Forest Ecology and Management 262 (2011) 1872–1886

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Regional and annual trends in Douglas-fir foliage retention: Correlations with climatic variables

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A R T I C L E I N F O

Article history:
Received 29 April 2011
Received in revised form 2 August 2011
Accepted 4 August 2011
Available online 3 September 2011

Keywords:
Swiss needle cast
Foliage retention
Foliage dynamics
Climatic drivers
Climate change

A B S T R A C T

Swiss needle cast imposes strong geographical patterns in Douglas-fir needle retention throughout the Coast Ranges of Oregon and southwestern Washington. These geographical patterns in foliage retention have been related to the spatial variability in average climatic conditions, with climate presumed a major causal factor in the spread and intensification of the fungus that causes Swiss needle cast. Annual fluctuations in foliage retention have likewise been hypothesized to follow fluctuations in annual climatic conditions. The objective of this analysis was to test a full suite of climatic variables for their ability to predict regional and annual patterns in Douglas-fir foliage retention on 296 permanent sample plots comprising six different Swiss needle cast studies. Foliage retention was estimated annually from 1996 to 2009 and climatic data were generated from the PRISM website through ClimateWNA (Wang et al., 2006). Among the 85 annual, seasonal, and monthly climate variables explored, average foliage retention was predicted most consistently by a temperature-based continentality index, mean annual precipitation, winter temperature, summer temperature, and spring or summer precipitation. The same 85 variables were tested for predicting annual fluctuations in foliage retention, allowing for lagged effects of climatic conditions 1–4 years prior to each year of observation. The annual foliage retention models had climate variables similar to the periodic average foliage retention models, but with a variety of lagged effects. The periodic average foliage retention model suggested that under future climate scenarios foliage retention would increase.

1. Introduction

Swiss Needle Cast (SNC) has become a major foliar disease of Douglas-fir (*Pseudotsuga menziesii*) in coastal areas of Oregon and Washington (Hansen et al., 2000). The causal fungus, *Phaeocryptopus gaeumannii* (T. Rohde) Petr., occludes the stomates with fruiting bodies, or pseudothecia, resulting in carbon starvation and premature foliage loss (Manter et al., 2003). Since 1990, SNC has intensified dramatically in coastal Oregon. The area of Douglas-fir forest with SNC symptoms detectable by aerial survey in the Coast Ranges of Oregon increased from 53,072 ha in 1996 to 159,483 ha in 2010 (Kanaskie and Mc Willianms, 2010). SNC had previously been a serious concern only where Douglas-fir was cultivated outside of its native range in western North America (Boyce, 1940). The influence of climatic factors on infection indices (Manter et al., 2005) has suggested that recent changes in local climatic conditions have facilitated emergence of the disease or that susceptible genotypes of Douglas-fir have been planted on coastal sites where climatic conditions are more favorable to the disease.

The reduction in needle retention symptomatic of SNC causes significant Douglas-fir growth losses (Maguire et al., 2002). Foliage retention has been routinely applied as an index of disease severity, and has been applied to estimate growth losses at the stand level. Individual-tree diameter and height growth predictions can also be modified by plot-level foliage retention in ORGANON, a growth model that can simulate growth of intensively managed Douglas-fir stands (Hann, 2006; Garber et al., 2007). In other species and regions of the world, needle retention has been correlated with a range of site factors, including inherent productivity (Pensa and Jalkanen, 2005), elevation (Reich et al., 1995), and various climatic factors correlated with elevation and latitude (Reich et al., 1995; Xiao, 2003); however, the proposed mechanisms have not included indirect effects through pathogens. Mild winter temperatures have been hypothesized to favor the development of fungal mycelia within the needles of infected Douglas-fir (Manter et al., 2005), and abundant spring moisture has been hypothesized to facilitate germination of spores on the surfaces of needles and allow hyphae to grow across the needle surface until they can enter a stomate.

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doi:10.1016/j.foreco.2011.08.008

Analyses to date have investigated the correlation between stand foliage retention averaged over a period of time and average climatic conditions for the same period and site. If the climate characterizing a site is driving part of the spatial variation in foliage retention, observed annual fluctuations in foliage retention should likewise be correlated with annual variation of the same climatic factors. These spatial and temporal relationships with climate have been verified for *P. gaeumannii* infection index (frequency of stomates occluded by pseudothecia; Manter et al., 2005). Spatial variability has been investigated for foliage retention, primarily because foliage retention has been regarded as the operational link to geographic risk rating systems. In contrast, annual climatic influences on epidemiology are better understood by directly observing annual responses of the pathogen itself. However, continuous monitoring of foliage retention on plots established by the Swiss Needle Cast Cooperative (SNCC; http://sncc.forestry.oregonstate.edu/) has provided a broader geographic scope and extended time series of observations than are currently available for pseudothecia counts. This database allowed extensive testing of the effects of both average climate characterizing a site and annual variation in climatic variables on foliage retention as the primary symptom of SNC. The objectives of this paper were to: (1) test a large set of site-specific climatic variables for their ability to predict geographic variation in plot average foliage retention over the period of observation; (2) test a large set of site-specific climatic variables for their ability to predict annual fluctuations in foliage retention, including lagged effects of climatic conditions; and (3) apply resulting models to forecast foliage retention under future climate scenarios at each plot. Identification of factors controlling geographic variation in average foliage retention have previously facilitated development of geographic risk-rating systems for SNC (Rosso and Hansen, 2003; Coop and Stone, 2007; Latta et al., 2009). Identification of lagged climatic variables that explain the largest possible proportion of variation in annual fluctuations in foliage retention should improve our understanding of climatic effects on SNC intensification, including the degree to which recent intensification can be attributed to corresponding trends in climate.

2. Material and methods

2.1. Field work

Plots were distributed across a range of SNC severity, stand density, aspect, and slope (Fig. 1). The study sites extended from 42.13°N to 46.65°N latitude and from 122.00°W to 124.35°W longitude. Elevation ranged from 9 to 1280 m above sea level. Over the last 40 years, the mean January minimum temperature for this region was 1.5 °C and the mean July maximum temperature was 22.8 °C. Total annual precipitation averaged approximately 240 cm, with approximately 80% of the total falling from October to March.

Data for all studies were collected by field crews trained by the Oregon Department of Forestry to ensure consistency and repeatability of measurements. Needle retention of individual trees was visually estimated by first dividing the live crown into thirds, with the base of the live crown defined as the lowest live branch. Secondary or lateral branches on a primary or main branch were then examined near the center of each third, and average number of needle age classes present at time of sampling was estimated to the nearest 0.5 year (Maguire et al., 2002). The needle retention of the tree was then estimated by averaging these values across the crown thirds (Fig. 2).

The Growth Impact Study (GIS) plots were established to monitor SNC symptoms and tree growth in 10–30 year-old Douglas-fir plantations between Astoria and Newport and within 18 miles of the Pacific Coast (Maguire et al., 2002, Maguire et al., submitted for publication). Needle retention was estimated on ten dominant trees per plot. Foliage retention was estimated at plot establishment in 1998, and annually just prior to bud break from 1999 to 2004. Plot-level foliage retention was computed as the average of the ten sample trees per plot.

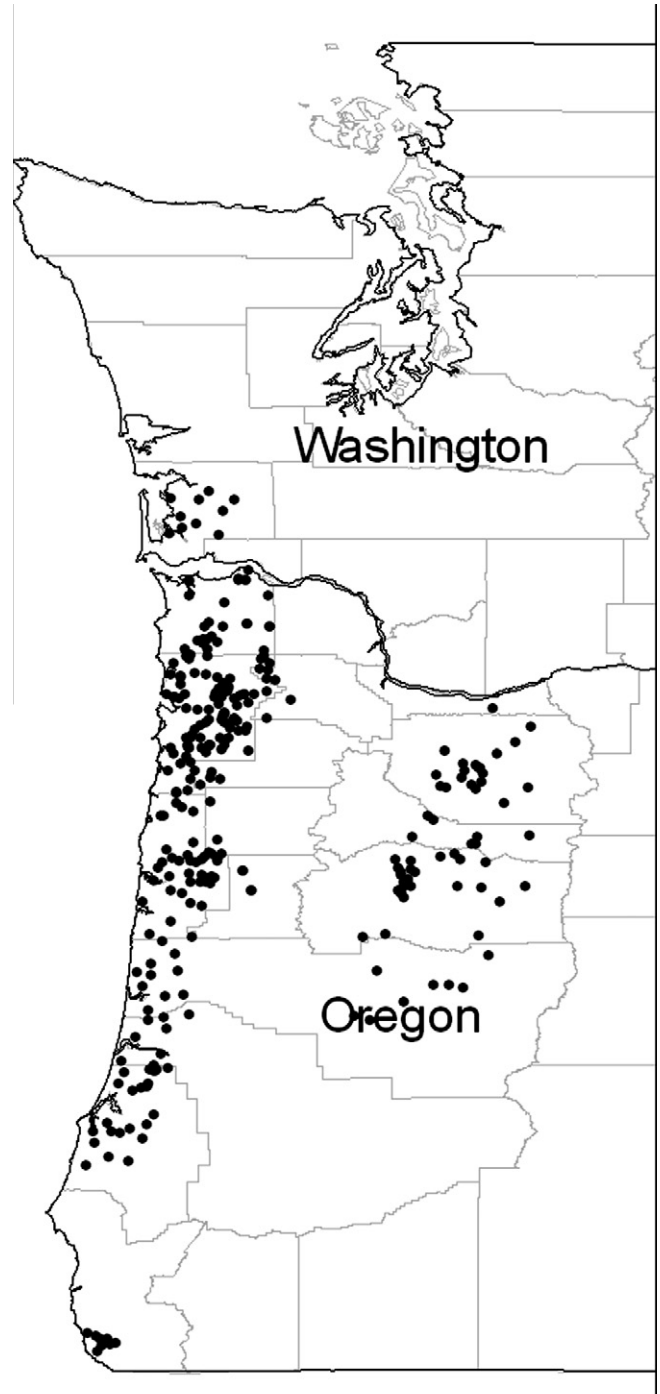

Fig. 1. Geographic distribution of plots and transects scored for Douglas-fir foliage retention.

The PCT study was designed to test the effect of thinning and initial SNC severity on symptom development and growth response (Maguire et al., in press). The treated plots were thinned before the growing season started in 1998. Spring (April–May)

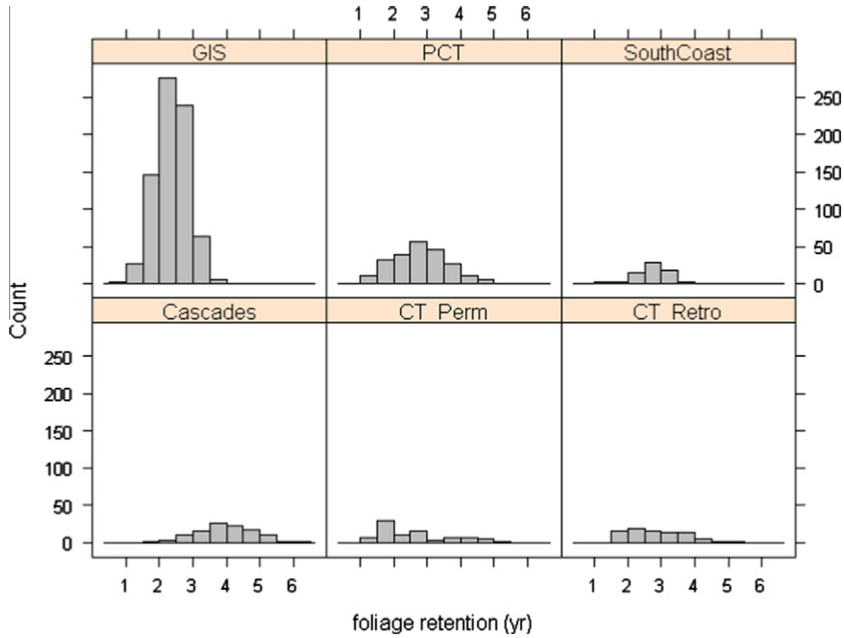

Fig. 2. Frequency histograms of foliage retention for six Swiss needle cast studies used in development of foliage retention models.

Table 1
Number of plots measured for Douglas-fir foliage retention by study and year of observation.

Plots type	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2009	Grand total
Cascades						55					55			110
CT_Perm							15	14	15	14	15	14		87
CT_Retro							24	20			23	17		84
GIS	77	77	77	77	76	76	76	76	72	72				756
PCT_Control			28	28	28	28	28	28	28	28				224
South coast									1				62	63
Grand total	77	77	105	105	104	159	143	138	116	114	93	31	62	1324

foliage retention was estimated annually at each of these study sites from 1998 to 2005 (Table 1) applying the same protocol as on the GIS plots.

Cascades growth impact study was installed in 2001 and remeasured in 2006 (Filip et al., 2006). Foliage retention was estimated by crown thirds as described above, but the ten sample trees were distributed along a randomly located 75-m transect within sample stands. Two dominant or codominant trees nearest to five equidistant points along the transect were scored for foliage retention. The same ten dominant or codominant trees were scored for foliage retention again in 2006, allowing for replacement with the nearest dominant or codominant tree if an original sample tree had died.

South coast foliage retention data were collected in 2009 on supplementary transects installed in randomly selected 10–30 year-old stands in the central and southern Oregon Coast Ranges and in the southern Washington Coast Ranges. The objective for measuring foliage retention in these stands was to extend the geographic and climatic range of previous SNCC work. The protocol for estimating foliage retention was identical to the protocol described above for the Cascades growth impact study.

CT_Perm and CT_Retro plots were established to investigate the interaction of thinning and SNC severity on growth of older stands ranging between 20 and 60 years of age (Table 1). All plots contained at least 75% Douglas-fir by basal area. The CT_Perm plots were unthinned control plots and CT_Retro plots had undergone commercial thinning 4–10 years prior to establishment (Mainwaring et al., 2005, Mainwaring and Maguire, 2008). Because these trees were much taller than those in other studies, foliage retention for each of ten trees per plot was estimated from secondary or lateral branches on a primary branch near the middle of the crown only (Table 2).

2.2. Climate data

Climate data for each plot and each year from 1992 to 2009 were calculated with ClimateWNA v4.62 (Tables 3 and 4). ClimateWNA extracts and downscales PRISM (Daly et al., 2002) monthly data (2.5 × 2.5 arcmin) for the reference period (1961–1990), and calculates seasonal and annual climate variables for specific locations in western North America based on latitude, longitude and elevation (optional). This software also downscales and integrates historical (1901–2009) (Mitchell and Jones, 2005; Mbogga et al., 2009) and future climate datasets generated by various global circulation models (GCM). Three future periods were explored, here referred to as 2020 (30 year average of 2010–2039), 2050 (30 year average of 2040–2069) and 2080 (30 year average of 2070–2099). The output included both measurable climate variables and derived climatic indices (Hamann and Wang, 2005).

GCM projections for future periods in ClimateWNA were obtained from the TYN SC 2.0 dataset (Mitchell et al., 2004) and from Pacific Climate Impact Consortium. These GCM predictions were obtained from the Intergovernmental Panel on Climate Change (IPCC) Fourth assessment (AR4) (IPCC, 2007). ClimateWNA used various combinations of ten GCMs and three emission scenarios

Table 2
Number of plots, average foliage retention (FR), slope, latitude, longitude, and elevation (elev) for plots in the six different SNC studies.

Region	N obs.	Variable	Mean	Std. dev.	Minimum	Maximum
CT_Perm	29	FR	2.60	1.02	1.26	4.78
		Slope	12.13	6.84	0.00	25.36
		Lat.	45.24	0.71	43.58	46.17
		Long.	−123.57	0.37	−123.99	−122.29
		Elev.	394.10	196.15	61.00	1024.00
CT_Retro	44	FR	2.85	0.80	1.65	4.58
		Slope	10.26	8.22	0.00	30.03
		Lat.	45.25	0.71	43.50	46.17
		Long.	−123.52	0.40	−124.06	−122.31
		Elev.	492.77	190.16	45.00	875.00
Cascades	55	FR	4.03	0.55	2.45	5.50
		Slope	10.58	8.06	0.00	34.88
		Lat.	44.72	0.42	43.85	45.50
		Long.	−122.45	0.25	−122.94	−122.00
		Elev.	652.64	312.93	152.00	1280.00
GIS	77	FR	2.38	0.42	1.26	3.35
		Slope	16.00	12.61	0.00	44.60
		Lat.	45.25	0.42	44.58	46.09
		Long.	−123.78	0.09	−123.99	−123.61
		Elev.	245.09	156.58	61.00	914.00
PCT	28	FR	2.79	0.78	1.28	4.43
		Slope	11.60	12.31	0.00	38.10
		Lat.	45.44	0.56	44.54	46.22
		Long.	−123.58	0.14	−123.89	−123.38
		Elev.	238.29	158.45	48.00	766.00
SouthCoast	63	FR	2.76	0.43	1.48	3.77
		Slope	7.83	7.06	0.00	22.05
		Lat.	43.98	1.32	42.10	46.64
		Long.	−124.02	0.19	−124.35	−123.57
		Elev.	227.08	139.61	9.00	609.00

(A1B, A2, and B1) to generate 13 sets of future climatic conditions for each period described above as 2020, 2050, and 2080.

2.3. Statistical analysis

All subsets regression and a mixed modelling approach were used to develop models for predicting foliage retention from climatic variables using PROC REG and PROC MIXED in SAS version 9.2. Both periodic average foliage retention and annual fluctuation in foliage retention were modeled, the former to understand fundamental site differences as determined by long-term climatic averages, and the latter to understand how annual fluctuations in the same or similar climatic variables caused the range and average of foliage retention to vary from year to year. For both periodic average and annual foliage retention models, 2/3 of all plots were used for model development and 1/3 was used for validation. Maximum acceptable variance inflation factor (VIF) was set at 10 to minimize the impact of collinearity among the variables. The best models were selected by optimal combinations of high R^2, low AIC, and low MSE.

2.3.1. Average periodic foliage retention

Periodic average foliage retention was modeled as a function of climatic variables averaged over the same period of observation plus the four-year period immediately preceding the first observation for a given dataset. Separate models were developed for annual, seasonal, and monthly weather variables. Models based on a mix of climate variables at different temporal resolutions were avoided to simplify interpretation of the results and to facilitate their application to climate data that are restricted to a specific resolution. Each observation of periodic average foliage retention was weighted by the length of the observation period. An all-subsets regression approach helped identify sets of models with strong statistical properties, and then specific models were selected based on their consistency with known aspects of SNC disease epidemiology and presumed causal factors. To facilitate comparison to previous work, the models developed by Coop and Stone (2007) and Latta et al. (2009) were also fitted to the comprehensive dataset.

Selected models were applied to the validation dataset and assessed by plotting predicted on observed foliage retention and computing the following validation statistics:

$$\mathrm{D} = \text{Mean difference} = \Sigma d/n_v$$

$$\mathrm{MAD} = \text{Mean absolute difference} = \Sigma|d|/n_v$$

where d is difference (observed retention − predicted retention), and n_v is number of observations in validation dataset.

The model selected as best using annual climatic variables was applied to the 13 future climate scenarios described above for 2020, 2050, and 2080. The average of the 13 predictions for each plot was then computed to generate frequency distributions across SNC severity for these three future periods.

2.3.2. Trends in annual foliage retention

Foliage retention in any single year was expected to have been influenced by climatic variables up to approximately 4 years prior to observation, because maximum needle longevity averaged slightly less than 4 years. Therefore, climate variables for foliage retention observed in any given year included seasonal or monthly variables in the current year up though May (month of observation), as well as climate variables from each of the previous 4 years to account for lagged and cumulative effects. Initial annual foliage retention models were developed by applying all-subsets regression to identify the best models based on annual, seasonal, and monthly variables separately. As was the case for periodic average retention, models based on a mix of climate variables at different

Table 3
Climatic variables tested as predictors of foliage retention in Douglas-fir.

Group		Predictor	Definition
Annual variables	*Direct variables*	MAT	Mean annual temperature (°C)
		MWMT	Mean warmest month temperature (°C)
		MCMT	Mean coldest month temperature (°C)
		TD	Temperature difference between MWMT and MCMT, or continentality (°C)
		MAP	Mean annual precipitation (mm)
		MSP	Mean annual summer (May to September) precipitation (mm)
		AHM	Annual heat:moisture index ((MAT+10)/(MAP/1000))
		SHM	Summer heat:moisture index ((MWMT)/(MSP/1000))
	Derived variables	DD0	Degree-days below 0 °C, chilling degree-days
		DD5	Degree-days above 5 °C, growing degree-days
		DDu18	Degree-days below 18 °C, heating degree-days
		DDa18	Degree-days above 18 °C, cooling degree-days
		NFFD	The number of frost-free days
		FFP	Frost-free period
		bFFP	The Julian date on which FFP begins
		eFFP	The Julian date on which FFP ends
		PAS	Precipitation as snow (mm) between August in previous year and July in current year
		EMT	Extreme minimum temperature over 30 years
		Eref	Hargreaves reference evaporation, calculated with the Hargreaves equation (EHar) with a latitude correction applied, i.e., Eref = EHar(1.18 − 0.0067latitude), n = 56, R^2 = 0.734, sexy = 0.039EHar and the latitude is in degrees.
		CMD	Hargreaves climatic moisture deficit, sum of the monthly difference between a reference evaporation (Eref) and precipitation.
Seasonal variables		Tave_wt, Tave_sp, Tave_sm, Tave_at	Mean temperature (°C) of winter (Dec.(previous year)–February), spring (March–May), summer (June–August), and autumn (September–November)
		Tmax_wt, Tmax_sp, Tmax_sm, Tmax_at.	Mean maximum temperature (°C) of winter, spring, summer, and autumn
		Tmin_wt, Tmin_sp, Tmin_sm, Tmin_at.	Mean minimum temperature (°C) of winter, spring, summer, and autumn
		PPT_wt, PPT_sp, PPT_sm, PPT_at	Precipitation (mm) of winter, spring, summer, and autumn
Monthly variables		Tave01–Tave12	January–December mean temperatures (°C)
		Tmax01–Tmax12	January–December maximum mean temperatures (°C)
		Tmin01–Tmin12	January–December minimum mean temperatures (°C)
		PPT01–PPT12	January–December precipitation (mm)

temporal resolutions were avoided to simplify interpretation of the results and to facilitate their application to climate data that are restricted to a specific resolution. Candidate models for annual foliage retention were restricted to those with parameter estimates that were all significant at $\alpha = 0.05$ and predictor variables with VIF < 10. Models with 2–4 variables for each of the three temporal resolutions were selected based on R^2 and MSE. The selected annual foliage retention models were required to have a combination of fewest predictors and high precision, but also contain predictors that were most consistent with known aspects of SNC epidemiology. Because foliage retention was measured repeatedly on plots, the independence of observations assumed in ordinary least squares was clearly violated. Mixed-effect models eliminated some of the autocorrelation by introducing plot as a random effect. The efficacy of random plot effects for addressing autocorrelation was further assessed by reductions in AIC obtained by modeling the variance-covariance structure of the residual errors directly.

3. Results

3.1. Average foliage retention model

Annual, seasonal, and monthly climatic variables all had reasonably strong predictive ability in the selected models ($R^2 \geqslant 0.62$; Table 5). Annual and monthly variables explained a greater proportion of the variation than seasonal variables, with R^2 ranging from 0.67 to 0.68, 0.62 to 0.66, and 0.65 to 0.72 for annual, monthly and seasonal variables, respectively (Table 5). Approximately 6% and 10% more of the variation in foliage retention was explained by these models relative to the models presented by Coop and Stone (2010) and Latta et al. (2009), respectively. The selected model from each of the annual, seasonal, and monthly sets (models 2, 4, and 7 in Tables 5 and 6) suggested that the geographic variation in periodic average foliage retention was driven by a variable representing winter temperature ($Tave_{wt}$, Tmin12), a variable representing summer temperature ($Tmax_{sm}$, Tave08), or a variable representing a combination of both (TD). All three models also included a variable representing precipitation (MAP in model 2), particularly precipitation received in the spring or early summer (PPTsp in model 4, PPT07 in model 7). In general, foliage retention at a given location increased with increasing summer temperature, decreasing winter temperature, or increasing difference between winter and summer temperatures (Fig. 3). Likewise, foliage retention decreased with greater precipitation, with spring and early summer precipitation imposing greatest influence (Table 6).

Validation statistics indicated that models with annual climate variables had relatively large differences between observed and predicted retention (D = −0.06 to −0.05), and low MAD (0.35–0.37). In contrast, models with seasonal climate variables had low D (−0.01 to 0.04), and high MAD (0.38–0.47). Between these extremes were models based on monthly climate variables, with intermediate values of D (−0.07 to 0.04), and MAD (0.35–0.46). Performance of the three selected models (2, 4, and 7 in Table 6) on the validation dataset suggested no serious problems in model behavior (Fig. 4).

3.2. Forecasts with the average foliage retention model

Under each of the 13 future climate scenarios, average foliage retention predicted for 2020, 2050, and 2080 differed among the annual, seasonal and monthly models (models 2, 4, and 7, respectively; the models selected as best among those based on annual, seasonal, and monthly climate predictors). Average foliage retention across all plots was predicted by the annual model (model 2) to increase gradually from 3.0 to 3.1 to 3.3 years in 2020,

Table 4
Averages, minima, and maxima for key climatic variables for predicting foliage retention in coastal Douglas-fir stands. Variables and their units are defined in Table 3.

Variable	Mean	Std. dev.	Minimum	Maximum
TD	12.42	1.62	8.21	15.92
AHM	9.51	2.56	4.07	16.65
MAP	2371.38	629.53	1348.00	4825.00
DD0	20.42	20.76	3.00	148.00
Tmax_sp	14.54	1.41	9.39	17.16
Tave_sm	16.17	0.91	13.81	18.62
Tmax_sm	22.27	1.47	18.44	26.23
Tmin_wt	1.81	1.35	−2.80	5.66
Tave_wt	5.57	1.48	0.57	8.84
PPT_sp	557.84	120.65	331.80	983.07
PPT_at	613.16	161.62	276.80	1243.56
Tmax06	19.87	1.24	15.17	22.82
Tave07	17.01	1.10	14.55	20.26
Tave08	17.26	0.91	14.46	19.86
Tmin12	1.75	1.36	−3.06	5.64
Tave12	5.04	1.45	0.16	8.10
PPT06	76.30	20.32	33.40	122.70
PPT07	20.69	10.34	3.80	41.80
PPT08	34.92	12.78	10.20	65.89
PPT09	63.92	22.98	22.40	129.22

2050, and 2080, respectively. In contrast, the seasonal model (model 4) predicted a gradual decline in foliage retention from 3.0 in 2020 to 2.9 in 2050 and 2.8 years in 2080. The monthly model predicted a trend in foliage retention similar to the annual model, with a gradual increase from 2.9 to 3.0 to 3.2 years. Consistent with these results, the frequency distributions for foliage retention in 2020, 2050, and 2080 indicated that in the future fewer plots would have foliage retention ⩽2 years, and more plots would also have foliage retention >5 years according to the annual and monthly models, but the reverse was true for the seasonal model (Fig. 5). Foliage retention on the majority of study plots was predicted to increase by about half a year from the current range of 2–3 years to a future range of 2.5–3.5 years in 2080 based on the annual and monthly models (Fig. 5). Predicted trends in specific climatic variables lend insight into predicted changes in foliage retention. The GCMs generally predicted a gradual increase in continentality index (TD), a slight increase in mean annual precipitation (MAP), and a marked decline in chilling degree days (DD0) (Fig. 6). With respect to seasonal climate conditions, GCMs predicted a gradual increase in maximum summer temperature (Tmax_sm) and average winter temperature (Tave_wt), and a slight decrease in spring precipitation (PPT_sp). At the monthly resolution, GCMs predicted a future increase in August temperature (Tave08), a decrease in July precipitation (PPT07), and a marked increase in December temperature (Tmin12).

Table 6
Parameter estimates and their standard errors for models predicting periodic average foliage retention from climatic variables.

Model	Parameter estimates and standard errors
Coop and Stone (2007)	FR = 7.6 − 0.0585RH7 − 0.142DDS − 0.000830asp (0.562) (0.00855) (0.0150) (0.000314)
Latta et al. (2009)	FR = 3.7 − 0.397Tm1 − 0.102CMI7 (0.275) (0.0277) (0.0204)
Annual	
1	FR = −1.0 + 0.372TD − 0.000292MAP (0.275) (0.0194) (0.0000541)
2	FR = −0.4 + 0.312TD − 0.000311MAP + 0.00855DD0 (0.335) (0.0270) (0.0000534) (0.00273)
Seasonal	
3	FR = −3.0 − 0.453Tmin_wt + 0.415Tave_sm (0.665) (0.0269) (0.0417)
4	FR = 2.2 + 0.175Tmax_sm − 0.394Tave_wt − 0.00188PPT_sp (0.663) (0.0241) (0.0251) (0.000302)
5	FR = 2.5 − 0.127Tmax_sp + 0.223Tmax_sm − 0.298Tave_wt − 0.00191PPT_sp (0.675) (0.0646) (0.0342) (0.0546) (0.000300)
Seasonal	
6	FR = −3.6 + 0.418Tave08 − 0.427Tmin12 (0.671) (0.0390) (0.0259)
7	FR = −1.8 + 0.330Tave08 − 0.388Tmin12 − 0.0162PPT07 (0.754) (0.0418) (0.0261) (0.00351)
8	FR = −2.2 + 0.666Tave08 − 0.259Tmax06 − 0.379Tmin12 − 0.0157PPT08 (0.701) (0.0820) (0.0585) (0.0244) (0.00287)

3.3. Annual foliage retention model

Fit statistics from both ordinary least squares (all-subsets) and mixed-effects models showed that the best annual, seasonal, and monthly models demonstrated comparable performance, with lowest AICs reaching 849 for the best seasonal model, 861 for the best monthly model and 885 for the best annual model (Table 7). A wide variety of alternative variance-covariance structures for the residual errors achieved no significant improvement in AIC. The best was the AR(1) model, but it reduced AIC by less than 2%. All three of the selected models (models 10, 12, and 15) suggested that foliage retention in any given year increased with increasing summer temperature (Tmax_sm2, Tmax081) and with either decreasing winter temperature (Tave_wt2, Tave123) or increasing difference between summer and winter temperature (TD2) (Tables 7 and 8). In addition to these temperature effects, greater spring precipitation (PPT_sp1, PPT064) was associated with lower foliage retention in the seasonal and monthly models, and mean annual precipitation (MAP) was likewise negatively correlated with foliage retention. In general, the best models contained

Table 5
Selected models for predicting periodic average foliage retention from annual, seasonal, and monthly climate variables averaged over the period of observation. All predictors are significant at $\alpha = 0.05$; bold type indicates variables with a positive effect on foliage retention; regular type indicates a negative effect.

Model authors or resolution	Model number	Number of predictors	Model statistics		Predictor variables	Validation statistics	
			R^2	MSE		D	MAD
Coop and Stone (2007)		3	0.56	1.09	RH7 DDS asp	0.01	0.50
Latta et al. (2009)		2	0.52	1.20	Tm1 CMI7	−0.09	0.56
Annual	1	2	0.67	0.83	**TD** MAP	−0.05	0.37
	2	3	0.68	0.80	**TD** MAP **DD0**	−0.06	0.35
Seasonal	3	2	0.62	0.94	Tmin_wt, **Tave_sm**	0.04	0.47
	4	3	0.65	0.87	**Tmax_sm**, Tave_wt, PPT_sp	0.02	0.42
	5	4	0.66	0.86	Tmax_sp, **Tmax_sm**, Tave_wt, PPT_sp	−0.01	0.38
Monthly	6	2	0.65	0.88	**Tave08**, Tmin12	0.04	0.46
	7	3	0.68	0.80	**Tave08**, Tmin12, PPT07	−0.01	0.39
	8	4	0.72	0.72	**Tave08**, Tmax06, Tmin12, PPT08	−0.07	0.35

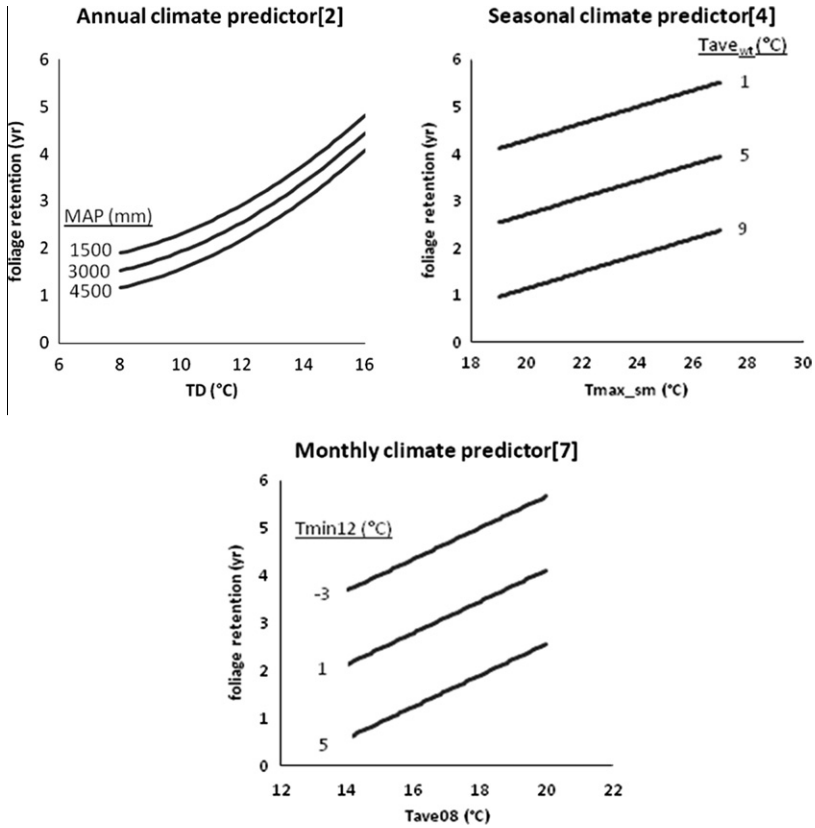

Fig. 3. Foliage retention predicted from three best periodic average retention models (model 2, 4, and 7). For model 2, DD0 was represented by its relationship to TD and MAP ($DD0 = 371.7 - 69.5 \cdot TD + 3.15 \cdot TD^2 + 0.00756 \cdot MAP$); for model 4, PPT_sp was set to the average of 557 mm; and for model 7, PPT07 was set to the average of 20 mm.

climate variables with lag times of 2 or 3 years. Comparison of predicted annual fluctuations in foliage retention to observed fluctuations for three randomly selected plots (one each with light, moderate, and severe SNC) suggested that the selected models tracked foliage retention best on the most severely impacted plots (Fig. 8).

Random effects for the plots in the validation dataset are unknown, so they cannot be accounted for when predicting foliage retention on the validation plots. As a result, the validation statistics were expected to indicate performance similar to fixed-effects models (Table 7). Validation statistics for the mixed-effects models showed that annual foliage retention models yielded a negative D (−0.16 to 0.00), indicating a slight underestimate of foliage retention in any given year. The annual, seasonal, and monthly models performed equally well on the validation dataset, although models based on annual climate variables yielded slightly better validation statistics, with D ranging from −0.04 to 0.00 and MAD ranging from 0.41 to 0.44). Performance of the three selected models (10, 12, and 15) on the validation dataset suggested no serious problems in model behavior (Fig. 7).

4. Discussion

The comprehensive screening of 85 climate variables in the present study was intended to measure the amount of predictive power that would potentially be sacrificed by a priori selection of climatic variables that are consistent with the working hypothesis for climatic drivers of SNC. The first phase of the analysis was intended to confirm previous work that established risk-rating systems based on geographic variation in needle retention and corresponding long-term climatic conditions at permanent plots. The second phase involved assessment of annual fluctuations in foliage retention to further confirm the influence of climatic drivers on fungal development and SNC severity. Results were generally consistent with the expectation that mild winter temperatures and greater late spring/early summer precipitation would be associated with greater Swiss needle cast severity and lower foliage retention. However, other variables like late summer temperature were consistently influential as well, and predictive ability was comparable among many alternative models based on annual, seasonal, or monthly climatic variables.

4.1. Climate data

ClimateWNA provided 85 climatic variables for the reference period 1961–1990 and for any location in western North America described by its longitude, latitude, and elevation. The earlier version of ClimateWNA, ClimateBC was widely applied as a tool for natural resource management, forest genecology and studies related to climate change (Spittlehouse, 2006). Variables from ClimateWNA performed well for predicting geographic variation in foliage retention, and helped make a convincing case for a link between Douglas-fir foliage retention and local climate. Preliminary analyses with climatic variables interpolated from PRISM data by geographically weighted regression (Latta et al., 2009) performed almost as well as ClimateWNA; however, the proportion of explained variation was consistently greater with climatic predictors from ClimateWNA.

4.2. Average foliage retention model

Previous research has supported the hypothesis that winter temperature and/or spring moisture are driving factors for the epidemiology of *P. gaeumannii* and Swiss needle cast intensity in

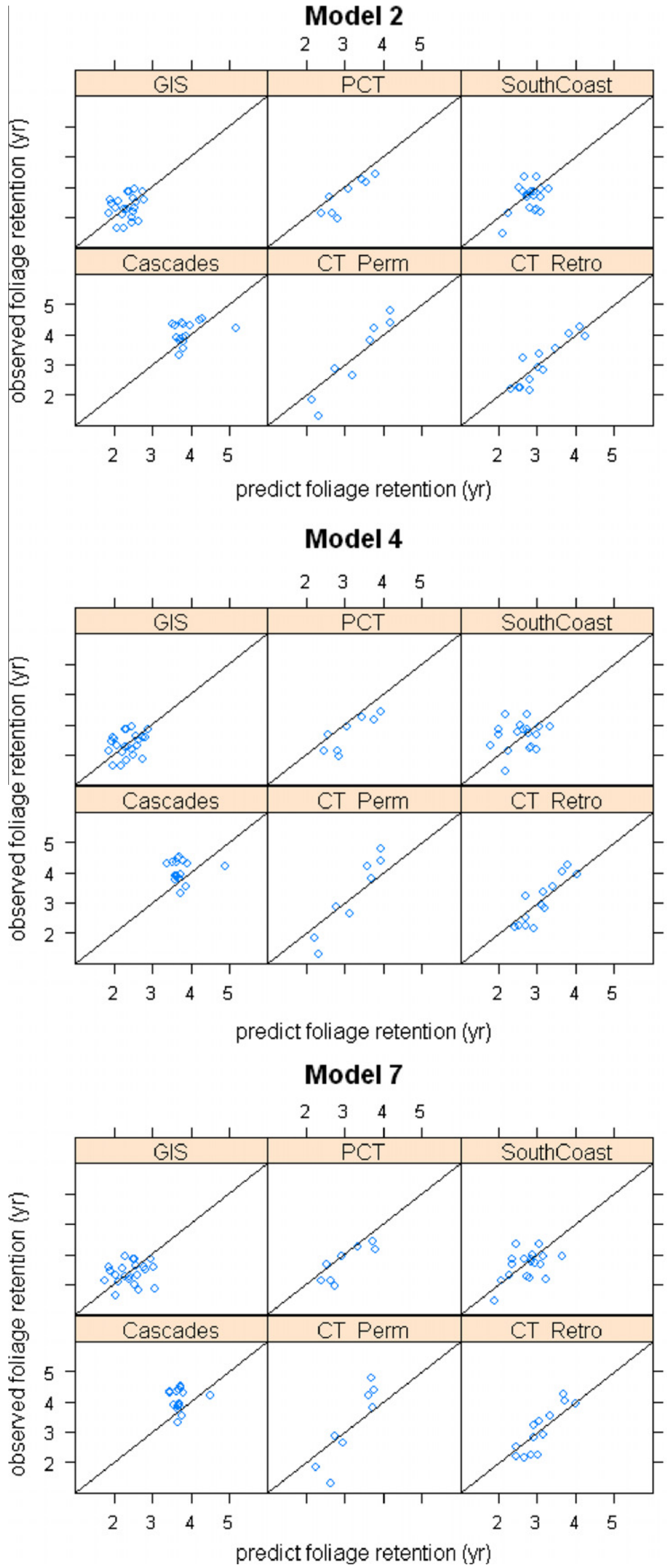

Fig. 4. Periodic average foliage retention predicted from selected models based on annual (model 2), seasonal (model 4), or monthly climatic variables (model 7) relative to observed retention for the validation dataset.

western Oregon (Rosso and Hansen, 2003; Manter et al., 2005; Stone and Coop, 2006). Coop and Stone (2007) developed a foliage retention model that predicted average foliage retention over a 12-year period from winter degree days, relative humidity in July,

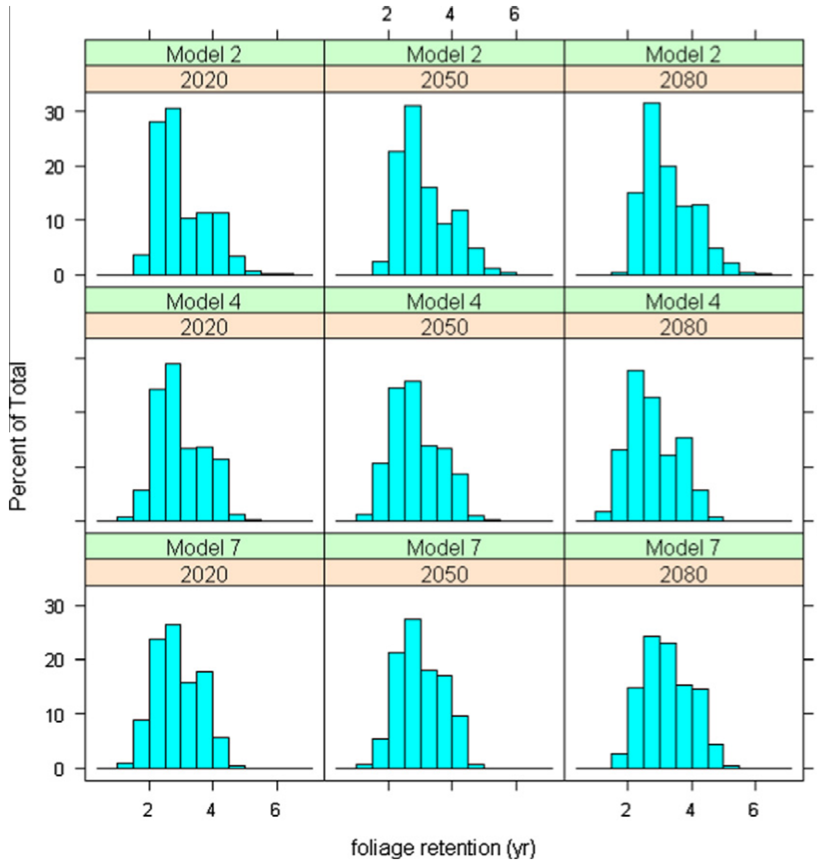

Fig. 5. Frequency distribution of future (predicted) foliage retention. Predicted retentions are based on climatic variables forecasted with ClimateWNA for 2020, 2050, and 2080.

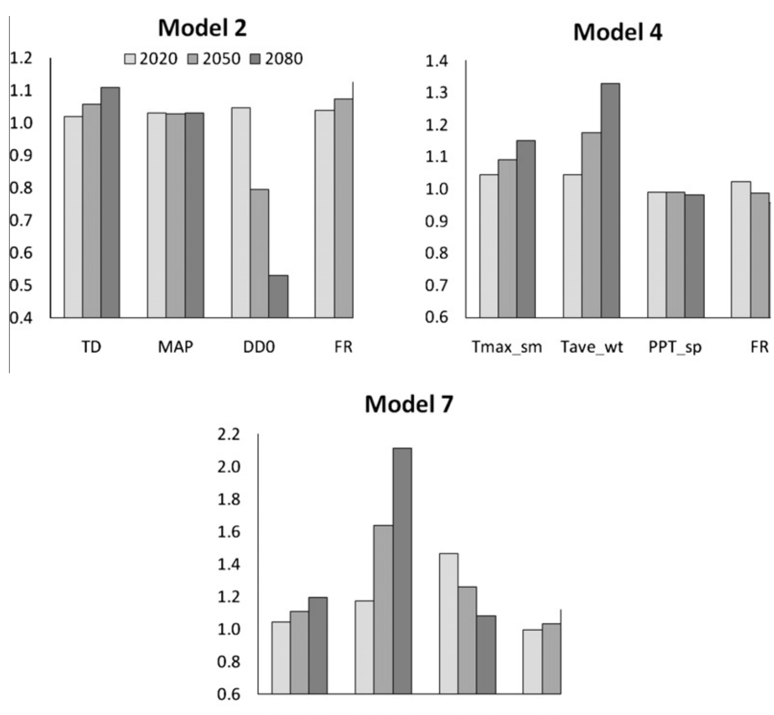

Fig. 6. The ratio of predicted to current average values of foliage retention and climatic variables from model 2, 4, and 7 for the 13 future climate scenarios predicted by ClimateWNA.

Table 7
Selected mixed-effects models for predicting foliage retention in any given year from annual, seasonal, and monthly climate variables. The numbers at the end of the symbols for annual and seasonal variables indicate the number of years the variable was lagged. The first two numbers of monthly variables indicate month, and the last number indicates the number of years the variable was lagged. All predictors are significant at $\alpha = 0.05$; bold type indicates variables with a positive effect on foliage retention; regular type indicates a negative effect.

Resolution	Model number	Number of predictors	Model statistics			Predictor variables	Validation statistics	
			R^2	MSE	AIC		D	MAD
Annual	9	2	0.56	0.29	946	MAP1, **TD2**	−0.04	0.44
	10	3	0.60	0.26	885	MAP1, **TD2**, **DD04**	0.00	0.41
Seasonal	11	2	0.55	0.29	919	Tmin_wt2, **Tave_sm2**	−0.06	0.48
	12	3	0.59	0.27	895	PPT_sp1, **Tmax_sm2**, Tave_wt2	−0.04	0.46
	13	4	0.59	0.27	849	Tave_wt0, Tmax_sp3, **Tmax_sm3**, PPT_sp4	−0.04	0.43
Monthly	14	2	0.51	0.32	1016	**Tmax081**, Tave122	−0.16	0.52
	15	3	0.57	0.28	992	**Tave081**, Tave123, PPT064	−0.15	0.47
	16	4	0.61	0.25	861	Tmax043, **Tmax073**, Tmin013, PPT043	−0.04	0.41

Table 8
Parameter estimates and their standard errors for mixed-effects models predicting foliage retention in any given year from climatic variables.

Model	Parameter estimates and standard errors
Annual	
9	FR = 0.2 − 0.000113MAP1 + 0.231TD2 (0.1644) (0.0000239) (0.0116)
10	FR = −0.0 − 0.000146MAP1 + 0.246TD2 + 0.00735DD04 (0.159) (0.0000233) (0.0111) (0.000821)
Seasonal	
11	FR = −3.2 − 0.311Tmin_wt2 + 0.408Tave_sm2 (0.313) (0.0169) (0.0204)
12	FR = 0.5 − 0.000764PPT_sp1 + 0.218Tmax_sm2 − 0.361Tave_wt2 (0.218) (0.0000938) (0.0110) (0.0172)
13	FR = 3.0 − 0.123Tave_wt0 − 0.227Tmax_sp3 + 0.182Tmax_sm3 − 0.000527PPT_sp4 (0.258) (0.0173) (0.0147) (0.0113) (0.0000851)
Monthly	
14	FR = 0.4 + 0.158Tmax081 − 0.230Tave122 (0.239) (0.0107) (0.0155)
15	FR = −0.2 + 0.291Tave081 − 0.288Tave123 − 0.00485PPT064 (0.275) (0.0183) (0.0178) (0.000340)
16	FR = 2.0 − 0.204Tmax043 + 0.194Tmax073 − 0.144Tmin013 − 0.00205PPT043 (0.216) (0.0114) (0.00912) (0.00939) (0.000173)

and aspect. Latta et al. (2009) developed a similar model for average foliage retention based on mean temperature in January and a Climate Moisture Index (calculated from precipitation and evaporation) in July. Although the working hypothesis in these analyses was that foliage retention in Douglas-fir is controlled completely or predominantly by *P. gaeumannii*, other climate and site variables with less obvious connection to development of foliar fungi have been found to explain geographic variation in conifer foliage retention (Xiao, 2003; Pouttu and Dobbertin, 2000). Characterization of prevailing climatic conditions at specific sites has been a useful approach for establishing risk-rating systems for growing Douglas-fir in north coastal Oregon (Rosso and Hansen, 2003; Coop and Stone, 2007), and application of climatic conditions as driving variables follow logically from observations about where the disease has become a problem both within and outside the native range of Douglas-fir (Boyce, 1940; Hood, 1982; Hansen et al., 2000). However, climatic conditions are spatially confounded with other environmental variables, and the significant marginal effects of additional variables such as aspect on disease severity (Rosso and Hansen, 2003; Coop and Stone, 2007) suggest a number of shortcomings that may include the following: (1) available climatic variables lack sufficient resolution; (2) the salient climatic variables are not available; (3) the functional integration of available climatic variables and their effects on the host and pathogen are not achieved by multiple regression; and (4) environmental factors other than climate are also influential. Like other analyses, ours has attempted to identify that portion of variation in foliage retention that is correlated with both spatial and temporal variation in climatic conditions.

Among the eight average foliage retention models presented (Table 5), the most common annual climate predictor was a continentality index computed as the temperature difference (TD) between mean warmest month temperature (MWMT) and mean coldest month temperature (MCMT). The two most common seasonal climate predictors were summer temperature (Tmax_sm) and winter temperature (Tave_wt or Tmin_wt), and the most common monthly predictors were temperature in December (Tmin12) and temperature in August (Tave08). Climatic predictors at all three temporal resolutions therefore reflected similar climatic effects; i.e., larger differences in temperature between the warmest and coldest month corresponded with greater foliage retention. Although the mechanisms by which these variables influence foliage retention can only be speculated on, some of our results confirm past work on SNC development, but some appear contradictory as described below.

Manter et al. (2005) defined three key seasons for *Phaeocryptopus* infection and development: May–June as the period of spore dispersion, deposition, germination and initial infection; August–October as the period of fungal development within infected needles; and December–February as the period critical to the rate of pseudothecia development. More severe SNC symptoms have been consistently observed on southerly aspects (Rosso and Hansen, 2003, Coop and Stone, 2007), and green house experiments have verified that, after initial field inoculation, pseudothecia proliferate

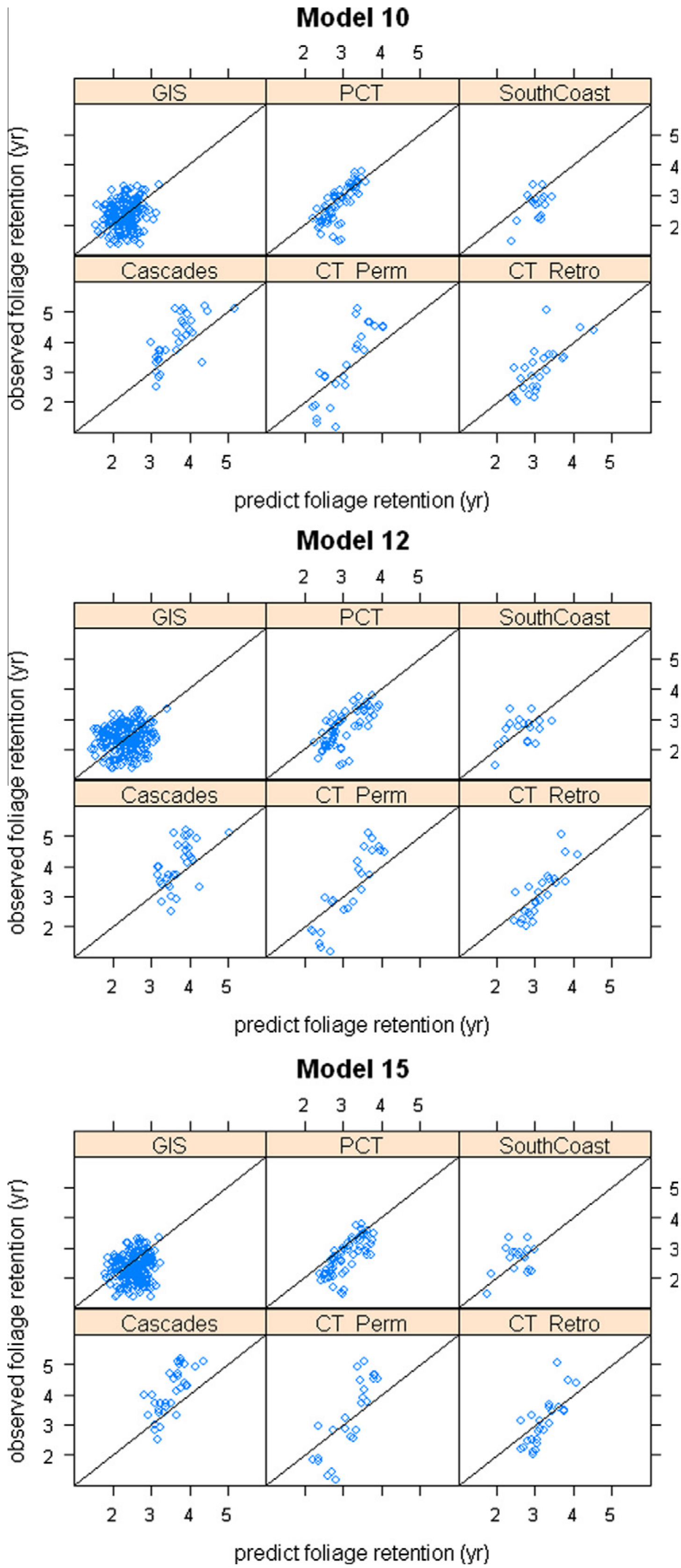

Fig. 7. Time series of foliage retention from 1995 to 2005 predicted from three selected annual retention models (models 10, 12, and 15) for three plots representing low, moderate, and severe Swiss needle cast (plots 37, 93, and 92, respectively).

best under full sun (vs. shading) and no misting from July through the following April (Manter et al., 2005). The positive effect of summer temperature on foliage retention in the current analysis appears contradictory, but the progression of pseudothecia counts

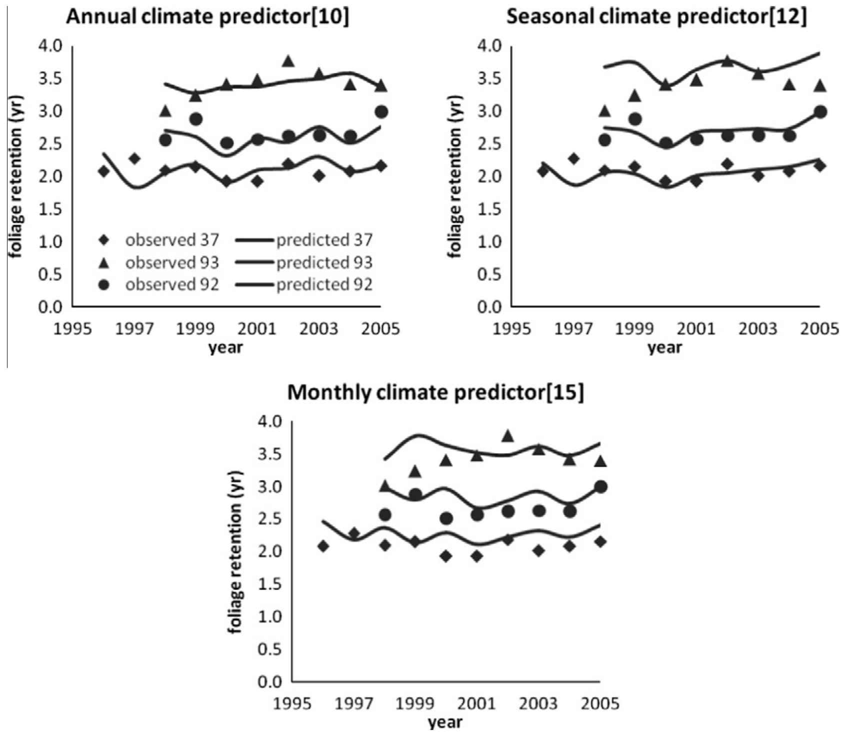

Fig. 8. Annual foliage retention predicted from the selected models using annual (model 10), seasonal (model 12), or monthly climatic variables (model 15) relative to observed retention in the validation dataset.

from July through April in Manter et al.'s (2005) study suggested that the promoting effect of more intense sun and presumably higher temperatures on pseudothecia development began only in November. It remains possible that higher temperatures during the summer may have stimulated fungal development within needles and contributed to the effect of higher winter temperatures on pseudothecia development. However, lacking any direct assessment of mycelia development during the summer, the consistently positive influence of summer temperature on needle retention in our analysis strongly suggested that other mechanisms must be operating during the summer. One alternative mechanism may be the negative effects of high vapor pressure deficits, low water potential within the foliage, and low water availability to fungal hyphae. Likewise, water stress on the tree itself may limit the amount or quality of feeding substrate available to the fungus. Littell et al. (2008) documented the influence of summer temperature on Douglas-fir growth, due to its influence on evapotranspirational demand and vapor pressure deficit. Also, the increase in foliage retention with lower productivity is well documented in the literature (Reich et al., 1995); therefore, climatic effects may have been influencing multiple drivers of needle retention in coastal Douglas-fir stands. It may also be important to note that summer temperature and continentality index were closely correlated with distance from the coast, a consistently strong predictor of Swiss needle cast intensity and foliage retention, even in the presence of the 85 climatic variables. Distance from coast represents a complex gradient of moisture, temperature, and fog. To start understanding the ultimate factors by which distance from coast influences foliage retention and SNC, our analysis intentionally focused on detailed climatic variables alone.

The continentality index was influenced by the lower or cold end of the temperature range as well as the high end of the range. Our results with respect to both continentality index and winter temperature alone (Tave_wt, Tmin_wt, or Tmin12) are therefore more consistent with both greenhouse and field studies (Manter et al., 2005); i.e., colder winters were inferred to impede hyphal and/or pseudothecia development. Furthermore, the positive effect of DD0 (degree-days below 0 °C) on foliage retention in our selected model ([2]) was consistent with the effect of winter degree days in the model presented by Coop and Stone (2007).

Another important annual climatic predictor was mean annual precipitation (MAP) as a general measure of moisture availability. The negative effect of this variable suggested that wetter conditions promoted disease development, probably by facilitating colonization of new foliage in the late spring and early summer. The finer resolution of models based on seasonal and monthly variables offered a potentially stronger case for specific mechanisms driving foliage retention. At the seasonal level, the combined negative effects of spring precipitation (PPT_sp) and spring mean maximum temperature (Tmax_sp) suggested that warm, wet springs did in fact create conditions that maximized colonization of new needles by *Phaeocryptopus*. Likewise, at a monthly resolution, precipitation during any of the summer months (PPT07 or PPT08) probably indicated potential leaf wetness (cf. Manter et al., 2005), and combined with the effect of maximum mean temperature in June (Tmax06), again suggested that warm wet conditions in spring and early summer were probably very conducive to infection of new foliage.

Stone et al. (2007) found that variation in SNC severity in New Zealand was influenced by climatic factors similar to those identified in western Oregon. Unfortunately, direct comparisons are complicated by use of a colonization index as the measure of SNC severity in New Zealand (Stone et al., 2007). Colonization index was the product of percent of needles with visible pseudothecia and the average proportion of occluded stomates. Its correlation with foliage retention has not been well quantified.

4.3. Forecasts with the average foliage retention model

According to the best foliage retention models based on annual or monthly climate variables (model 2 or 7), foliage retention was predicted to increase gradually from 2020 to 2080. These predicted increases could be attributed primarily to increasing continentality indices (TD) predicted by the GCMs at the annual resolution, and to increasing August average temperature (Tave08) and decreasing July precipitation (PPT07) predicted at the monthly resolution. Apparently the strong decline in chilling degree days (DD0) and relative stability in annual precipitation (MAP) predicted by the GCMs were not great enough relative to the increase in continentality to imply a net decrease in foliage retention in the annual model. Likewise, the increase in December minimum temperature (Tmin12) in the monthly model was not great enough relative to the increase in August average temperature and decrease in July precipitation to cause a net decrease in foliage retention in the monthly model. However, according to the best seasonal model (model 4), average foliage retention was predicted to decrease gradually from 2020 to 2080, primarily due to the marked increase in average winter temperature predicted by the GCMs.

Stone et al. (2008) suggested that the severity and distribution of Swiss needle cast is likely to increase in the coming decades as a result of climate change, with significant consequences for Pacific Northwest forests. It is significant to note that their model, like model 4 in the current analysis, was based on seasonal climatic variables, and that both models predicted a gradual decline in foliage retention under future climate scenarios. Uncertainty in future climate variables would probably be least at the annual resolution, moderate at the seasonal resolution, and relatively high at a monthly resolution. However, the fact that the monthly and annual models were consistent and different from the seasonal model suggested that differences could not be attributed to the relative uncertainty associated with climatic predictions at different temporal resolutions. Of possible relevance was the relatively small decline in spring precipitation compared to the more dramatic decline in July precipitation predicted by the GCMs (Fig. 6). If spring moisture becomes limiting to successful colonization by *P. gaeumannii*, then winter temperatures may become irrelevant to disease severity and foliage retention. Unfortunately, the uncertainty in GCM predictions of future precipitation is considered greater than that for temperature (Buytaert et al., 2009), underscoring the challenge of predicting the course of Swiss needle cast under future climate scenarios.

With respect to actual observations over the last 14 years in western Oregon, annual foliage retention has fluctuated too widely within specific sets of plots and geographic locations to claim a long-term increase or decrease over the period between 1996 and 2009 (Fig. 9). Annual aerial surveys for SNC suggested the total area with SNC symptoms detectable from the air increased about 3-fold from 1996 to 2010; however, annual variation in these symptoms similarly limits any conclusions about long-term trends (Kanaskie and Mc Willianms, 2010).

Across the age range, management intensity, and site conditions sampled in the Swiss needle cast growth impact study in north coastal Oregon, Douglas-fir retained foliage up to almost 4 years, but under severe Swiss needle cast as low as 1 year (Maguire et al., 2002). Fewer plots were predicted to retain foliage for less than 2 years under future climate scenarios, and the number of plots retaining foliage for longer than 5 years was also predicted to increase. Because averaging the 13 predictions for each plot potentially damped the effect of extreme values and narrowed the potential variability and frequency distributions, it was important to consider the range of plot-level maxima and minima as well. However, the same general conclusion was reached with regard to a slight increase in foliage retention under predicted future climates.

4.4. Annual foliage retention model

Previous analyses of needle retention focused on geographic variation; i.e., retention was averaged over a period of approximately

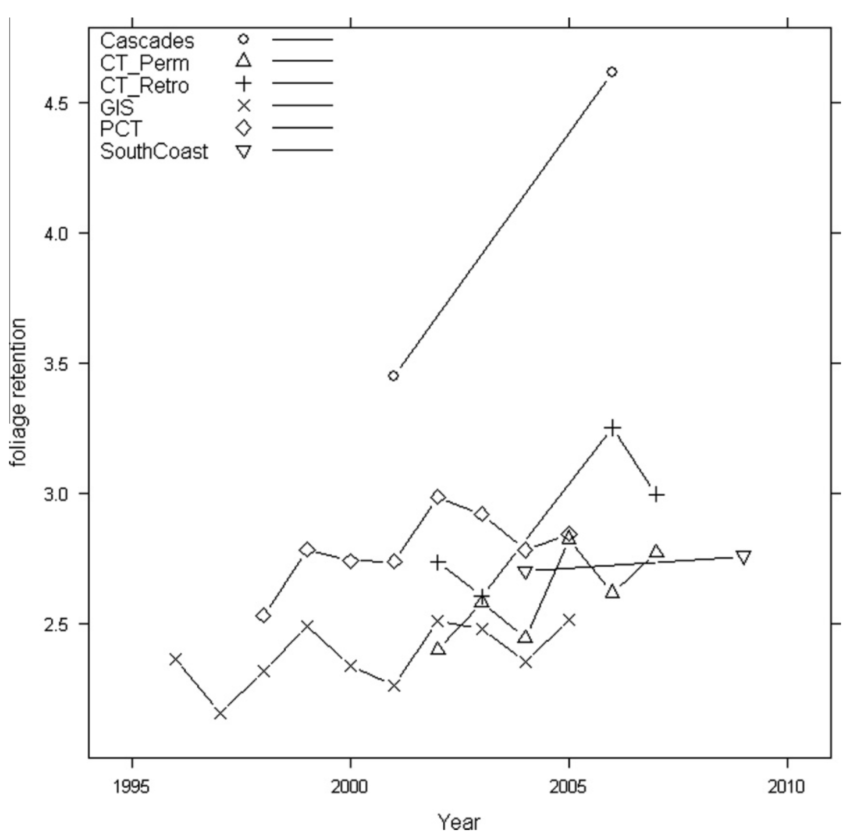

Fig. 9. Average foliage retention for each year of observation in the six Swiss needle cast studies used in development of foliage retention models.

10 years for a number of sites and then was correlated with long-term climatic variables specific to those sites. From this correlation between needle retention and climatic conditions, the link between weather, *P. gaeumannii*, and foliage retention was inferred. Contemporaneous fluctuation in annual foliage retention and climatic variables lent further support to the hypothesis that weather controls foliage retention either directly through physiological effects or indirectly through mediating processes such as colonization by *P. gaeumannii* and subsequent development of Swiss needle cast. Coop and Stone (2010) developed a model to predict normalized colonization index (CI) averaged over a five-year period (2001–2005). Because this colonization index requires pseudothecia counts, only 29 sites were available for model development, and climatic variables presumably represented 10-year averages from PRISM. In this and other studies using either CI or foliage retention as an index of SNC severity, monthly or bi-monthly climatic variables were considered rather than annual variables to ensure a closer match between known and hypothesized mechanisms driving SNC epidemiology. However, our mixed-effects model predicted annual foliage retention surprisingly well from annual climatic variables lagged by one to 4 years.

The best annual and seasonal predictors in the models for describing annual fluctuations in foliage retention were consistent with the best predictors in the geographic analysis of periodic average foliage retention. A lag time of 2 years generally was most effective for predicting annual retention. However, in the models fitted using monthly climatic variables, the predictors were often quite different from the monthly variables in the periodic average retention models, especially in those models with four predictors. Optimal lag times generally shifted to 3 years, which is consistent with the large majority of plots holding foliage for 2–3 years; i.e., climatic conditions during the year of formation of two- and three-year-old needles has a strong influence on their continued longevity. However, due to close correlations between monthly climate variables in adjacent months of the same year, and between monthly climate variables in different years, the specific predictors that perform best in alternative models depended on their relationship with other variables already in the model.

Alternative models were screened based on ordinary least squares in an all-subsets approach, with selected models required to have all parameter estimates significantly different from zero at $\alpha = 0.05$. A random plot effect appeared sufficient for addressing autocorrelation among repeated observations within a plot, with no additional gains from modeling the variance-covariance structure of the residual errors directly. Introducing the random plot effect led to adjustments in parameter estimate standard errors and accompanying shifts in significance of parameter estimates. Given the evidence in this large dataset, the annual foliage retention model with annual climate predictors (model 10) is probably most appropriate for regional risk rating assessments, but if large changes occur in the relationship between annual, seasonal, and monthly variables, or if extreme events become predominant drivers, models with climatic variables at finer temporal resolution may be required.

5. Conclusions

Geographic variation in long-term average foliage retention, as well as annual fluctuation in foliage retention, were predicted well by climate variables from ClimateWNA. Climatic variables at an annual resolution (versus seasonal or monthly) seemed adequate for explaining both the geographic and temporal variation in recent past foliage retention. However, monthly climatic variables may have a more dominating influence on foliage retention if future climates are characterized by greater monthly variation and relatively little change in annual averages. When predicting average foliage retention under future climate scenarios, the periodic average foliage retention model with climatic variables at an annual resolution may be more reliable because this resolution more appropriately matched the precision of GCM predictions. The average foliage retention model developed from the six Swiss needle cast studies suggested that foliage retention would increase under current predictions from GCMs. The GCMs predicted greater continentality (difference between mean warmest month temperature and mean coldest month temperature) and only a very slight increase in mean annual precipitation. However, predictions of foliage retention were very sensitive to the monthly distribution of precipitation, underscoring the importance of finer resolution in climatic variables for predicting the consequences of climate change. Models for predicting annual fluctuations in foliage retention are probably more appropriate for understanding the mechanisms driving the effect of *P. gaeumannii* or other factors on the survival of individual foliage cohorts. Ultimately, models describing geographical and temporal trends in foliage retention should be similar to those that describe the same trends in counts or indices of pseudothecia frequency (e.g., Manter et al., 2005; Stone et al., 2007).

Acknowledgements

This project was funded by the Swiss Needle Cast Cooperative (SNCC) hosted at Oregon State University. We gratefully acknowledge field work performed by many different field crews working for the SNCC and the Oregon Department of Forestry.

References

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

Buytaert, W., Ćelleri, R., Timbe, L., 2009. Predicting climate change impacts on water resources in the tropical Andes: effects of GCM uncertainty. Geophys. Res. Lett. 36, L07406. doi:10.1029/2008GL037048.

Coop, L.B., Stone, J.K., 2007. Prediction maps of Swiss needle case needle retention based on climate factors. In: Shaw, D. (Ed.) Swiss Needle Cast Cooperative Annual Report 2007, College of Forestry, Oregon State University, Corvallis, OR, pp. 15–21.

Coop, L.B., Stone, J.K., 2010. Prediction maps of Swiss needle case needle retention based on climate factors. In: Mulvey, R., Shaw, D. (Eds.) Swiss Needle Cast Cooperative Annual Report 2010, College of Forestry, Oregon State University, Corvallis, OR, pp. 66–80.

Daly, C., Gibson, W.P., Taylor, G.H., Johnson, G.L., Pasteris, P., 2002. A knowledge-based approach to the statistical mapping of climate. Clim. Res. 22, 99–113.

Filip, G., Kanaskie, A., Littke, W., Browning, J., Hildebrand, D., Maguire, D., 2006. Impacts of Swiss needle cast on Douglas-fir in the Cascade foothills of northern Oregon after five years. In: Shaw, D. (Ed.), 2006 Swiss Needle Cast Cooperative Annual Report, pp. 12–19.

Garber, S., Maguire, D., Mainwaring, D., Hann, D., 2007. Swiss Needle Cast ORGANON Module Update. In: Shaw, D. (Ed.), 2007 Swiss Needle Cast Cooperative Annual Report, pp. 63–66.

Hamann, A., Wang, T.L., 2005. Models of climatic normals for genecology and climate change studies in British Columbia. Agric. For. Meteorol. 128, 211–221.

Hann, D.W., 2006. ORGANON user's manual: Edition 8.0. Department of Forest Resources, Oregon State University, Corvallis, Oregon, p. 129.

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

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

IPCC, 2007. Climate change 2007: the physical science basis. Working Group I, Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Kanaskie, A., Mc Willianms, M., 2010. Response of Swiss needle cast severity and tree growth to pre-commercial thinning in north coastal Oregon. In: Mulvey, R., Shaw, D. (Eds.), 2010 Swiss Needle Cast Cooperative Annual Report, pp. 7–10.

Latta, G., Adams, D., Shaw, D., 2009. Mapping western Oregon Douglas-fir foliage retention with a simultaneous autoregressive model. In: Shaw, D., Woolley, T. (Eds.), 2009 Swiss Needle Cast Cooperative Annual Report, pp. 37–51.

Littell, J.S., Peterson, D.L., Tjoelker, M., 2008. Douglas-fir growth in mountain ecosystems: water limits tree growth from stand to region. Ecol. Monogr. 78, 349–368.

Maguire, D.A., Mainwaring, D.A., Kanaskie, A. Ten-year growth and mortality in young Douglas-fir stands experiencing a range in Swiss needle cast severity. Can. J. Forest. Res., in press.

Maguire, D.A., Mainwaring, D.A., Kanaskie, A. Response of Swiss needle cast infected trees Douglas-fir to pre-commercial thinning in coastal northwestern Oregon, submitted for publication.

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

Mainwaring, D., Maguire, D., 2008. Growth responses to pre-commercial thinning under different levels of initial SNC severity of north coastal Oregon. In: Shaw, D., Woolley, T. (Eds.), Swiss Needle Cast Cooperative Annual Report 2008, College of Forestry, Oregon State University, Corvallis, OR, pp. 18–20.

Mainwaring, D.B., Maguire, D.A., Kanaskie, A., Brandt, J., 2005. Growth responses to commercial thinning in Douglas-fir stands with varying severity of Swiss needle cast in Oregon. USA Can. J. For. Res. 35, 2394–2402.

Manter, D.K., Bond, B.J., Kavanagh, K.L., Stone, J.K., Filip, G.M., 2003. Modelling the impacts of the foliar pathogen, *Phaeocryptopus gaeumannii*, on Douglas-fir physiology: net canopy carbon assimilation, needle abscission and growth. Ecol. Model. 164, 211–226.

Manter, D.K., Reeser, P.W., 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.

Mbogga, M., Hamann, A., Wang, T., 2009. Historical and projected climate data for natural resource management in western Canada. Agric. For. Meteorol. 149, 881–890.

Mitchell, T.D., Jones, P.D., 2005. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. Int. J. Climatol. 25, 693–712.

Mitchell, T. D., Carter, T. R., Jones, P. D., Hulme, M., and New, M., 2004. A comprehensive set of climate scenarios for Europe and the globe. Tyndall Centre for Climate Change Research.

Pensa, M., Jalkanen, R., 2005. Variation in needle longevity is related to needle-fascicle production rate in *Pinus sylvestris*. Tree Physiol. 25, 1265–1271.

Pouttu, A., Dobbertin, M., 2000. Needle retention and density patterns in *Pinus sylvestris* L. In the Rhone Valley of Switzerland: comparing results of the needle-trace method with visual defoliation assessments. Can. J. For. Res. 30, 1973–1982.

Reich, P.B., Koike, T., Gower, S.T., Schoettle, A.W., 1995. Causes and consequences of variation in conifer leaf life-span. In: Smith, W.K., Hinckley, T.M. (Eds.), Ecophysiology of Coniferous Forests. Academic Press, New York, pp. 225–254.

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

Spittlehouse, D.L., 2006. ClimateBC: your access to interpolated climate data for BC. Streamline Watershed Manage. Bull. 9, 16–21.

Stone, J.K., Coop, L.B., 2006. Predicting spatial variation in Swiss needle cast western Oregon. In: Shaw, D. (Ed.), Swiss Needle Cast Cooperative Annual Report 2006, College of Forestry, Oregon State University, Corvallis, OR, pp. 54–59.

Stone, J.K., Hood, I.A., Watt, I.A., Kerrigan, J.L., 2007. Distribution of Swiss needle cast in New Zealand in relation to winter temperature. Aust. Plant Pathol. 36, 445–454.

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

Wang, T., Hamann, A., Spittlehouse, D.L., Aitken, S.N., 2006. Development of scale-free climate data for western Canada for use in resource management. Intl. J. Climatol. 26, 383–397.

Xiao, Y., 2003. Variation in needle longevity of *Pinus tabulaeformis* forests at different geographic scales. Tree Physiol. 23, 463–471.