NRC Research Press

ARTICLE

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

E. Henry Lee, Peter A. Beedlow, Ronald S. Waschmann, Connie A. Burdick, and David C. Shaw

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

Résumé : La sévérité de la rouille suisse (RS), une maladie cryptogamique du douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco), a augmenté partout dans son aire de répartition naturelle et dans les régions où elle a été introduite au cours du dernier demi-siècle. Le rôle joué par les changements climatiques et les pratiques d'aménagement dans cette augmentation est nébuleux. Nous avons analysé des séries dendrochronologiques dans six peuplements de douglas en fin de succession dans la chaîne côtière de l'Oregon à l'aide de l'analyse d'intervention en séries chronologiques (AISC) dans le but de déterminer de quelle façon le climat influence l'impact de la RS sur la croissance des arbres. Les séries dendrochronologiques de la pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.), une espèce non sensible au champignon *Phaeocryptopus gaeumannii* (Rhode) Petrak, ont été utilisées dans l'AISC comme données indirectes liées au climat. Nous avons trouvé que les réductions de croissance associées à la RS remontaient aux années 1950, la période correspondant aux plus anciennes de nos données dendrométriques. Les réductions de croissance étaient synchrones dans les six stations, indiquant que la sévérité de la maladie était largement influencée par les conditions climatiques. L'impact de la RS a culminé en 1984 à 1986 dans les six stations faisant partie de l'étude, suivi d'impacts sans précédent de la maladie atteignant 100% en 1996 et 2004 dans une station, alors qu'ils diminuaient pour revenir à des niveaux antérieurs dans les cinq autres stations. Notre indice d'impact de la RS était significativement corrélé avec les températures hivernales et estivales et avec la précipitation estivale. Les conditions hivernales étaient plus étroitement associées à l'impact de la maladie dans les stations plus humides et plus fraîches tandis que les conditions estivales étaient plus importantes dans les stations moins humides et plus chaudes. Avec les changements climatiques, les impacts de la RS risquent d'augmenter dans les zones côtières où la précipitation durant les mois de juin et juillet est beaucoup plus élevée que le seuil de ~110 mm, le minimum requis pour le développement de *P. gaeumannii*, et de diminuer dans les endroits où la précipitation estivale est égale ou inférieure à ce seuil. Les hivers plus chauds vont augmenter la sévérité de la maladie à plus haute altitude, au nord le long de la côte allant du nord de l'Oregon à la Colombie-Britannique et dans les endroits situés à l'intérieur des terres où les températures hivernales actuelles limitent la croissance des champignons. [Traduit par la Rédaction]

Introduction

Swiss needle cast (SNC) is an economically important disease of both coastal (*Pseudotsuga menziesii* (Mirb.) Franco) and interior (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) forms of Douglas-fir, as well as bigcone Douglas-fir (*Pseudotsuga macrocarpa* (Vasey) Mayr) in New Zealand (Boyce 1940; Gadgil 2005). SNC disease is caused by the fungus *Phaeocryptopus gaeumannii* (Rhode) Petrak and is widespread throughout the natural and introduced range of the host, but it is most severe in forests and plantations on the western slopes of the Oregon Coast range within the coastal fog belt (Hansen et al. 2000). Epidemic outbreaks of SNC have been reported in coastal Oregon, Washington, and British Columbia since the mid-1980s, (Hansen et al. 2000; Omdal and Ramsey-Kroll 2010) and have caused widespread symptoms of chlorosis and premature needle loss (Shaw et al. 2011). Thought to be innocuous in western North American forests prior to 1950 (Boyce 1940; Peace 1962; Hood 1982), increased severity since that time is

Received 11 February 2013. Accepted 1 May 2013.

E.H. Lee, P.A. Beedlow, R.S. Waschmann, and C.A. Burdick.* US Environmental Protection Agency, 200 SW 35th Street, Corvallis, OR 97333, USA.
D.C. Shaw. Oregon State University, Department of Forest Engineering, Resources and Management, 218 Richardson Hall, Corvallis, OR 97331, USA.
Corresponding author: E. Henry Lee (e-mail: Lee.EHenry@epa.gov).
*Retired.

Can. J. For. Res. **43**: 677–690 (2013) dx.doi.org/10.1139/cjfr-2013-0062

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

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

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

The impact of SNC on Douglas-fir growth is further influenced by climatic factors associated with the infection and development of the fungus over multiple years. A delay of several years between climate conditions favorable to reproduction and growth of the fungus and visible symptoms of growth reduction in the trees is expected because the pathogen infects only the newly emerged needles each year (Stone et al. 2008*b*). Further, needle abscission typically occurs after 50% or more of the stomata are occluded by fruiting bodies (Hansen et al. 2000). Pseudothecia can be commonly found on 4- to 7-year-old needles in the Cascade Mountains of Oregon and Washington, and on 1- to 2-year-old needles in some areas of the Coast Range where more favorable climatic conditions allow the fungus to develop faster (Stone et al. 2008*b*). Consequently, the proportion of stomata occluded depends upon current and previous years' climatic conditions associated with inoculum abundance, ascospore dispersal and germination, and pathogen colonization in each needle age class. Douglas-fir trees on the coast typically retain up to 4 years of needles, but may only have current and 1-year-old foliage due to premature needle abscission in severely affected plantations (Hansen et al. 2000; Maguire et al. 2002; Zhao et al. 2011).

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

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

Methods

Study sites

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

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

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

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

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

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

Field sampling

Different field-sampling methods and plot sizes were used to sample tree cores from Douglas-fir and western hemlock trees at the six sites depending upon the origin, source, and focus of the study. Species, diameter, and canopy class were recorded for all trees >10 cm diameter at breast height (DBH; at 1.3 m) at the three study sites chosen by Black et al. (2010) and for trees >20 cm DBH at CH and SM. At TL, TU, and EM, trees were systematically sampled within circular plots of 0.02 ha in area along transects through the forest interior at approximately 20 m intervals (Black et al. 2010). There were 19–23 tree cores of each tree species collected in 2007 and 2008 at these three sites (Table 1).

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

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

Dendrochronological methods

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

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

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

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

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

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

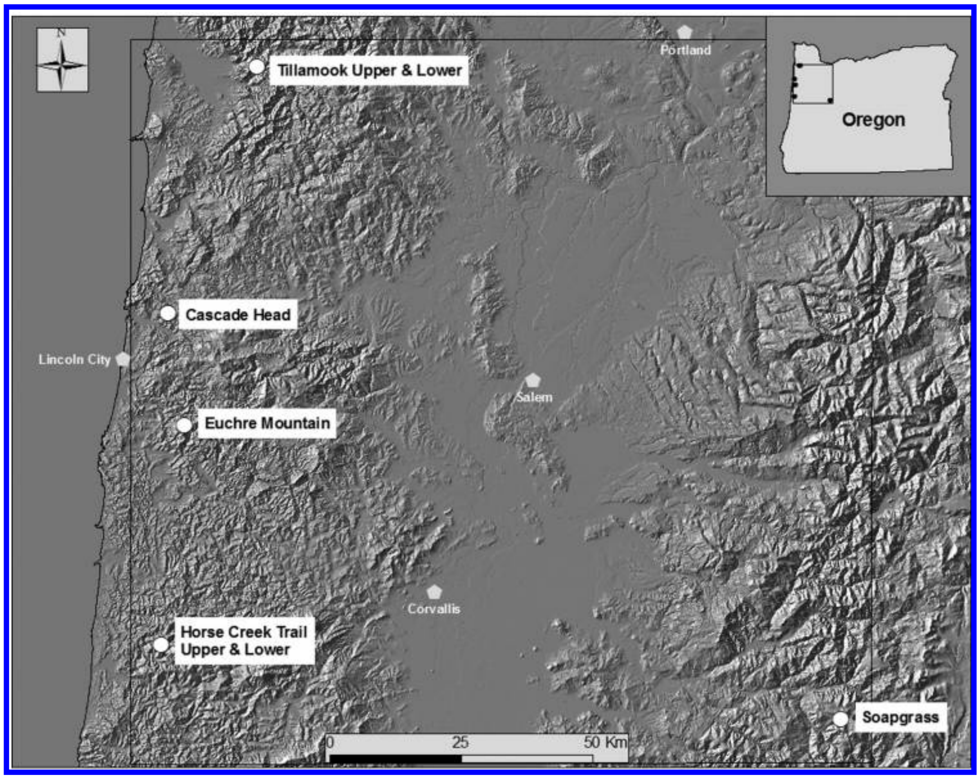
Statistical procedures

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

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

where X is the mean daily maximum temperature (°C) for June and July, T = Year − 1980 for Year > 1980 and 0 otherwise for $t = 1, 2, \ldots, N$ years. The model parameters (β_0, β_1, β_2, β_3, and β_4) are unknown and estimated from the data for each site. Because trend was present in the master chronology of Douglas-fir only at TL, β_4 was set equal to 0 at the other five study sites. To account for autocorrelation (Fritts 1976), the Douglas-fir master chronology of annual ring width was modeled as a third-order autoregressive

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



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

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

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

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

Additive pulse interventions were identified sequentially as significant divergences between the master chronology of Douglas-fir and its mean given in eq. (1). The identification of pulse intervention years is analogous to the detection of outliers from the AR(3) model given in eq. (2). The TSIA model approach assumes the mean function is the sum of a climatic signal given in eq. (1) and an additional component for disease disturbance, following Cook (1987) but implemented using a traditional time-series approach (Box and Tiao 1975; Tsay 1988). When β_1 = 1, our approach is comparable to commonly used dendroecological approaches that use the difference in chronologies between the disturbed and reference species to test for divergences in growth rates (e.g., Black et al. (2010)). Given that reductions in stem growth owing to SNC range from 25% to 55% in the PNW (Maguire et al. 2002, 2011), pulse interventions were initially defined as a 25% or greater reduction in the master chronology of Douglas-fir adjusted for climatic factors. Years prior to and following a >25% reduction in growth were also identified as interventions when reductions in growth exceeded 10%. Additional pulse events were identified as multiple consecutive years of reduced growth with a peak reduction <25% at less severely diseased sites that were synchronous with growth reductions >25% at the more severely diseased sites. Several reconstructions of forest disturbance history showed an increase in growth rate following a disturbance event (Henry and Swan 1974; Oliver and Stephens 1977). Consequently, candidate years with enhanced growth >10% were identified as pulse interventions associated with release.

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

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

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

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

Results

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

Swiss needle cast index

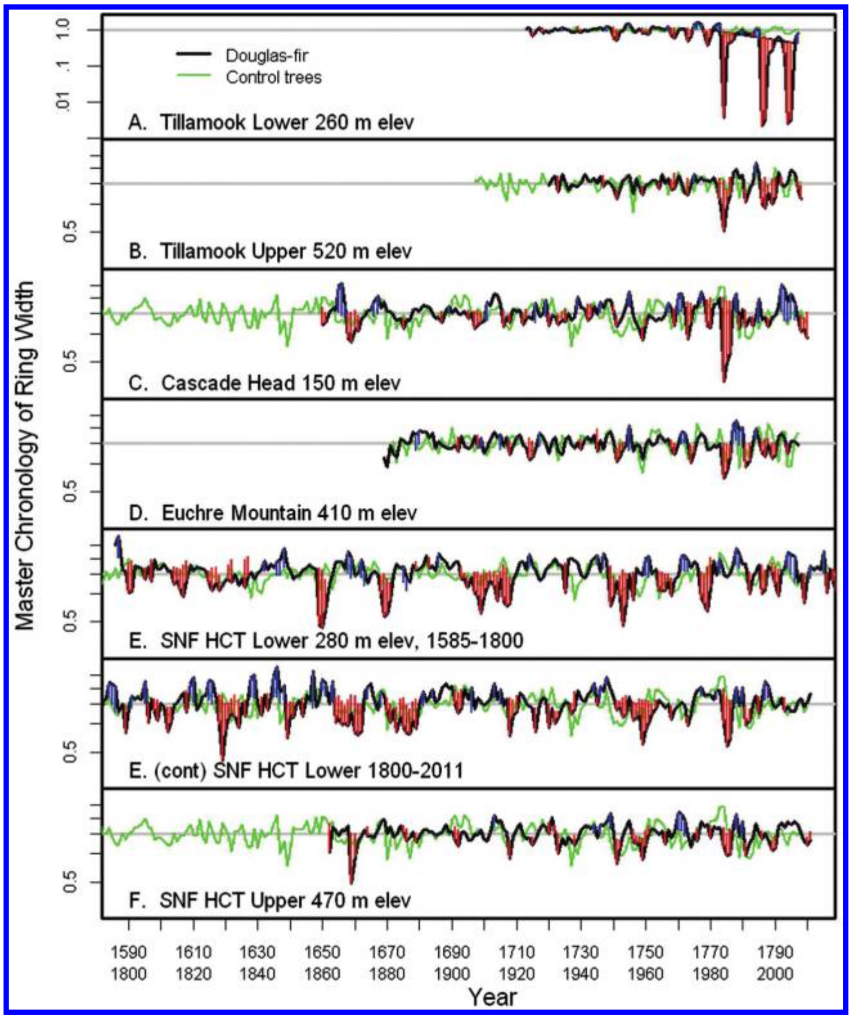
The time-series intervention models accounted for at least 86% of the total variation in the Douglas-fir chronologies for the six study sites. Similar tree-ring-based reconstructions of the SNC impact for each site were obtained by using either the local western hemlock chronology or the Douglas-fir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

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

Cyclical patterns of Swiss needle cast

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

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



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

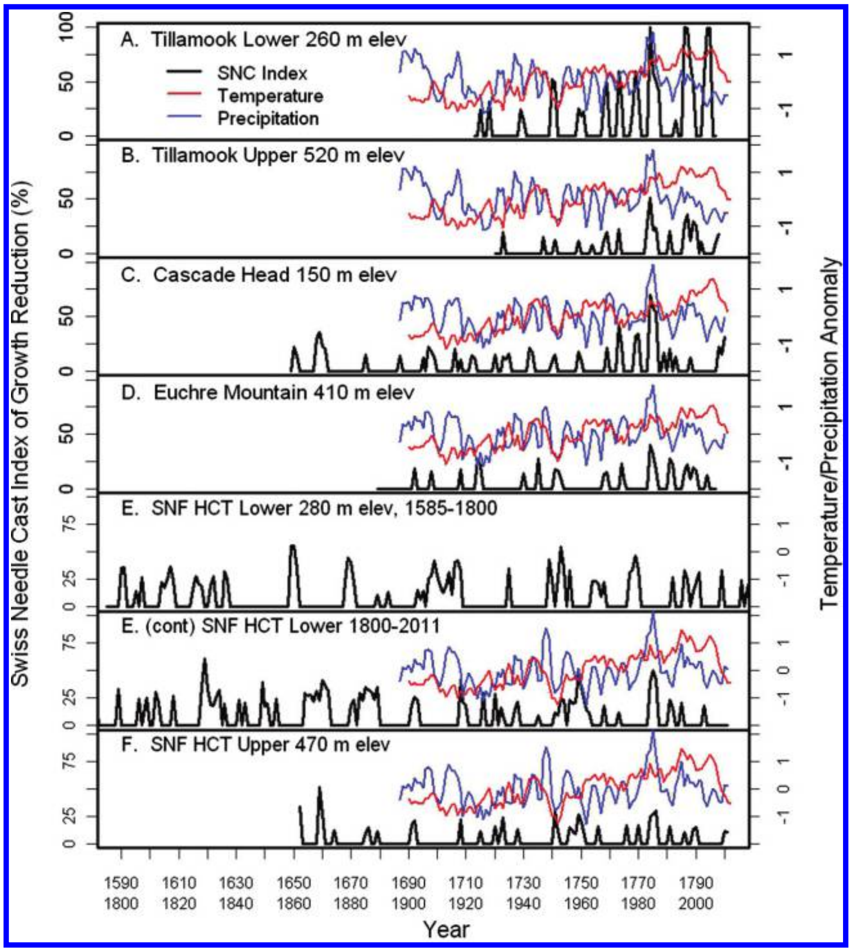
Co-spectrum analysis indicated that the SNC indices for all sites were coherent and in phase at the key frequencies (not shown). The synchronization of SNC impact on Douglas-fir across the landscape indicated that there were climate factors, which favored disease conditions at these sites in coastal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

Seasonal climate factors

The climatic factors associated with the SNC index were examined for each site, focusing on the three lower elevation sites where the magnitude and frequency of disease impacts and the statistical power of the test for correlation were greater. The impact of SNC on stem growth lagged the seasonal averages of winter and summer temperatures and summer precipitation and DPD by 1–25 years to varying degrees at all study sites (Fig. 5). A statistically significant cross-correlation represented a past year when growth loss was affected primarily by climatic factors rather than biotic factors (e.g., abundance of fruiting bodies). A nonsignificant cross-correlation indicted either no linear association between impact and past climate or a potential interaction between biotic and abiotic factors.

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

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

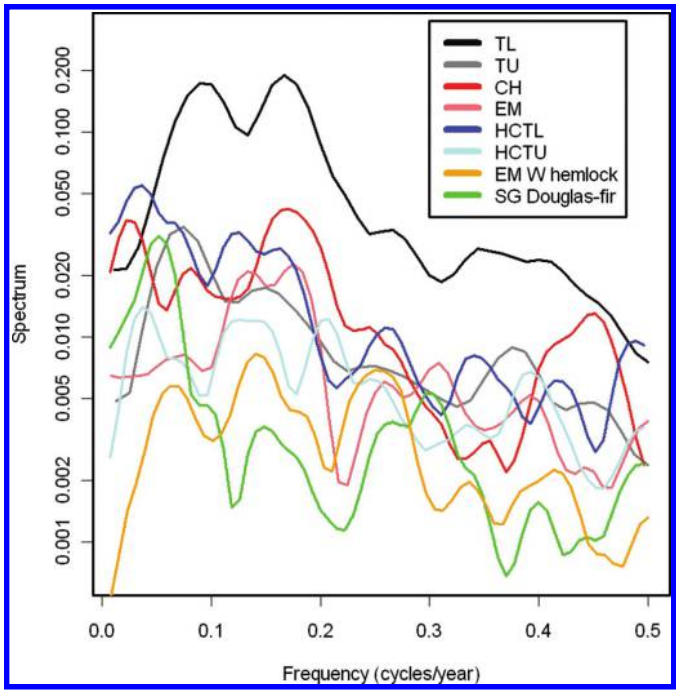


precipitation was the primary limiting factor of disease impacts at HCTL (Figs. 5G–5I) and HCTU (not shown) because the warmer, less humid summers at these sites were likely less favorable conditions for infection and colonization. The interactive effects of SNC and climate factors over several decades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

Canonical correlation analysis was used to generate a climate index for each seasonal climate factor and study site based on a weighting scheme of current and previous years to optimize the correlation with the SNC index of impact (Table 2). The canonical factors for summer and winter temperatures and summer precipitation and DPD included only those years having a cross-correlation >0.2 (or <–0.2 for summer temperature and DPD). Much stronger associations between the SNC index and seasonal temperature, precipitation, and DPD were obtained when the climatic variables were averaged across current and past years than for individual years. Overall, canonical correlations with the SNC index were strong and ranged from 0.50 to 0.86 for winter temperature, from 0.68 to 0.78 for summer precipitation, from –0.81 to –0.48 for summer DPD, and from –0.95 to 0.84 for summer temperature. Disease impact related to winter temperature, summer precipitation, and DPD consistently across all study sites. The lagged relationship between SNC impact and summer temperature was complex and varied by the range of local summer temperature in relation to two temperature optima — 18 °C for ascospore germination and 22 °C for germ-tube growth.

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

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



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

Discussion

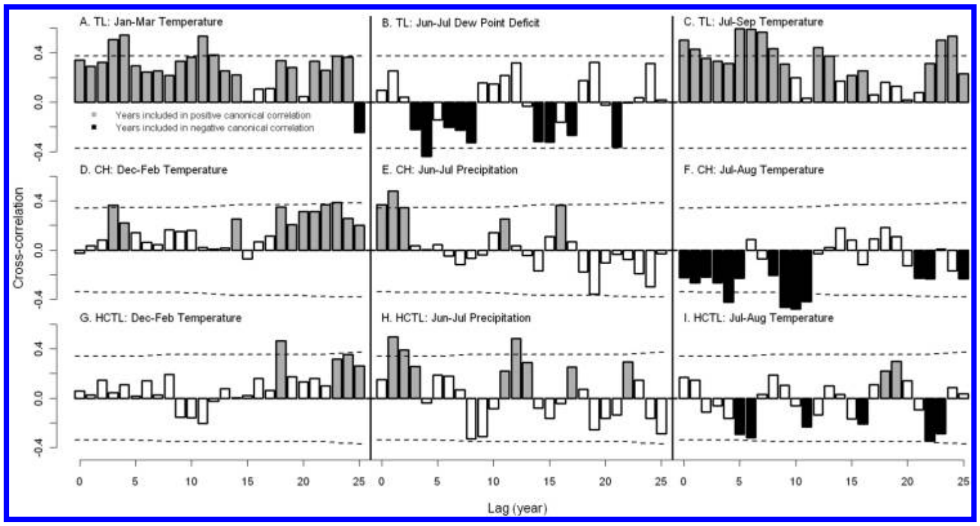
Using the time-series intervention and spectral analyses of tree-ring data, we identified several patterns of growth suppression and release associated with SNC. Intervention analysis was adapted from econometrics to dendroecology for the decomposition of a tree-ring time series into discrete signals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

Defoliation owing to SNC was the most likely cause of the significant divergences in chronologies of annual-ring-width increment between coastal Douglas-fir and the reference trees. Evidence from past foliar assessment surveys (Boyce 1940), historical records, epidemiological studies (Maguire et al. 2002), and a previous study of tree-ring data (Black et al. 2010) also identified SNC disease as the most likely cause of annual growth suppressions of coastal Douglas-fir in Oregon. Regular cyclical patterns of growth suppression having periodicities of 6, 12, and ~25 years were synchronous across study sites and associated with current and past winter and summer conditions, indicative of SNC. The fundamental periodicity of ~25 years and its harmonic periodicities of 6 and 12 years were associated with climate and its effect on the intensification of *P. gaeumannii* abundance over one or more decades. Because *P. gaeumannii* almost exclusively infects the newly emerged needles (Stone et al. 2008*b*), the 6-year periodicity in the SNC index was likely the result of a delayed growth response to climate conditions favorable to the infection and ensuing pathogen colonization in each needle age class. Close correlations have been found between growth impacts and needle retention, pseudothecia density, and pathogen biomass (Hansen et al. 2000; Manter et al. 2001; Maguire et al. 2002; Winton et al. 2002, 2003), suggesting that the SNC index of impact correlates with these indices. Pathogen abundance likely peaked during a year with severe impact, followed by a decrease to a minimum because of the loss of foliage, and increased in intensity to a peak after one or more decades in synchrony with the SNC index. At the most severely impacted site, the intensification of pathogen abundance was much faster because of the more favorable conditions for pathogen development as evidenced by abundant pseudothecia on 1- and 2-year-old needles in this area (Stone et al. 2008*b*). This likely explains the lack of a 25-year periodicity in the SNC index at this site.

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

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

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



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

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

Our dendrochronological study corroborates the findings of greenhouse and field studies that associate SNC severity with winter temperature and spring–summer needle surface wetness (Manter et al. 2005; Stone et al. 2008a) when summer temperature is relatively low (Rosso and Hansen 2003). Our findings are generally consistent with earlier studies but indicate a more complex site-specific climate–growth relationship between SNC impact and current and previous winter and summer temperatures and summer precipitation having lags of up to 25 years. Unlike previous climate–disease models that associate disease severity and needle retention with current and past winter and summer conditions having lags of up to 4 years (Zhao et al. 2011), our findings indicate a delayed growth response to past climate conditions associated with the intensification of *P. gaeumannii* abundance over several decades. Inferences of these lagged climate–growth relationships are possible with the long time series of tree-ring data but not with laboratory or field studies conducted over a limited number of years.

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

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

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

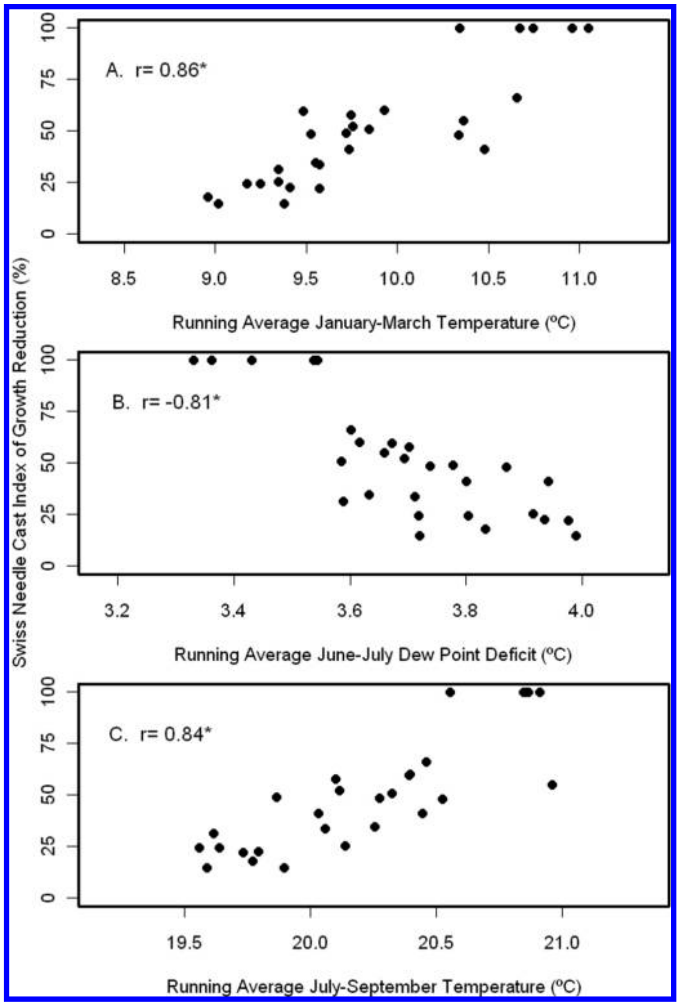
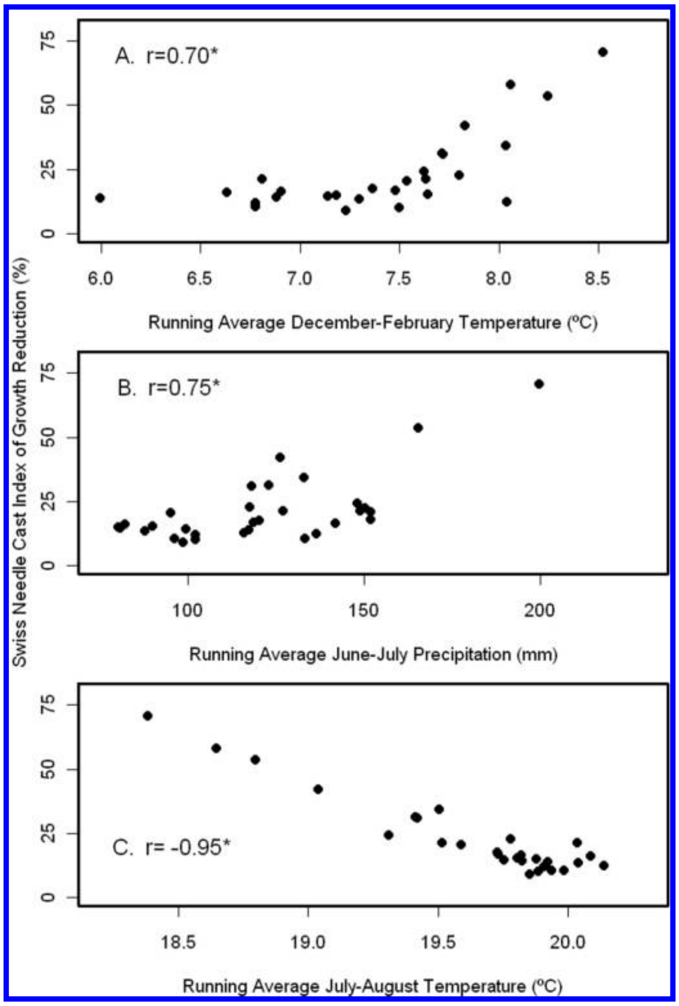


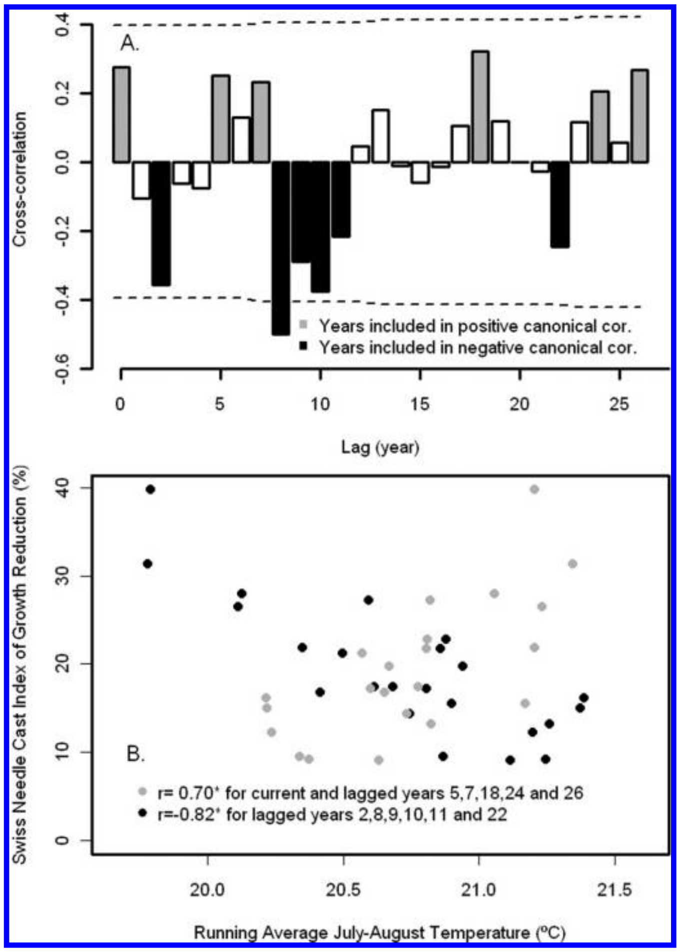
Fig. 7. Canonical correlations between current-year Swiss needle cast index of impact and (A) the weighted mean daily maximum winter temperature averaged across the previous 3–23 years, (B) the weighted mean total summer precipitation averaged across the current and the previous 1–11 years, and (C) the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



summer) since 1966 (NOAA 2005). The decline in SNC impact at the warmer, drier sites after 1996 was related to summer temperature increasing at a rate of about 0.3 °C·decade^{-1} and summer precipitation in July decreasing at a rate of about 8 mm·decade^{-1} since 1970, resulting in less favorable conditions for ascospore germination of *P. gaeumannii*. Our findings are consistent with previous studies that suggest disease severity in young Douglas-fir plantations in coastal Oregon is best explained by climate variables in the summer months, most notably July (Rosso and Hansen 2003; Coop and Stone 2007; Latta et al. 2009). Climate conditions in July correlate best with SNC impact and severity because higher temperature combined with lower moisture in July may be more inhibiting to *P. gaeumannii* development than in other months (Rosso and Hansen 2003). A negative relationship between impact and summer temperature is consistent with the findings of Zhao et al. (2011), who reported a positive effect of summer temperature on foliage retention. Zhao et al. (2011) postulated that warmer summer temperatures are associated with higher vapor pressure deficit and lower water potential within the foliage, which negatively affect fungal development and increase needle retention. Where summer temperature along the Oregon coast exceeds the optimum of 18 °C for spore germination (Capitano 1999), we postulate that warmer summer temperature is associated with less SNC impact because the establishment efficiency (i.e., proportion of spores that successfully infect the newly emerged needles) is reduced under warmer, drier conditions.

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

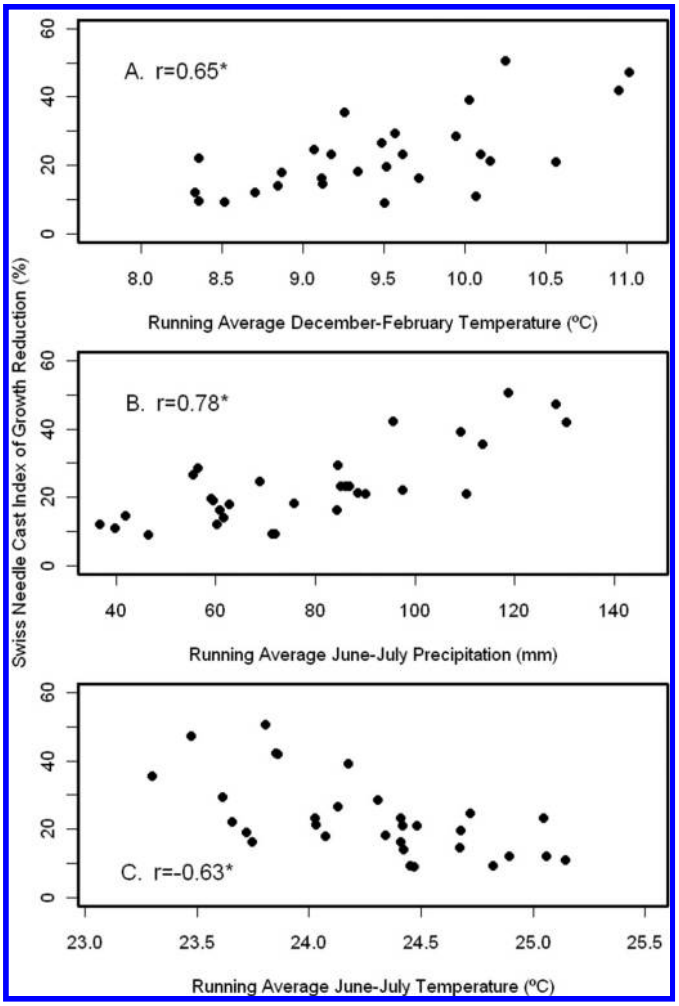
Fig. 8. (A) Cross-correlations between the current-year Swiss needle cast (SNC) index of impact and the current and past July–August temperature at Euchre Mountain. (B) Canonical correlation between the SNC index and the weighted mean daily maximum July–August temperature averaged across current and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



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

Our findings suggest that the geographic area affected by severe SNC may expand overall, but the intensity and frequency in coastal Oregon may increase or decrease under future climate conditions. Peak SNC impacts since 1984 were most frequent and severe at TL where the warmer winter and wet summer conditions promoted faster hyphal development in the intercellular spaces of the needle and faster pseudothecia formation (Manter et al. 2005). In some high-severity areas of the Coast Range, pseudothecia are abundant on 1- and 2-year-old needles (Hansen et al. 2000; Stone et al. 2008*b*) and only current and 1-year-old needles of Douglas-fir are retained in some years (Hansen et al. 2000; Maguire et al. 2002; Zhao et al. 2011). Continued warming during winter and summer will likely increase SNC intensity and frequency in areas within the coastal fog zone where needle wetness is maintained by coastal fog and drizzle. Conversely, continued warming and drying in the summer will likely decrease SNC intensity and frequency in areas where warm, dry summers currently limit ascospore germination. Needle retention is predicted to decrease or increase gradually from 2020 to 2080 under future climate scenarios depending upon whether winter or summer conditions are the primary driver of pathogen development (Zhao et al. 2011). Based on annual area surveys conducted by the Swiss Needle Cast Cooperative at Oregon State University, the spatial extent of infected forests increased from 53 000 ha in 1996 to 210 000 ha in 2012 at a rate of about 3.2 km·year^{-1} inland. This inland movement of disease was likely due to an expansion of area in the Coast Range where the winter temperature threshold was exceeded and disease conditions became more favorable. The disease will continue to spread inland, north, and to higher elevations in the Coast Range under a projected climate change scenario of warmer winter and summer temperatures, which will become more favorable for fungal germination and development.

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



Conclusion

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

Acknowledgements

The authors thank Michael Bollman, Cailie Carlile, Katie Steele, Isaac Bolduc, Steve Cline, and Don Phillips for their assistance in the field. The authors thank Bryan Black for providing his tree-ring data of Douglas-fir and western hemlock for three study sites. The authors thank Robert Nowak, Timber Contracting Officer of the Siuslaw National Forest, US Forest Service, for permission to collect tree core samples in the Siuslaw National Forest. The research described in this article has been funded wholly by the US Environmental Protection Agency. It has been subjected to review by the National Health and Environmental Effects Research Laboratory's Western Ecology Division and approved for publication. Approval does not signify that the contents reflect the views of the Agency, nor does mention of trade names or commercial products constitute endorsement or recommendation for use.

References

Avery, T.E. 1975. Natural resources measurement. McGraw-Hill, New York.

Beedlow, P.A., Lee, E.H., Tingey, D.T., Waschmann, R.S., and Burdick, C.A. 2013. The importance of seasonal temperature and moisture patterns on growth of Douglas-fir in western Oregon, U.S.A. Agric. For. Meteorol. **169**: 174–185. doi:10.1016/j.agrformet.2012.10.010.

Black, B.A., Shaw, D.C., and Stone, J.K. 2010. Impacts of Swiss needle cast on overstory Douglas-fir forests of the western Oregon Coast Range. For. Ecol. Manag. **259**: 1673–1680. doi:10.1016/j.foreco.2010.01.047.

Box, G.E.P., and Jenkins, G.M. 1970. Time series analysis: forecasting and control. Holden-Day, San Francisco, Calif.

Box, G.E.P., and Tiao, G.C. 1975. Intervention analysis with applications to economic and environmental problems. J. Am. Stat. Assoc. **70**: 70–79. doi:10.1080/01621459.1975.10480264.

Boyce, J.S. 1940. A needle cast of Douglas-fir associated with *Adelopus gaeumannii*. Phytopathology, **30**: 649–659.

Capitano, B. 1999. The infection and colonization of Douglas-fir by *P. gaeumannii*. M.Sc. thesis, Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon. Available from http://sncc.forestry.oregonstate.edu/sites/default/files/CapitanoBryanR1999.pdf.

Carpenter, S.R., Frost, T.M., Heisey, D., and Kratz, T.K. 1989. Randomized intervention analysis and the interpretation of whole-ecosystem experiments. Ecology, **70**: 1142–1152. doi:10.2307/1941382.

Cook, E.R. 1987. The decomposition of tree-ring series for environmental studies. Tree-Ring Bull. **47**: 37–59.

Cook, E.R., Briffa, K., Shiyatov, S., and Mazepa, V. 1990. Tree-ring standardization and growth-trend estimation. *In* Methods of dendrochronology. *Edited by* E.R. Cook and L.A. Kairiukstis. International Institute for Applied Systems Analysis, Netherlands. pp. 104–123.

Coop, L.B., and Stone, J.K. 2007. Prediction maps of Swiss needle cast needle retention based on climate factors. *In* Swiss Needle Cast Cooperative annual report 2007. *Edited by* D. Shaw. College of Forestry, Oregon State University, Corvallis, Oregon. pp. 15–21.

Druckenbrod, D.L. 2005. Dendroecological reconstructions of forest disturbance history using time-series analysis with intervention detection. Can. J. For. Res. **35**(4): 868–876. doi:10.1139/x05-020.

Franklin, J.F., and Dyrness, C.T. 1973. Natural vegetation of Oregon and Washington. U.S. For. Serv. Gen. Tech. Rep. PNW-8.

Fritts, H.C. 1976. Tree rings and climate. Academic Press, New York.

Fuller, W.A. 1976. Introduction to statistical time series. John Wiley & Sons, New York.

Gadgil, P.D. 2005. Fungi on trees and shrubs in New Zealand. Fungal Diversity Press, Hong Kong.

Hadfield, J., and Douglas, B. 1982. Protection of Douglas-fir Christmas trees from Swiss needle cast in Oregon. Am. Christmas Tree J. **26**: 31–33.

Hansen, E.M., Stone, J.K., Capitano, B.R., Rosso, P., Sutton, W., Winton, L., Kanaskie, A., and McWilliams, M.G. 2000. Incidence and impact of Swiss needle cast in forest plantations of Douglas-fir in coastal Oregon. Plant Dis. **84**: 773–778. doi:10.1094/PDIS.2000.84.7.773.

Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., Ostfeld, R.S., and Samuel, M.D. 2002. Climate warming and disease risks for terrestrial and marine biota. Science, **296**: 2158–2162. doi:10.1126/science.1063699.

Henry, J.D., and Swan, J.M.A. 1974. Reconstructing forest history from live and dead plant material — An approach to the study of forest succession in southwest New Hampshire. Ecology, **55**: 772–783. doi:10.2307/1934413.

Holmes, R.I. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. **43**: 69–78.

Hood, I.A. 1982. *Phaeocryptopus gaeumannii* on *Pseudotsuga menziesii* in southern British Columbia. N.Z. J. For. Sci. **12**: 415–424.

Hood, I.A., and Kershaw, D.J. 1975. Distribution and infection period of *Phaeocryptopus gaeumannii* in New Zealand. N.Z. J. For. Sci. **5**: 201–208.

Kimberley, M.O., Hood, I.A., and Knowles, R.L. 2011. Impact of Swiss needle-cast on growth of Douglas-fir. Phytopathology, **101**: 583–593. doi:10.1094/PHYTO-05-10-0129.

Lee, E.H., Tingey, D.T., Beedlow, P.A., Johnson, M.G., and Burdick, C.A. 2007. Relating fine root biomass to soil and climate conditions in the Pacific Northwest. For. Ecol. Manage. **242**: 195–208. doi:10.1016/j.foreco.2007.01.033.

Maguire, D.A., Kanaskie, A., Voelker, W., Johnson, R., and Johnson, G. 2002. Growth of young Douglas-fir plantations across a gradient in Swiss needle cast severity. West. J. Appl. For. **17**: 86–95.

Maguire, D.A., Mainwairing, D.B., and Kanaskie, A. 2011. Ten-year growth and mortality in young Douglas-fir stands experiencing a range in Swiss needle cast severity. Can. J. For. Res. **41**(10): 2064–2076. doi:10.1139/x11-114.

Manter, D.K., Bond, B.J., Kavanagh, K.L., Rosso, R.H., and Filip, G.M. 2000. Pseudothecia of Swiss needle cast fungus, *Phaeocryptopus gaeumannii*, physically block stomata of Douglas-fir, reducing CO_2 assimilation. New Phytol. **148**: 481–491. doi:10.1046/j.1469-8137.2000.00779.x.

Manter, D.K., Kelsey, R.G., and Stone, J.K. 2001. Quantification of *Phaeocryptopus gaeumannii* colonization in Douglas-fir needles by ergosterol analysis. For. Pathol. **31**: 229–240. doi:10.1046/j.1439-0329.2001.00243.x.

Manter, D.K., Winton, L.M., Filip, G.M., and Stone, J.K. 2003. Assessment of Swiss needle cast disease: temporal and spatial investigations of fungal colonization and symptom severity. J. Phytopathol. **151**: 344–351. doi:10.1046/j.1439-0434.2003.00730.x.

Manter, D.K., Reeser, P.W., and Stone, J.K. 2005. A climate-based model for predicting geographic variation in Swiss needle cast severity in the Oregon Coast Range. Phytopathology, **95**: 1256–1265. doi:10.1094/PHYTO-95-1256.

McLaughlin, S.D., Downing, D.J., Blasing, T.J., Cook, E.R., and Adams, H.S. 1987. An analysis of climate and competition as contributors to decline of red spruce in high elevation Appalachian forests of the Eastern United States. Oecologia, **72**: 487–501. doi:10.1007/BF00378973.

Michaels, E., and Chastagner, G.A. 1984. Distribution, severity and impact of Swiss needle cast in Douglas-fir Christmas trees in western Washington and Oregon. Plant Dis. **68**: 939–942. doi:10.1094/PD-69-939.

Mote, P.W., and Salathé, E.P., Jr. 2010. Future climate in the Pacific Northwest. *In* The Washington climate change impacts assessment: evaluating Washington's future in a changing climate. Climate Impacts Group, University of Washington, Seattle, Washington. Chapter 1.

National Oceanic and Atmospheric Administration (NOAA). 2005. U.S. temperature and precipitation trends [online]. US Department of Commerce, National Oceanic and Atmospheric Administration, National Weather Service, Climate Prediction Center, Camp Springs, Maryland. Available from http://www.cpc.noaa.gov/trndtext.shtml.

Oliver, C.D., and Stephens, E.P. 1977. Reconstruction of a mixed-species forest in central New England. Ecology, **58**: 562–572. doi:10.2307/1939005.

Omdal, D., and Ramsey-Kroll, A. 2010. Swiss needle cast on Washington State lands, 1999–2009. Washington Department of Natural Resources, Olympia, Wash. Forest Health Note 2010-001.

Peace, T.R. 1962. Pathology of trees and shrubs. Oxford University Press, Oxford, UK.

Rosso, P.H., and Hansen, E.M. 2003. Predicting Swiss needle cast disease distribution and severity in young Douglas-fir plantations in coastal Oregon. Phytopathology, **93**: 790–798. doi:10.1094/PHYTO.2003.93.7.790.

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

Stone, J.K., Hood, I.A., Watt, M.S., and Kerrigan, J.L. 2007. Distribution of Swiss needle cast in New Zealand in relation to winter temperature. Austral. Plant Pathol. **36**: 445–454. doi:10.1071/AP07049.

Stone, J.K., Coop, L.B., and Manter, D.K. 2008*a*. Predicting effects of climate change on Swiss needle cast disease severity in Pacific Northwest forests. Can. J. Plant Pathol. **30**: 169–176. doi:10.1080/07060661.2008.10540533.

Stone, J.K., Capitano, B.R., and Kerrigan, J.L. 2008*b*. The histopathology of *Phaeocryptopus gaeumannii* on Douglas-fir needles. Mycologia, **100**: 431–444. doi:10.3852/07-170R1.

Tsay, R.S. 1988. Outliers, level shifts, and variance changes in time series. J. Forecasting, **7**: 1–20.

Watt, M.S., Stone, J.K., Hood, I.A., and Palmer, D.J. 2010. Predicting the severity of Swiss needle cast on Douglas-fir under current and future climate in New Zealand. For. Ecol. Manage. **260**: 2232–2240. doi:10.1016/j.foreco.2010.09.034.

Watt, M.S., Stone, J.K., Hood, I.A., and Manning, L.K. 2011. Using a climatic niche model to predict the direct and indirect impacts of climate change on the distribution of Douglas-fir in New Zealand. Global Change Biol. **17**: 3608–3619. doi:10.1111/j.1365-2486.2011.02486.x.

Welsh, C., Lewis, K., and Woods, A. 2009. The outbreak history of Dothistroma needle blight: an emerging forest disease in northwestern British Columbia, Canada. Can. J. For. Res. **39**(12): 2505–2519. doi:10.1139/X09-159.

Winton, L.M., Stone, J.K., Watrud, S., and Hansen, E.M. 2002. Simultaneous one-tube quantification of host and pathogen DNA with real-time polymerase chain reaction. Phytopathology, **92**: 112–116. doi:10.1094/PHYTO.2002.92.1.112.

Winton, L.M., Manter, D.K., Stone, and Hansen, E.M. 2003. Population structure suggests reproductively isolated lineages of *Phaeocryptopus gaeumannii*. Mycologia, **98**: 781–791. doi:10.3852/mycologia.98.5.781.

Woods, A.J. 2003. Species diversity and forest health in northwest British Columbia. For. Chron. **79**: 892–897.

Woods, A., Coates, K.D., and Hamann, A. 2005. Is an unprecedented Dothistroma needle blight epidemic related to climate change? BioScience, **55**: 761–769. doi:10.1641/0006-3568(2005)055[0761:IAUDNB]2.0.CO;2.

Zhao, J., Mainwaring, D.B., Maguire, D.A., and Kanaskie, A. 2011. Regional and annual trends in Douglas-fir foliage retention: correlations with climatic variables. For. Ecol. Manage. **262**: 1872–1886. doi:10.1016/j.foreco.2011.08.008.