle:year2017	0.25	0.48	0.53	0.599		−0.73	1.05	−0.70	0.485	
canopyLower:year2017	0.68	0.61	1.11	0.267		0.19	0.72	0.27	0.791	
siteKlickitat Mt:year2017	−0.45	0.61	−0.74	0.457		−1.92	0.62	−3.08	0.002	**
siteWoods Creek:year2017	−3.51	1.79	−1.96	0.050	*	−1.15	1.12	−1.02	0.308	
siteFalls Creek:year2017	−0.02	0.98	−0.02	0.986		−1.71	0.84	−2.02	0.044	*
siteMoose Mt:year2017	−0.57	0.86	−0.66	0.507		−2.92	0.70	−4.18	<0.001	***
treeageYoung:canopyMiddle:siteKlickitat Mt	0.43	0.82	0.52	0.601		1.89	1.42	1.33	0.183	
treeageYoung:canopyLower:siteKlickitat Mt	0.71	0.99	0.72	0.472		0.41	1.33	0.31	0.757	
treeageYoung:canopyMiddle:siteWoods Creek	3.54	1.83	1.94	0.053	.	3.76	1.73	2.17	0.030	*
treeageYoung:canopyLower:siteWoods Creek	−0.09	0.77	−0.12	0.907		1.31	1.65	0.80	0.425	
treeageYoung:canopyMiddle:siteFalls Creek	0.16	1.18	0.14	0.891		1.89	1.69	1.12	0.262	
treeageYoung:canopyLower:siteFalls Creek	−0.80	1.13	−0.71	0.478		−1.40	1.48	−0.95	0.345	
treeageYoung:canopyMiddle:siteMoose Mt	0.44	0.97	0.46	0.647		2.52	1.46	1.73	0.084	.
treeageYoung:canopyLower:siteMoose Mt	0.84	1.21	0.70	0.486		1.11	1.42	0.78	0.434	
treeageYoung:canopyMiddle:year2017	−0.66	0.57	−1.16	0.246		0.44	1.91	0.23	0.818	
treeageYoung:canopyLower:year2017	−0.58	0.71	−0.82	0.414		−0.48	1.75	−0.28	0.782	
treeageYoung:siteKlickitat Mt:year2017	−1.37	0.75	−1.83	0.067	.	0.70	1.36	0.51	0.609	
treeageYoung:siteWoods Creek:year2017	1.74	1.83	0.95	0.340		−1.92	1.59	−1.21	0.227	
treeageYoung:siteFalls Creek:year2017	−0.37	1.04	−0.35	0.723		1.15	1.56	0.74	0.458	
treeageYoung:siteMoose Mt:year2017	−0.93	0.97	−0.96	0.338		0.09	1.35	0.07	0.947	
canopyMiddle:siteKlickitat Mt:year2017	−0.15	1.15	−0.13	0.899		1.97	1.16	1.70	0.089	.
canopyLower:siteKlickitat Mt:year2017	−1.49	1.76	−0.85	0.397		−0.82	1.03	−0.80	0.421	
canopyMiddle:siteWoods Creek:year2017	−12.37	3909.49	0.00	0.997		0.73	1.67	0.44	0.662	
canopyLower:siteWoods Creek:year2017	−0.72	2.57	−0.28	0.781		−0.91	1.41	−0.65	0.517	
canopyMiddle:siteFalls Creek:year2017	−2.65	2.79	−0.95	0.341		0.65	1.37	0.48	0.632	
canopyLower:siteFalls Creek:year2017	−2.56	1.90	−1.34	0.179		−1.46	1.16	−1.26	0.209	
canopyMiddle:siteMoose Mt:year2017	1.08	1.20	0.90	0.371		−0.83	1.37	−0.61	0.544	

(Continued)

TABLE 1 | (Continued)

	Density				Incidence			
	Estimates	**SE**	**z value**	**p value**	**Estimates**	**SE**	**z value**	**p value**
canopyLower:siteMoose Mt:year2017	0.31	1.50	0.21	0.835	−1.30	1.07	−1.22	0.224
treeageYoung:canopyMiddle:siteKlickitat Mt:year2017	0.04	1.40	0.03	0.977	−2.04	2.09	−0.98	0.329
treeageYoung:canopyLower:siteKlickitat Mt:year2017	1.74	1.90	0.92	0.360	0.30	2.02	0.15	0.880
treeageYoung:canopyMiddle:siteWoods Creek:year2017	11.94	3909.49	0.00	0.998	−2.08	2.44	−0.85	0.393
treeageYoung:canopyLower:siteWoods Creek:year2017	0.16	2.63	0.06	0.951	−0.65	2.30	−0.28	0.779
treeageYoung:canopyMiddle:siteFalls Creek:year2017	2.52	2.84	0.89	0.374	−0.40	2.47	−0.16	0.873
treeageYoung:canopyLower:siteFalls Creek:year2017	1.54	2.00	0.77	0.440	1.06	2.21	0.48	0.633
treeageYoung:canopyMiddle:siteMoose Mt:year2017	−0.81	1.36	−0.60	0.550	0.07	2.22	0.03	0.975
treeageYoung:canopyLower:siteMoose Mt:year2017	−0.47	1.64	−0.29	0.776	0.86	2.09	0.41	0.681

Only 2-year-old needles were used. Asterisks indicate significance at the 0.05 (*), 0.01 (**), and 0.001 (***) levels. Estimates are based on a logit transformation.

Within Crown and Site Patterns of Mature Trees

Pseudothecia density varied by canopy position, site, and year depending upon needle age class (**Figures 5**, **6** and **Table 3**). Site differences in pseudothecia density of 2-year-old needles were statistically significant at the 0.05 level, with greater pseudothecia density at the Cascade Head site than the inland sites (**Figures 4**, **5**). Canopy position differences in pseudothecia density of 3- and 4-year-old needles were statistically significant at the 0.05 level, with greater pseudothecia density in the upper canopy than in the lower canopy (**Figure 6**).

Site differences in pseudothecia density were statistically significant at the 0.05 level of significance (**Table 3**), indicating that temporal and spatial variability might exist in response to local weather variability. Only current year foliage is infected by *N. gaeumannii,* and variability of weather during the year foliage emerges can influence infection success (Stone et al., 2008a). Year-to-year variation in temperature in winter and rainfall in summer is common (**Figure 3**). Pseudothecia density of 2-year-old needles was greatest at Cascade Head, notably in 2017, whereas that of 4-year-old needles in 2016 was greatest at Woods Creek (**Figure 5** and **Table 2**). Pseudothecia density peaked in either 2- or 3-year-old needles at Cascade Head and 3- or 4-year-old needles at the inland sites depending upon year (**Figure 5**).

Canopy position differences were statistically significant at the 0.05 level (**Table 3**). Needles from upper canopy position had significantly higher pseudothecia density than the needles from middle (p = 0.024, **Table 3**) and lower canopies (p < 0.001, **Table 3**). In addition, these trends in canopy position also persisted over time for needles that emerged from the same year. For example, the canopy position trends in 2-year-old needles in 2016 was similar to the canopy position trends in 3-year-old needles in 2017, which they both emerged from 2014. The canopy position trends are particular for the 2- and 3-year old needles in 2016. In contrast, the canopy position trends in 3-year-old needles in 2016 did not persist in 4-year-old needles in 2017 due, in part, to a combination of pseudothecia density in the upper canopy peaking in 2016 followed by greater needle abscission in 2017 (**Figure 6**). The needle cohorts that emerged from the same year had similar trends among sites, implying a weather effect.

DISCUSSION

Swiss needle cast is an important disease of plantation Douglas-fir along the coast, yet mature stands are apparently not currently severely infected except in limited areas such as Tillamook, Oregon (Black et al., 2010). Older trees have lower disease severity on 2-year-old needles (Lan et al., 2019) and older stands rarely show up in Swiss needle cast aerial detection surveys (Mildrexler et al., 2019). In this study, pseudothecia density, as well as disease severity, peaks on 3-, and 4-year-old needle age classes in mature Douglas-fir trees (**Figure 4**). This is consistent with previous findings that pseudothecia incidence peaks on 3-year or older needles for mature Douglas-fir (Lan et al., 2019). Pseudothecia density is also very low across all our mature tree samples compared to young tree 2-year-old needles, with density never exceeding 10% for any needle age class (**Table 2**). Manter et al. (2000) states that carbon assimilation decreases proportionally with increasing stomate occlusion, while Hansen et al. (2000) suggest leaves are cast above 50% occlusion and Manter et al. (2003) suggest casting with as low as 25% stomate occlusion. Therefore, it is likely that the levels of stomate occlusion found in older trees do not influence needle function as strongly as in younger trees, although we did not test this.

The combination of lower pseudothecia density and the emergence of pseudothecia on 3- or 4-year-old needles, rather than 2-year-old needle age class, is potentially the key difference between Swiss needle cast disease expression in young and mature Douglas-fir. This supports our hypothesis, that the reason mature stands do not typically suffer from disease caused by *N. gaeumannii* is because needle retention is typically above 3 years (Lan et al., 2019). The lower pseudothecia density on mature trees also makes needle casting due to disease less likely in mature needles.

Why Do Pseudothecia Emerge on Older Needles in Mature Forests?

The factors that control timing of pseudothecia emergence from needles are not well understood, yet they may be critical to explaining disease epidemiology because the *N. gaeumannii* is an endophyte that appears to only impact leaves when

TABLE 2 | Disease incidence (%) and pseudothecia density (%) of 2-year old needles of young plantations (data used to determine disease severity in Lan et al., 2019) and 2–6 year age classes on mature trees (n = 15).

Sites	**Young plantation 2 year**		**Mature 2 year**		**Mature 3 year**		**Mature 4 year**		**Mature 5 year**		**Mature 6 year**	
	2016	**2017**	**2016**	**2017**	**2016**	**2017**	**2016**	**2017**	**2016**	**2017**	**2016**	**2017**
Incidence												
Cascade Head	99.78 ± 0.22	100 ± 0	91.78 ± 2.32	97.78 ± 1.31	86.4 ± 9.27	93.11 ± 5.43	77.96 ± 3.79	90.01 ± 7.26	81.57 ± 7.97	97.22 ± 2.78	84.51 ± 1.35	85.71 ± 14.29
Klickitat Mountain	96.22 ± 1.61	85.78 ± 4.06	26.44 ± 7.39	10 ± 5.36	69.78 ± 7.03	41.12 ± 9.3	39.18 ± 6.96	50.19 ± 10.15	26.59 ± 12.55	34.65 ± 8.82	15.53 ± 7.99	28.04 ± 11.67
Woods Creek	94.89 ± 3.27	44.44 ± 8.07	2.22 ± 0.91	1.33 ± 0.58	30.22 ± 7.68	8.44 ± 2.84	33.78 ± 5.97	22.44 ± 4.71	8.12 ± 1.64	27.78 ± 4.2	9.33 ± 3.25	6.29 ± 2.29
Moose Mountain	96.89 ± 1.57	68.67 ± 9.88	22.44 ± 6.97	1.78 ± 0.91	54.89 ± 13.96	34.44 ± 10.94	52.51 ± 12.41	40 ± 12.41	51.59 ± 14.25	34.79 ± 11.06	39.5 ± 19.19	33.5 ± 12.82
Falls Creek	98.89 ± 0.59	97.33 ± 1.15	7.78 ± 2.3	2.44 ± 0.87	62.67 ± 10.39	38 ± 7.26	51.95 ± 6.97	65.79 ± 10.72	56.57 ± 8.21	51.66 ± 9.08	56.16 ± 12.14	53.64 ± 11.65
Density												
Cascade Head	12.82 ± 1.84	17.89 ± 3.08	4.56 ± 1.03	6.51 ± 1.34	7.52 ± 0.91	6.28 ± 0.7	6.63 ± 1.09	6.4 ± 0.88	7.36 ± 1.08	4.12 ± 0.57	9.33 ± 2.48	6.1 ± 0.7
Klickitat Mountain	6.22 ± 0.73	2.07 ± 0.38	1.84 ± 0.5	1.16 ± 0.52	2.04 ± 0.68	2.02 ± 0.47	2.68 ± 0.68	3.06 ± 1.18	2.36 ± 0.46	4.05 ± 1.96	1.42 ± 0.57	2.44 ± 1.42
Woods Creek	20.82 ± 2.07	4.65 ± 1.09	2.07 ± 1.14	0.07 ± 0.05	7.78 ± 2.41	1.59 ± 0.81	8.41 ± 1.78	6.94 ± 0.87	6.91 ± 1.6	5.7 ± 0.9	4.44 ± 1.24	2.72 ± 1.22
Moose Mountain	8.63 ± 1.18	3.18 ± 0.44	0.84 ± 0.15	1.25 ± 0.73	3.9 ± 0.7	4.51 ± 1.49	3.2 ± 0.73	8.82 ± 1.49	3.27 ± 1.07	6.63 ± 2.17	2.14 ± 0.51	4.07 ± 1.07
Falls Creek	7.93 ± 0.97	6.15 ± 1.75	0.71 ± 0.13	0.35 ± 0.27	8.55 ± 2.08	2.69 ± 0.58	5.54 ± 1.69	6.89 ± 1.36	3.98 ± 0.48	3.46 ± 1.05	3.95 ± 0.79	3.51 ± 0.89

pseudothecia emerge and block gas exchange (Manter et al., 2000, 2005). Manter et al. (2005) has shown that winter temperature may explain timing of pseudothecial development, while Lan et al. (2019) showed that leaf wetness and leaf nitrogen do not explain differences in Swiss needle cast disease severity using 2-year-old needles of young and mature trees. Evidence from dendrochronological studies suggest winter temperature is strongly associated with disease impact at wetter, cooler sites while summer conditions are more important at less humid, warmer sites (Lee et al., 2013). In 2015, the PNW experienced the warmest winter on record with winter temperatures 3.4°C above historical average (Mote et al., 2019). The anomalously warm winter of 2015 likely contributed to the high disease severity at the coast site while below-average spring and summer precipitation and above-average summer temperatures in 2015 likely decreased pseudothecia incidence and density at inland sites outside of the coastal fog zone (Lee et al., 2013, 2017).

What Factors Could Control Timing of Pseudothecia Emergence?

Although we did not specifically test why pseudothecia emerge on older needles of mature trees, canopy architecture is distinct between young plantations and mature tree crowns. The mature trees are taller, with longer vertical foliage distribution and more complex microclimatic variation (Parker et al., 2002). Leaf temperature in winter may be reduced in mature trees compared to younger stands due to age differences in canopy height and architecture, and this could slow the development of pseudothecia production (Manter et al., 2005). Spore dispersal could also be different within older forest stands with complex crowns compared to even-structured young stands where canopy connectivity and homogeneity may allow for better colonization of needles. Other factors that might influence pseudothecia development time could be related to differences in leaf structure or chemistry between young and mature trees (Lan et al., 2019).

Patterns Within Mature Tree Crowns

We found that *N. gaeumannii* pseudothecia density varies year to year depending on needle age and canopy position in mature Douglas-fir of western Oregon. Needles emerging from the same year, for example, 2-year-old needles in 2016 and 3-year-old needles in 2017 both emerged in 2014, have similar patterns of pseudothecia density across needle ages which likely relates to differences in weather during the year that needles are infected (**Figure 5**). *Nothophaeocryptopus gaeumannii* only infects the current-year needles from May–August when pseudothecia disperse spores (Michaels and Chastagner, 1984) and leaf wetness is important for fungal colonization (Manter et al., 2005). The weather during these months may cause the similar pseudothecia occlusion for the same-year needle cohorts due to similarities in weather-driven fungal colonization. The site effect was important for 2-year-old needles in our study, with highest pseudothecia densities at the Cascade Head site, but site was also important for 3- and 4-year-old needles. Distance from coast is important to Swiss needle cast disease severity and needle retention in young stands, with Swiss needle cast impacts greater

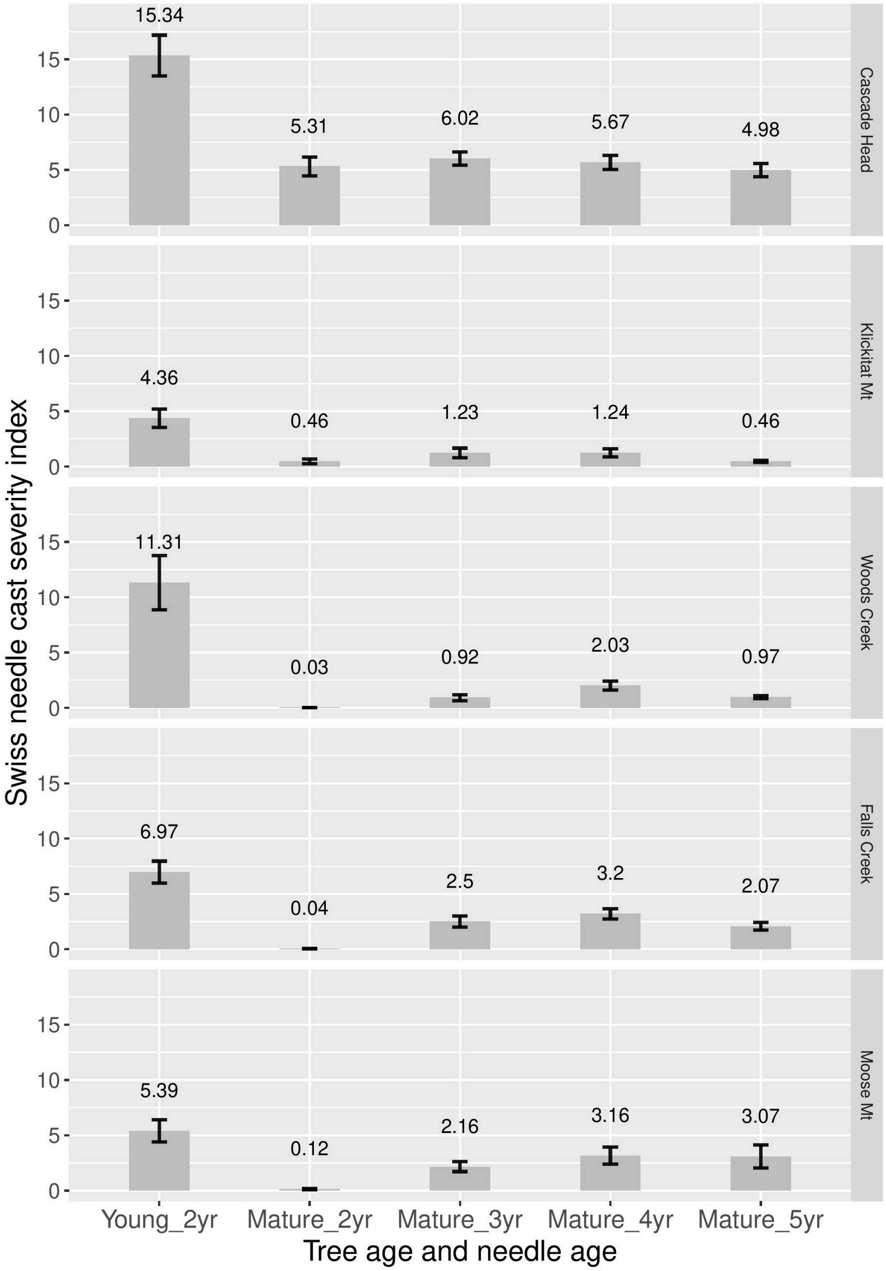


FIGURE 4 | Swiss needle cast average disease severity (incidence × density) for 2-year-old needles in young nearby plantations, and for 2, 3, 4, and 5-year old needles in mature stands. Two years and three canopy positions were averaged at each site.

at lower elevation areas and closer to coast (Hansen et al., 2000; Rosso and Hansen, 2003; Lee et al., 2013; Shaw et al., 2014, 2021; Ritóková et al., 2021).

Disease severity and pseudothecial density measured on 2-year-old needles is highest in the upper crowns of plantation-grown Douglas-fir compared to middle and lower crown positions (Hansen et al., 2000; Manter et al., 2005; Shaw et al., 2014; Lan et al., 2019; Ritóková et al., 2021). Our pseudothecia density data across older needles is generally consistent with Douglas-fir crown vertical patterns for 2-year-old needles in plantations. The lower canopy position had consistently lowest density of pseudothecia for all needle age classes (**Figure 6** and **Table 3**), while the upper canopy had the highest density, except the mid canopy of 4-year old needles in 2017.

Foliage diseases are generally thought to be most impactful in the highest humidity regions of a tree crown, which is typically the lower and inner crown (Tattar, 1989; Scharpf, 1993). In Christmas tree plantation settings in Pennsylvania and western Washington, *N. gaeumannii* was most severe in the lower and inner portion of the tree crown (Merrill and Longenecker, 1973;

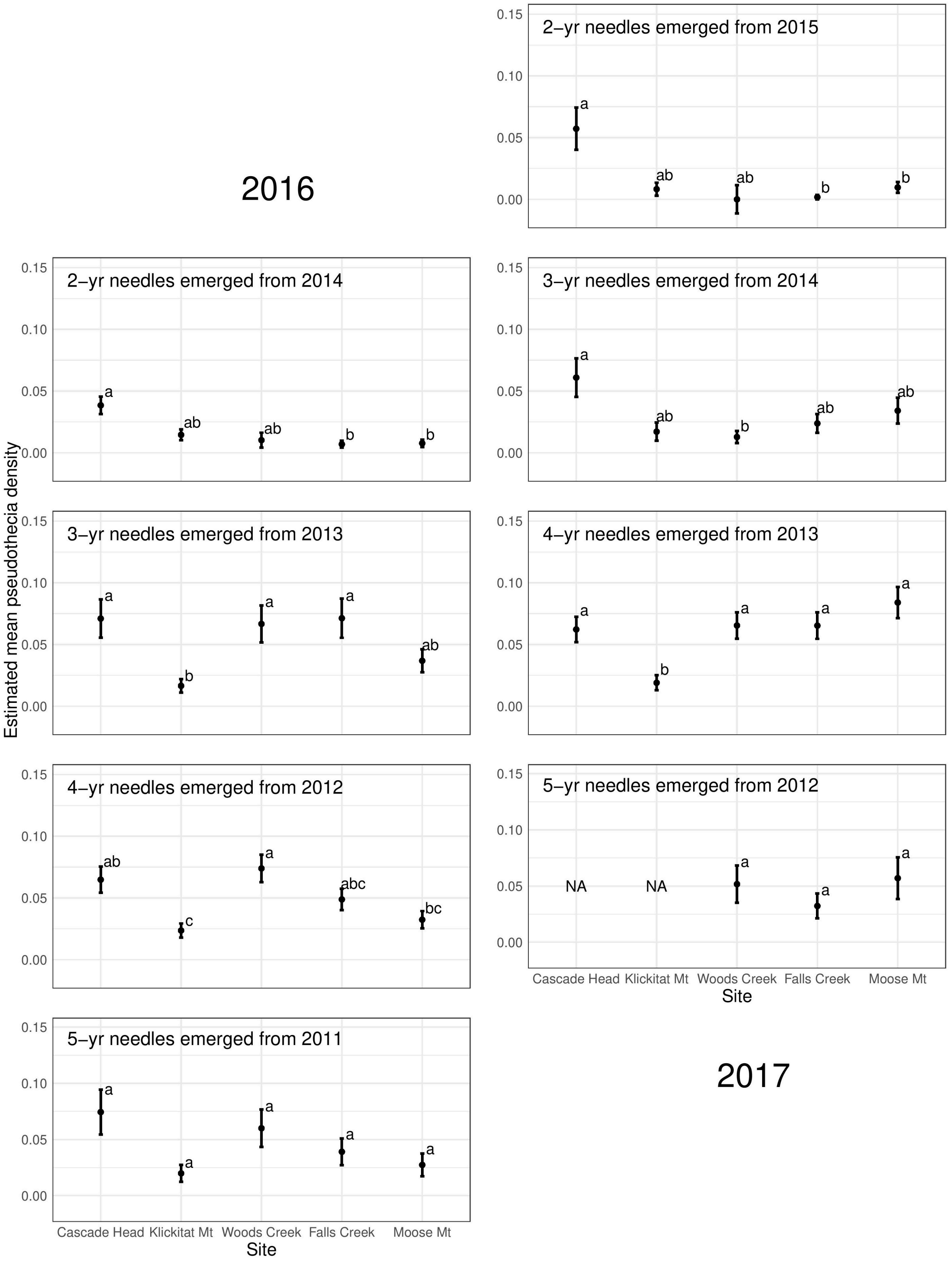


FIGURE 5 | Pseudothecia density by site for 2- to 5-year old needles in 2016 and 2017 from mature Douglas-fir trees in western Oregon. Sites listed on the *X*-axis are from coast (left) to inland (right). Different letters represent that the two groups are statistically different.

Chastagner and Byther, 1983). However, in western Oregon, disease severity of *N. gaeumannii* is consistently greatest in the upper crown for plantation trees (Hansen et al., 2000; Shaw et al., 2014; Ritóková et al., 2021), while the mid- and upper crown of mature trees show greater pseudothecia density in our study. This implies that environmental conditions for the fungus are more favorable in the mid and upper crown of mature trees, consistent with younger trees in western Oregon forests. Dye et al. (2020) analyzed the 22-year mean May through September low cloudiness (i.e., stratus, stratocumulus, and fog) and found

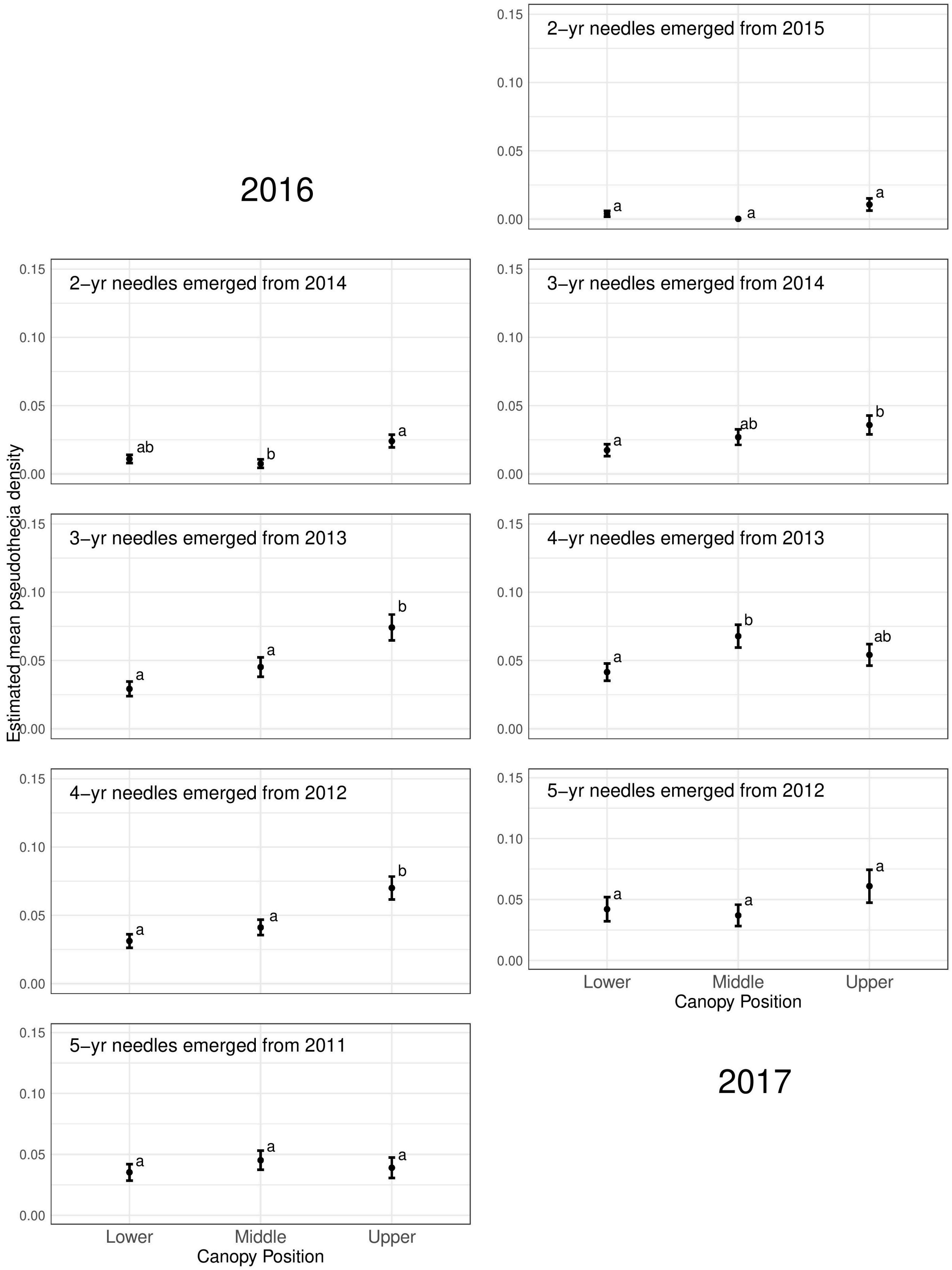


FIGURE 6 | Pseudothecia density by canopy position for 2- to 5-year old needles in 2016 and 2017 from mature Douglas-fir trees in western Oregon. Different letters represent that the two groups are statistically different.

a strong decline of low clouds in May and June, and a peak in July in the terrestrial highlands mode (Moose Mt. and Falls Creek). Seasonally, coastal fog frequency increases to a peak in August and is highest from June to September (Johnstone and Dawson, 2010). The coastal summer fog maintains needle wetness during the period of low summer precipitation and high summer temperatures. The coastal mode (Cascade Head, Klickitat Mt. and Woods Creek) had consistent low cloudiness that also peaked in late summer. The fog may wet the upper and mid crowns of co-dominant and dominant trees more

TABLE 3 | Summary of GLMM of pseudothecia density across five study sites (15 trees) in western Oregon, needle age (2–5-year-old), year, canopy position and their interactions.

	Estimate	SE	*z* value	*p* value	
(Intercept)	−2.32	0.26	−8.88	<0.001	***
canopyMiddle	−0.53	0.23	−2.25	0.024	*
canopyLower	−1.16	0.29	−4.07	<0.001	***
needleage3 year	−0.06	0.21	−0.31	0.759	
needleage4 year	−0.43	0.24	−1.78	0.075	.
needleage5 year	−0.20	0.28	−0.72	0.473	
siteKlickitat Mt	−0.99	0.42	−2.37	0.018	*
siteWoods Creek	−1.79	0.47	−3.80	<0.001	***
siteFalls Creek	−2.50	0.58	−4.33	<0.001	***
siteMoose Mt	−2.35	0.52	−4.48	<0.001	***
year2017	−0.14	0.06	−2.62	0.009	**
canopyMiddle:needleage3 year	0.45	0.32	1.41	0.159	
canopyLower:needleage3 year	0.69	0.37	1.84	0.065	.
canopyMiddle:needleage4 year	0.92	0.34	2.71	0.007	**
canopyLower:needleage4 year	1.14	0.39	2.92	0.004	**
canopyMiddle:needleage5 year	0.41	0.37	1.11	0.265	
canopyLower:needleage5 year	0.73	0.42	1.73	0.084	.
canopyMiddle:siteKlickitat Mt	−0.63	0.55	−1.14	0.253	
canopyLower:siteKlickitat Mt	−0.68	0.72	−0.95	0.341	
canopyMiddle:siteWoods Creek	−2.82	1.78	−1.59	0.113	
canopyLower:siteWoods Creek	1.20	0.54	2.21	0.027	*
canopyMiddle:siteFalls Creek	−0.47	0.93	−0.50	0.615	
canopyLower:siteFalls Creek	0.81	0.78	1.04	0.301	
canopyMiddle:siteMoose Mt	0.86	0.57	1.50	0.133	
canopyLower:siteMoose Mt	0.59	0.72	0.82	0.412	
needleage3 year:siteKlickitat Mt	0.18	0.40	0.44	0.663	
needleage4 year:siteKlickitat Mt	0.42	0.43	0.97	0.332	
needleage5 year:siteKlickitat Mt	−0.46	0.62	−0.73	0.465	
needleage3 year:siteWoods Creek	1.56	0.42	3.67	<0.001	***
needleage4 year:siteWoods Creek	2.49	0.43	5.79	<0.001	***
needleage5 year:siteWoods Creek	1.93	0.46	4.23	<0.001	***
needleage3 year:siteFalls Creek	2.67	0.53	5.02	<0.001	***
needleage4 year:siteFalls Creek	3.02	0.55	5.52	<0.001	***
needleage5 year:siteFalls Creek	2.03	0.59	3.46	<0.001	***
needleage3 year:siteMoose Mt	1.81	0.48	3.74	<0.001	***
needleage4 year:siteMoose Mt	2.61	0.50	5.22	<0.001	***
needleage5 year:siteMoose Mt	1.92	0.55	3.48	<0.001	***
canopyMiddle:needleage3 year:siteKlickitat Mt	−0.30	0.75	−0.40	0.692	
canopyLower:needleage3 year:siteKlickitat Mt	−0.13	0.91	−0.15	0.883	
canopyMiddle:needleage4 year:siteKlickitat Mt	−0.07	0.72	−0.10	0.918	
canopyLower:needleage4 year:siteKlickitat Mt	−0.09	0.89	−0.11	0.916	
canopyMiddle:needleage5 year:siteKlickitat Mt	1.12	0.85	1.32	0.186	
canopyLower:needleage5 year:siteKlickitat Mt	1.22	0.99	1.23	0.220	
canopyMiddle:needleage3 year:siteWoods Creek	2.63	1.81	1.45	0.147	
canopyLower:needleage3 year:siteWoods Creek	−1.76	0.67	−2.62	0.009	**
canopyMiddle:needleage4 year:siteWoods Creek	2.03	1.81	1.12	0.262	
canopyLower:needleage4 year:siteWoods Creek	−2.16	0.65	−3.31	<0.001	***
canopyMiddle:needleage5 year:siteWoods Creek	2.69	1.82	1.48	0.138	
canopyLower:needleage5 year:siteWoods Creek	−1.46	0.68	−2.15	0.031	*
canopyMiddle:needleage3 year:siteFalls Creek	−0.27	0.98	−0.27	0.785	
canopyLower:needleage3 year:siteFalls Creek	−1.55	0.86	−1.80	0.072	.
canopyMiddle:needleage4 year:siteFalls Creek	−0.49	0.99	−0.50	0.620	
canopyLower:needleage4 year:siteFalls Creek	−1.71	0.86	−1.98	0.048	*

(Continued)

TABLE 3 | (Continued)

	Estimate	SE	*z* value	*p* value	
canopyMiddle:needleage5 year:siteFalls Creek	0.40	1.02	0.40	0.693	
canopyLower:needleage5 year:siteFalls Creek	−0.82	0.90	−0.90	0.366	
canopyMiddle:needleage3 year:siteMoose Mt	−1.15	0.67	−1.72	0.086	.
canopyLower:needleage3 year:siteMoose Mt	−0.85	0.82	−1.04	0.299	
canopyMiddle:needleage4 year:siteMoose Mt	−1.51	0.67	−2.26	0.024	*
canopyLower:needleage4 year:siteMoose Mt	−1.21	0.81	−1.49	0.137	
canopyMiddle:needleage5 year:siteMoose Mt	−1.14	0.74	−1.54	0.123	
canopyLower:needleage5 year:siteMoose Mt	0.10	0.84	0.12	0.904	

Asterisks indicate significance at the 0.05 (*), 0.01 (**), and 0.001 (***) levels. Estimates are based on a logit transformation.

than the lower canopy, and help explain canopy differences of *N. gaeumannii* density, although leaf wetness was not consistently higher on upper canopy foliage (Lan et al., 2019).

In western Oregon, winter temperature influences disease severity at a range of spatial and temporal scales (Manter et al., 2005; Stone et al., 2008a,b; Zhao et al., 2012; Lee et al., 2013, 2017; Wilhelmi et al., 2017). Leaf canopy temperature may be a key predictor of variations in *N. gaeumannii* density within the canopy of mature Douglas-fir. A wide range of biological responses from leaf photosynthesis (Jordan and Ogren, 1984) to net ecosystem exchange (Kim et al., 2016) are better predicted by leaf temperature than air temperature. Several thermal imaging and radiation absorption modeling studies show leaf temperature is higher in the upper crown than in the lower crown and understory (Still et al., 2019; Miller et al., 2021) due to more direct daytime solar irradiation at the treetop than at the bottom of the canopy (Sinoquet et al., 2001). The gradients in leaf canopy temperature are most likely an important factor for fungal development, notably in the cool winter months when temperatures are most limiting to the formation of pseudothecia. In coastal Oregon, pseudothecial primordia form in epistomatal chambers October to April following initial infection in the summer months (Stone et al., 2008a). Pseudothecia density was generally low ($< 10\%$) for all needle age classes in mature trees, implying less colonization of the needles or slower growth within the needles. Winton et al. (2003) have demonstrated that pseudothecia density is significantly correlated with quantitative PCR, or the abundance of fungi within the needle. Therefore, other factors may be influencing colonization success of needles in mature trees. Although more recently, Montwé et al. (2021) contend that there is not a clear relationship between pseudothecia density, fungal DNA load and needle retention. They propose that there is a more complex unknown pathology involved in needle loss.

CONCLUSION

Nothophaeocryptopus gaeumannii causes disease in plantation and forest trees when over 25% of the stomates of young (1 and 2-year-old) foliage are occluded, causing early needle casting. Our hypothesis that disease severity is lower in mature trees because pseudothecia emerge later on older needles is supported. Within the mature tree crowns, we also found that pseudothecia density varied with needle age, canopy position, and site. In older and mature trees, pseudothecia *of N. gaeumannii* were most abundant on 3- and 4-year-old needles and density of pseudothecia on all needles was very low ($< 10\%$). Something about mature forest canopies and foliage appears to decrease the success of needle colonization or increase the time it takes for pseudothecia to emerge from the needles, in contrast to younger plantations (Lan et al., 2019), thus allowing the mature trees to have greater needle retention. Tree crown and canopy architectural differences may help explain these results, because mature trees have more complexities in microenvironmental patterns with deeper crowns, more shade, and less crown connectivity between trees, but this needs more studies in the future.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

Y-HL contributed to the study design, field sampling, data process and analysis, and writing. DS contributed to the study design and writing and especially for the discussion. EL contributed to the data analysis cooperation and stats interpretation. PB contributed to the study design, field sampling, especially organizing the climbing crew, and discussion. All authors contributed to the article and approved the submitted version.

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List of Refereed Publications

Disease Distribution, Severity and Epidemiology

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