Trees (2012) 26:1361–1371
DOI 10.1007/s00468-012-0711-x

ORIGINAL PAPER

Climatic influences on needle cohort survival mediated by Swiss needle cast in coastal Douglas-fir

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Received: 25 October 2011 / Revised: 9 February 2012 / Accepted: 10 March 2012 / Published online: 23 March 2012

Abstract Swiss needle cast (SNC) severity in Douglas-fir (*Pseudotsuga menziesii*) has been shown to vary spatially and temporally in response to climatic factors both within its native range and in regions where it has been planted as an exotic species. Survival models were developed for different Douglas-fir needle cohorts to enhance our understanding of how climatic influences on needle longevity are mediated by SNC in the Oregon Coast Range. The climate-based models were based on repeated measurement of 100 plots between 1998 and 2005 coupled with downscaled PRISM climate data. Potential predictors of needle survival by annual cohort were selected from numerous climatic variables at annual, seasonal, and monthly scales. Needle survival probability was positively associated with maximum summer temperature, and negatively associated with minimum winter temperature and spring precipitation. Seasonal climate variables associated with needle longevity are consistent with current epidemiological understanding of *Phaeocyrptopus gaeumannii*, as well as with previous analyses of climatic influences on SNC severity as measured by average years of foliage retention and frequency of fungal fruiting bodies, or pseudothecia, in stomates.

Communicated by W. Oßwald.

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Keywords Cohort survival · Needle longevity · Climatic effects · Survival probability

Introduction

Needles of most conifers can live for many years, and within a species needle longevity can vary tremendously (Reich et al. 1994). Coastal Douglas-fir has been observed to hold needles for up to 7 years in western Oregon and Washington (Mitchell 1974) and 10 years in British Columbia (Silver 1962). Variation in needle longevity is related to many factors, including latitude (Reich et al. 1996; Xiao 2003), climate (Xiao 2003; Coop and Stone 2007), site fertility (Balster and Marshall 2000; Niinemets and Lukjanova 2003), and insect and disease history (Hansen et al. 2000; Kurkela et al. 2005).

Coastal stands of Douglas-fir are among the most productive native conifer forests in the world due to a long growing season, abundant nitrogen, high precipitation, and relatively warm winter temperatures (Waring and Franklin 1979). In general, conifer needle longevity is negatively correlated with site productivity (Niinemets and Lukjanova 2003); therefore, needle retention on Douglas-fir growing in coastal zones is expected to be relatively low compared to less productive interior regions. In fact, foliage retention on interior Douglas-fir trees may be as high as 20 years (Gower et al. 1992), but healthy Douglas-fir stands in the Oregon Coast Range typically retain approximately 4 years of needles (Maguire et al. 2002). Since the mid 1980s (Black et al. 2010), Douglas-fir productivity in many coastal stands has diminished significantly due to Swiss needle cast (SNC), a foliar disease that causes premature needle loss. SNC is an endemic foliar disease specific to Douglas-fir and is caused by the fungus *Phaeocryptopus* *gaeumanii* (Boyce 1940). In the last 25 years, this disease has reached epidemic levels along the northwestern coast of the United States, resulting in varying levels of tree defoliation and growth loss (Maguire et al. 2002, 2011). Although the cause of this epidemic is hypothesized to result from numerous factors (Hansen et al. 2000), epidemiological research has identified climate factors as playing a large role in intensification of SNC (Rosso and Hansen 2003). Specifically, fungal spore germination and growth of hyphae into stomates have been shown to require wet springtime conditions (Capitano 1999), and development of the fungus in intercellular spaces of the needles appears to be enhanced by relatively cool summers (Rosso and Hansen 2003) and warm winters (Manter et al. 2005).

As part of an effort to monitor SNC disease levels, estimate growth impacts, and investigate potential silvicultural mitigation of impacted stands, a network of permanent fixed-area plots was installed in north coastal Oregon in 1998. Although many different indices have been used to rank stands for symptom severity, average foliage retention (the number of annual needle cohorts remaining on a tree) has been the surrogate of choice for describing SNC intensity due to its relative objectivity, operational ease of estimation, and its correlation with tree growth (Maguire et al. 2002, 2011).

Across the age range, management intensity, and site conditions sampled in the permanent plot network, Douglas-fir foliage retention ranged from a maximum of approximately 4 years in healthy stands to as low as 1 year in the most severely infected stands (Maguire et al. 2002, 2011). Due to the significant positive correlation between tree growth and foliage retention in infected stands, foliage retention has been used to estimate regional volume growth losses from SNC (Maguire et al. 2002, 2011; Mainwaring et al. 2005), and has also been incorporated into regional growth models (Garber et al. 2007) and applied in financial analyses (Latta and Adams 2010).

In the effort to create hazard rating maps for SNC in the Coast Ranges of Oregon and Washington, quantitative links between foliage retention and climate variables have been established using varying methodologies (Rosso and Hansen 2003; Manter et al. 2005; Coop and Stone 2007; Latta et al. 2009; Zhao et al. 2011). In each of these analyses, tree-level foliage retention is calculated as the summed proportions of needles surviving in each annual cohort. This foliage retention is generally interpreted as number of annual cohorts with 100 % survival plus the surviving fraction of the oldest cohort that is experiencing needle abscission. Older foliage is generally cast before younger foliage, but this pattern is not universal because: (1) only new emerging foliage can be infected by hyphae growing across the surface of the needles and into stomates and (2) annual variation in climatic conditions creates annual variability in infection success or intensity. As a result, some younger annual cohorts may start to lose foliage before older cohorts. Zhao et al. (2011) analyzed the influence of local climatic factors on spatial and temporal variation on SNC as measured by average foliage retention. Modeling the effect of climatic factors on individual needle cohorts may further advance our understanding of mechanisms behind infection and mycelial development, and subsequent intensification of SNC. The objectives of this study were: (1) to identify climate variables that account for variability in survival patterns of annual cohorts of Douglas-fir needles; (2) to develop a needle survival model that explains observed variation in needle longevity by specific climatic conditions that prevailed during year of needle formation and (3) to explore implied survival curves for needle cohorts formed under the full range of climatic conditions observed over the last 10 years.

Methods

Field work

Plots were distributed across a range of SNC severity, stand density, aspect, and slope (Table 1). The study sites ranged from 44.53° to 46.23°N latitude and from 123.38° to 124.00°W longitude (Fig. 1). Elevation ranged from 48 to 914 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 80 % of the total typically occurring from October to March.

Measurements

Data for this analysis were compiled from two ongoing studies established to investigate growth losses under the influence of SNC: the Growth Impact Study (GIS) and the Precommercial Thinning (PCT) study. The GIS plots were established in 1998 to monitor SNC symptoms and tree growth in 77 randomly selected 10- to 30-year-old Douglas-fir plantations within 18 miles of the Pacific coast in northwestern Oregon (Maguire et al. 2002, 2011). The PCT plots were established in 23 stands in 1998 and to test the effect of thinning and initial SNC severity on subsequent symptom development and tree growth (Mainwaring et al., review). Only control plots from the PCT study were included in this analysis.

Just prior to budbreak in each spring (April–May), foliage retention was recorded using two different methods

Table 1 Initial (1998) attributes of Douglas-fir control plots included in the SNCC Precommercial Thinning (PCT) Study and Growth Impact Study (GIS)

Variables	PCT study			GIS study		
	Mean (SD)	Minimum	Maximum	Mean (SD)	Minimum	Maximum
Douglas-fir tree density (trees ha^{-1})	1,020.8 (313.3)	629.9	2,001.0	628.1 (290.7)	86.5	1,630.2
Douglas-fir basal area (m^2 ha^{-1})	15.76 (6.32)	3.92	27.05	17.62 (8.59)	0.62	38.71
Douglas-fir breast height age (years)	10.9 (2.4)	5.0	15.5	20.0 (5.6)	11.0	32.0
Douglas-fir QMD (cm)	14.1 (3.1)	7.2	19.7	18.6 (6.2)	3.8	34.0
Douglas-fir top height (m)	11.7 (2.1)	7.8	15.6	26.2 (8.4)	5.8	44.6
Douglas-fir site index (m at 50 years)	43.0 (6.7)	32.1	62.5	44.9 (7.6)	14.6	61.7
Basal area of other conifers (m^2 ha^{-1})	1.75 (6.14)	0.00	29.62	2.76 (5.24)	0.00	24.03
Basal area of broadleaved species (m^2 ha^{-1})	1.21 (1.14)	0.00	3.97	1.05 (2.03)	0.00	13.40
Total tree density (trees ha^{-1})	1,496.6 (950.2)	629.9	5,101.0	848.4 (413.7)	259.4	2,037.8
Total plot basal area (m^2 ha^{-1})	18.72 (8.79)	3.92	60.64	21.43 (10.17)	0.66	48.65
Foliage retention (years)	2.4 (0.5)	1.3	3.3	2.3 (0.4)	1.1	3.1

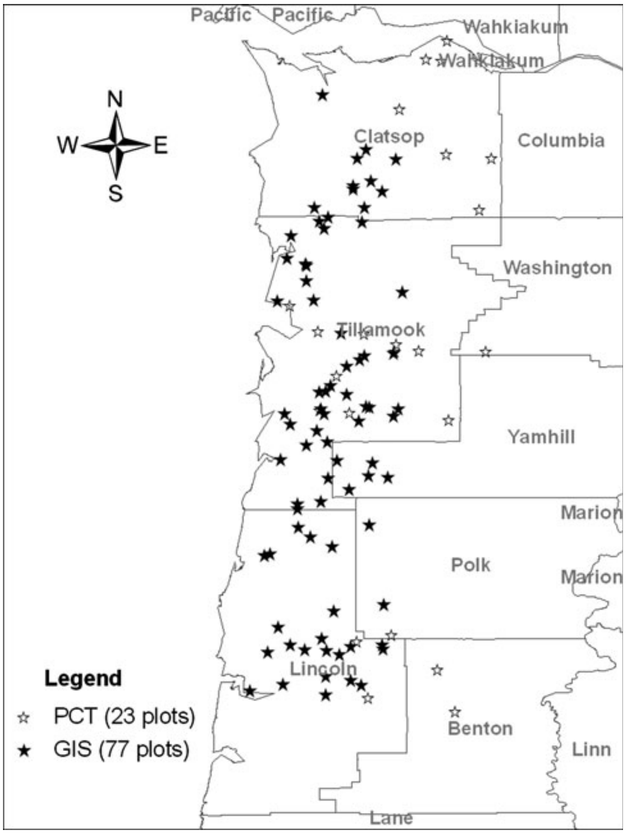


Fig. 1 Location of 100 permanent plots on which Douglas-fir needle survival was monitored from 1998 to 2003. Locations are indicated by county in northwestern Oregon

on ten dominant or codominant trees on each plot. The first method involved estimating the average number of annual needle cohorts held by the tree, and has been referred to in past analyses as foliage retention (Hansen et al. 2000; Maguire et al. 2002). The second approach yielded the data used in this analysis and called for estimating separately the percentage of surviving needles from each of the four youngest annual cohorts. Specifically, cohort retention was scored on each of the four most recent shoot age classes on secondary laterals. This retention score was recorded as 0, 1,…, or 9, with 0 representing 0–10 %, 1 representing 11–20 %,…, and 9 representing 91–100 %. These measurements were generally repeated on the same trees on each plot from 1998 to 2005; however, if a tree died or was badly damaged, a tree similar in size was chosen as a replacement.

Climate data

Climate data corresponding to the year that each needle cohort emerged were calculated with the software ClimateWNA v4.60. ClimateWNA extracts and downscales PRISM (Daly et al. 2002) monthly data (2.5 × 2.5 arcmin) for the reference period (1961–1990), and calculates annual, seasonal and monthly climate variables for specific locations based on latitude, longitude, and elevation for western North America. This program also downscales and integrates historical climate data (1901–2009) (Mitchell and Jones 2005; Mbogga et al. 2009). The output included both measurable climate variables and derived climatic indices (Hamann and Wang 2005).

In total, ClimateWNA can produce 85 climate variables, including 48 monthly, 16 seasonal and 21 annual variables (Tables 2, 3). The monthly and seasonal variables included minimum, maximum, and average temperatures and precipitation. Of the 21 annual climate variables, eight were directly calculated from the monthly data including mean annual temperature (MAT), mean coldest month temperature (MCMT), mean warmest temperature (MWMT), continentality (TD, the difference between MWMT and

Table 2 Climatic variables tested as predictors of Douglas-fir needle cohort survival

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–September) precipitation (mm)
	AHM	Annual heat:moisture index (MAT + 10)/(MAP/1,000))
	SHM	Summer heat:moisture index ((MWMT)/(MSP/1,000))
Derived variables	DD < 0	Degree-days below 0 °C, chilling degree-days
	DD > 5	Degree-days above 5 °C, growing degree-days
	DD < 18	Degree-days below 18 °C, heating degree-days
	DD > 18	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 (1.18–0.0067 latitude), $n = 56$, $R^2 = 0.734$, $se_{xy} = 0.039$EHar 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 (December (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)

MCMT), mean annual precipitation (MAP), mean May to September precipitation (MSP), annual heat-moisture index (AHM), and summer heat-moisture index (SHM). Calculations of other annual variables, such as growing degree-days (DD >5 °C), cooling degree-days (DD <0 °C), frost-free period (FFP), required daily weather data. ClimateWNA derived these variables using either linearly interpolated monthly data or relationships between these daily variables and monthly climate variables (Wang et al. 2006).

Statistical analysis

Annual cohort retention scores were expressed as the midpoint of each interval of percent retention, i.e., 5, 15,…, and 95 %. We first generated the observed life-table survival and hazard probabilities (Lawless 1982) to obtain descriptive information using PROC LIFETEST in SAS version 9.2 (SAS Institute 2009). A proportional hazards model (Lawless 1982) was first fitted to the data with PROC PHREG in SAS version 9.2 to select best subsets of

Table 3 Averages, minima, and maxima for key climatic and physiographic variables for predicting needle survival probability in coastal Douglas-fir stands

	Mean (SD)	Minimum	Maximum
Longevity (years)	2.5 (1.2)	0.5	4.0
Latitude (°N)	45.3 (0.4)	44.5	46.2
Longitude (°W)	−123.7 (0.1)	−124.0	−123.4
Elevation (m)	243.5 (156.8)	48.0	914.0
Slope (°C)	8.7 (6.9)	0.0	24.0
Aspect (°C)	166.1 (110.2)	−1.0	358.0
Tave02 (°C)	6.7 (1.3)	1.2	9.5
Tave09 (°C)	15.6 (1.4)	11.1	18.9
Tmax03 (°C)	12.3 (1.5)	6.2	16.2
PPT03 (mm)	299.7 (109.8)	95.0	752.0
PPT10 (mm)	229.3 (79.3)	40.0	533.0
Tmax_sm (°C)	21.3 (1.4)	17.1	25.6
Tmin_wt (°C)	2.6 (1.3)	−2.2	5.8
Tmin_sm (°C)	10.2 (0.7)	7.2	12.2
Tave_wt (°C)	6.2 (1.2)	1.6	9.0
Tave_sp (°C)	9.9 (1.1)	5.1	12.5
PPT_sp (mm)	633.1 (148.3)	275.0	1,281.0
TD (°C)	11.1 (1.4)	6.8	15.9
MSP (mm)	416.0 (134.2)	136.0	892.0
NFFD (days)	317.2 (18.0)	232.0	349.0
eFFP	319.0 (14.2)	267.0	350.0

climate variables for predicting needle longevity of individual cohorts. Climate variables at different scales (annual, seasonal and monthly climate variables) were tested as potential predictors, and only those pertaining to the year of foliage emergence and first year of foliage development were considered as predictors for each corresponding foliage cohort. The criterion to determine "best" subsets was based on the highest global score Chi-square statistic (Lawless 1982).

The final needle survival model was generated with PROC LIFEREG in SAS version 9.2. This method uses maximum likelihood to fit parametric regression models to the cohort survival data (Lawless 1982; Allison 2010). This procedure considers the scale and shape of the distribution of failure times (time to needle abscission) as conditional on specified covariates.

The relationship between needle longevity and potential covariates was assessed by accelerated failure time analysis. The response variable was average needle longevity for each plot expressed as 0.5, 1, 2, 3, or 4 years. Assuming that each cohort started with 100 total needles, the number of needles with a lifetime of n years was calculated as the difference between the % cohort survival at age n and the % cohort survival at age $n + 1$, yielding a value between 0 and 100. This number was weighted by the number of needles in each age class. Because needles were not monitored past 4 years to determine their full lifetimes, right-censoring was specified in PROC LIFEREG. We tested whether a normal, lognormal, Weibull, Gamma, exponential, or log-logistic function provided the best fit to the needle longevity and survival data and selected the function that gave the lowest AIC (indicating goodness-of-fit), the fewest number of parameters, and best fit to individual populations. The selected model was then assessed by examining the survival probability plot from a modified Kaplan–Meier method that adjusts for covariates. If the specified model is adequate, the graph of the transformed survival estimates against the log of time should appear as a straight line (Allison 2010).

Results

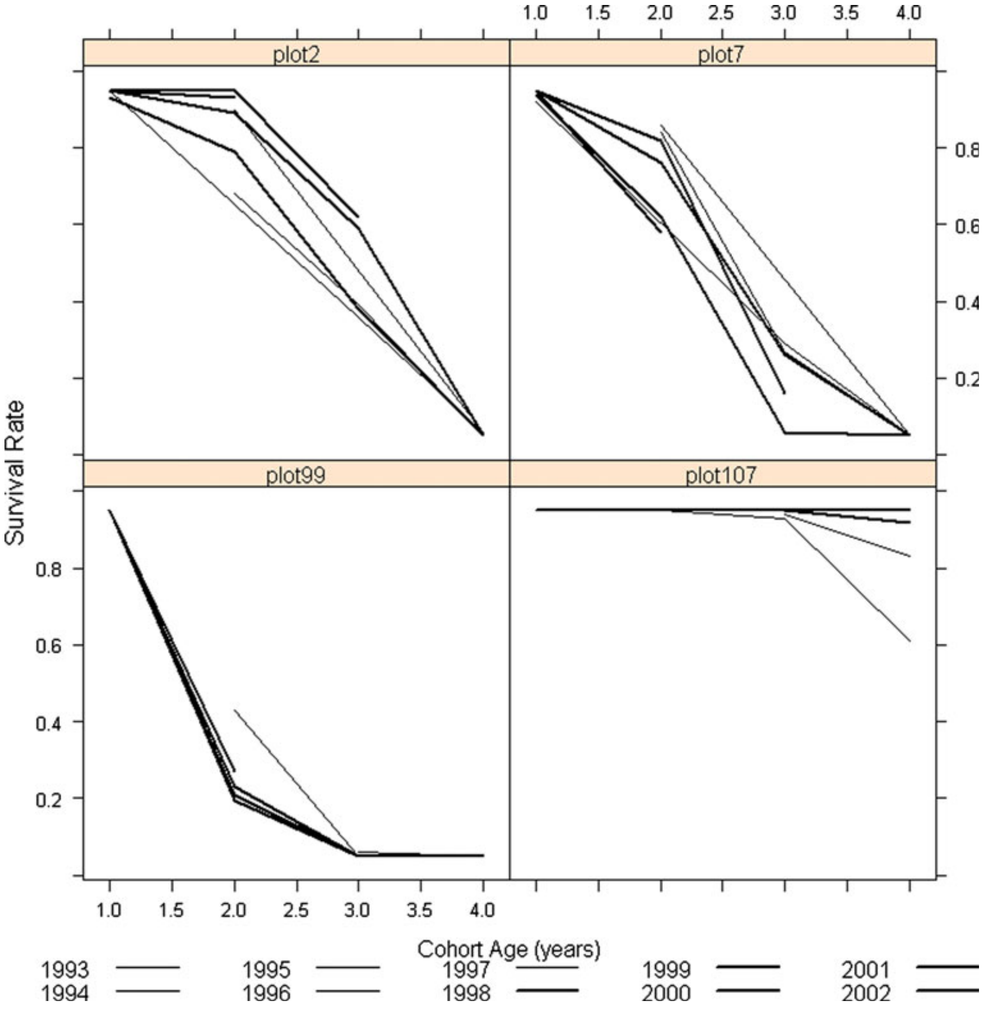
Survival and hazard probabilities

The overall average needle longevity was 2.45 years. The majority of plots had needle survival curves that indicated moderate declines in needle retention over time (plots 2 and 7 in Fig. 2), with the most healthy plots retaining needles for a long time (plot 107 in Fig. 2), and the most severely affected plots showing rapid decline in needle retention (plot 99 in Fig. 2). The distribution of survival probabilities in different age classes demonstrated the declining survival rates with increasing needle age (Fig. 3). For ages 1 and 4, the majority of survival probabilities was 95 and 5 %, respectively. The average probabilities of survival to ages 1–4 years were 0.99, 0.73, 0.42 and 0.19, respectively (Table 4). Corresponding probabilities of abscission were 0.01, 0.30, 0.55 and 0.73, respectively (Table 4). In short, most needles survived the first 2 years, but were likely to die shortly afterwards.

Best climate predictors

The climate predictors that appeared in the best proportional hazards models varied somewhat among the three temporal resolutions (Table 5). Based on variables identified in previous epidemiological research (Capitano 1999; Rosso and Hansen 2003; Manter et al. 2005), and on statistical scores (global Chi-square statistic), models based on seasonal climate variables (models 4–6 in Table 5), were judged most suitable. Model 5 included maximum temperature in summer (Tmax_sm), minimum temperature in winter (Tmin_wt), and precipitation in spring (PPT_sp), so was selected as the optimal subset because it had the best combination of few predictors and high accuracy (high score).

Fig. 2 Empirical needle survival curves for two average plots (*2* and *7*), a relatively healthy plot (*107*), and a severely impacted plot (*99*)



Needle longevity model

The relative performance of the normal, lognormal, Weibull, Gamma, exponential, and log-logistic models differed considerably (Table 6). Gamma and lognormal distributions had the lowest AIC, but the Gamma distribution also has an additional parameter to estimate. In addition, the equation using the Gamma function is more complicated, making it difficult to judge the shape of the survival curve from the estimated parameters (Allison 2010). Therefore, we chose the lognormal distribution as the preferred model. The estimated scale parameter was 0.5591 with 95 % confidence limits of 0.5552 and 0.5630 (Table 7), suggesting that the rate of needle loss is increasing with time. All covariates (Table 5) were significantly related to the probability of needle loss (all $p < 0.0001$), and the probability plot indicated close conformity to the specified model (Fig. 4).

To view differences in the survival curve for needles formed under different climatic conditions, survival probabilities were predicted from the final model based on minimum and maximum values of the covariates represented in this dataset (maximum PPT_sp, Tmax_sm, and Tmin_wt of 1,281 mm, 25.6, and 5.8 °C, respectively; minimum PPT_sp, Tmax_sm, and Tmin_wt of 275 mm, 17.1, and −2.2 °C, respectively). The highest survival probabilities occurred for a cohort formed in a year with low PPT_sp, high Tmax_sm, and low Tmin_wt, with survival probabilities exceeding 90 % through year four (Fig. 5). The lowest survival probabilities occurred for a cohort formed in a year with high PPT_sp, low Tmax_sm, and high Tmin_wt, with survival probabilities dropping below 20 % by year four.

Discussion

Swiss needle cast can be sufficiently severe that foliage retention reaches slightly <1 year in populations where the maximum foliage retention would otherwise be approximately 4 years (Hansen et al. 2000; Maguire et al. 2002). In general, needle loss progresses from the oldest to the

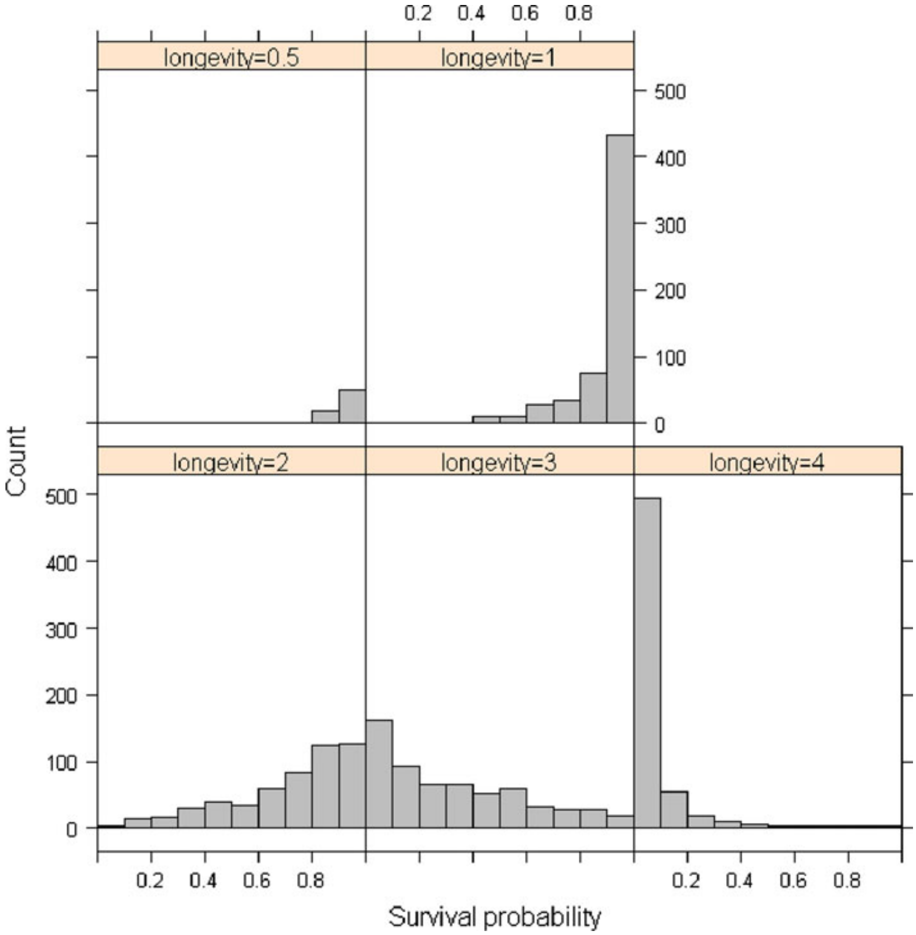


Fig. 3 Survival probability of Douglas-fir needles by age class

Table 4 Life table analysis of Douglas-fir needle survival in different age classes

Age interval	Number failed	Number censored	Effective sample size	Survival		Hazard	
				Probability	SE	Probability	SE
0–1	625	0	60,661	1.0000	0.0000	0.0104	0.0004
1–2	15,644	0	60,036	0.9897	0.0004	0.2996	0.0024
2–3	17,766	6,651	41,066.5	0.7318	0.0018	0.5520	0.0040
3–4	9,180	5,690	17,130	0.4152	0.0021	0.7321	0.0071
4–	0	5,105	2,552.5	0.1927	0.0019		

youngest needles, but it is not uncommon for a younger needle cohort to start losing needles before an older cohort. Presumably this sequence is a result of environmental conditions that are more favorable for infection of new foliage during the year that the younger cohort was formed. Survival analysis provided a methodology to describe differential rates of survival for specific needle cohorts, and to test the effects of weather conditions specific to the year in which each cohort emerged and developed. In our analysis of Douglas-fir needle dynamics, patterns in needle longevity and survival probability were first assessed by nonparametric estimation of empirical survival rates and hazard probabilities, indicating that survival probability declines rapidly after 2 years in the population sampled. The semi-parametric proportional hazard models illustrated that a relatively small set of climatic variables describing conditions during year of foliage emergence could explain a significant amount of variation in cohort survival. These key variables were then introduced into alternative parametric models, identifying the lognormal distribution as best and providing a model that could be compared to previous work analyzing the spatial and temporal variability in foliage retention (Manter et al. 2005; Stone et al. 2007; Zhao et al. 2011).

The climate variables with greatest efficacy for predicting survival of Douglas-fir needle cohorts were consistent with the strongest variables for predicting spatial and temporal patterns in average foliage retention (Zhao

Table 5 Selected models for predicting Douglas-fir needle cohort survival from climatic variables

No.	Climate variables	Number of predictors	Predictors	Score
1	Annual	2	**TD** MSP	6,131.7829
2	Annual	3	MSP NFFD **eFFP**	7,631.4501
3	Annual	4	**TD** MSP NFFD **eFFP**	8,428.1364
4	Seasonal	2	Tmin_wt PPT_sp	5,929.6470
5	Seasonal	3	Tmin_wt **Tmax_sm** PPT_sp	6,780.4181
6	Seasonal	4	Tave_wt Tmin_sm **Tave_sp** PPT_sp	7,680.2884
7	Monthly	2	Tave02 **Tmax03**	9,123.6956
8	Monthly	3	PPT03 Tave02 **Tave09**	9,828.2675
9	Monthly	4	Tave02 **Tave09** **Tmax03** PPT10	10,469.6083

Bold type indicates positive effects and regular type indicates negative effects

Table 6 Goodness-of-fit statistics of different distributions fitted to Douglas-fir needle survival data

Distribution	2 Log likelihood	AIC	AICC	BIC
Exponential	132,023.9	132,031.9	132,031.9	132,054.7
Normal	157,245.0	157,255.0	157,255.0	157,283.5
Lognormal	99,508.83	99,518.83	99,518.86	99,547.36
LLogistic	100,475.4	100,485.4	100,485.4	100,513.9
Logistic	157,402.6	157,412.6	157,412.6	157,441.1
Weibull	105,373.5	105,383.5	105,383.5	105,412.0
Gamma	99,358.9	99,370.9	99,370.9	99,405.1

et al. 2011). In general both cohort survival rates and average foliage retention declined as winter temperatures and spring precipitation increased, and increased as summer temperature increased (Zhao et al. 2011 and results presented above). Similar climatic variables have also been shown to influence indices of SNC infection intensity based on the frequency of stomatal occlusion by pseudothecia (Manter et al. 2005; Stone et al. 2007).

The covariates for describing needle cohort survival patterns were selected to represent an optimal combination of strong predictive ability and consistency with biological mechanisms known to influence SNC epidemiology. As a group, the monthly climate variables accounted for the greatest amount of variation in needle survival patterns, and represented some of the factors previously hypothesized to influence SNC severity. For example, winter temperature was represented in all three monthly models by average February temperature. However, the other climatic factor most commonly associated with SNC severity in previous studies was spring precipitation, but this variable was absent in some of the models, probably due to its collinearity with other climatic variables. Furthermore, while March precipitation appeared in some of the monthly models, the fact that *Phaeocryptopus* spores can infect new needles only after budbreak and shoot elongation in May–June (Chastagner and Byther 1983) suggested strongly that March precipitation served as a general surrogate for spring wetness, probably due to its correlation with precipitation later in the spring. Similarly, the combination of March and October precipitation in some models may have simply indicated relatively wet years or sites, including high leaf wetness during the period of spore germination and hyphal growth into stomates.

Annual climate variables also accounted on average for a greater proportion of the variability in needle survival than did seasonal climate variables. Growing season precipitation (MSP) was probably a coarse surrogate for spring wetness, and continentality (TD) probably indicated the combined effects of low winter temperature and high summer temperature, both of which have been shown to influence spatial and temporal patterns in average foliage retention (Zhao et al. 2011). Variables representing the number of frost-free days (NFFD, eFFP) likewise probably integrate the positive effect of warmer and/or shorter winters on SNC intensification. Although TD is a combination of maximum summer temperature and minimum winter temperature, the individual covariates constituting TD may be more important to represent in the model if the inherent correlations with TD and other climatic variables

Table 7 Parameter estimates and statistical tests for the lognormal regression regression model fitted to Douglas-fir needle survival data

Parameter	DF	Estimate	Standard error	95 % Confidence limits		Chi-square	Pr > Chisq
Intercept	1	−0.4170	0.0371	−0.4898	−0.3442	126.13	<.0001
Tmin_wt	1	−0.1582	0.0020	−0.1621	−0.1543	6,327.82	<.0001
Tmax_sm	1	0.0931	0.0016	0.0899	0.0964	3,211.51	<.0001
PPT_sp	1	−0.0006	0.0000	−0.0007	−0.0006	1,548.46	<.0001
Scale	1	0.5591	0.0020	0.5552	0.5630		

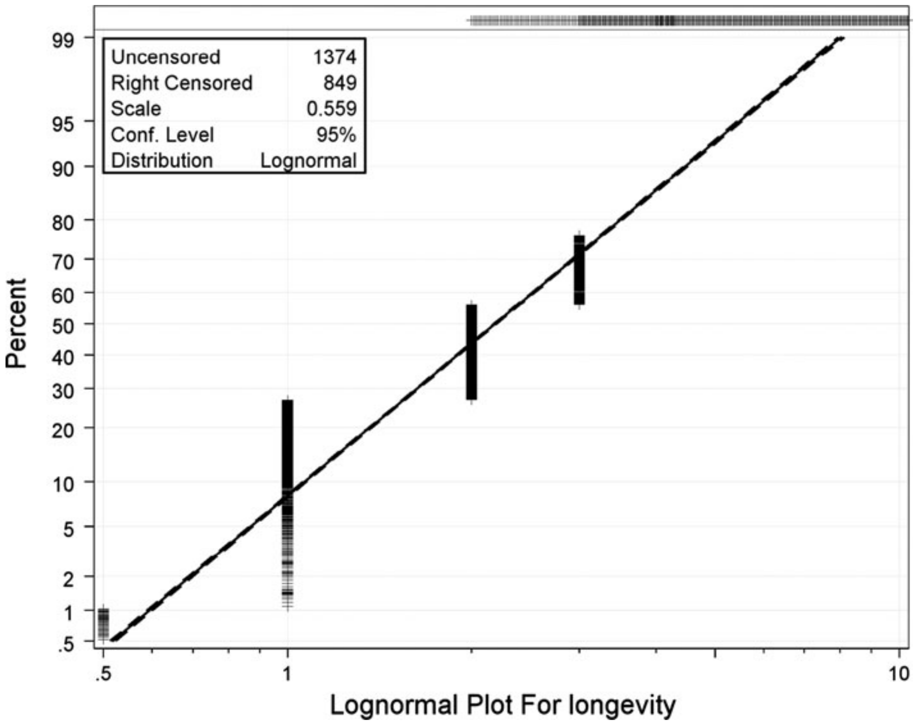


Fig. 4 Lognormal probability plot for Douglas-fir needle longevity data

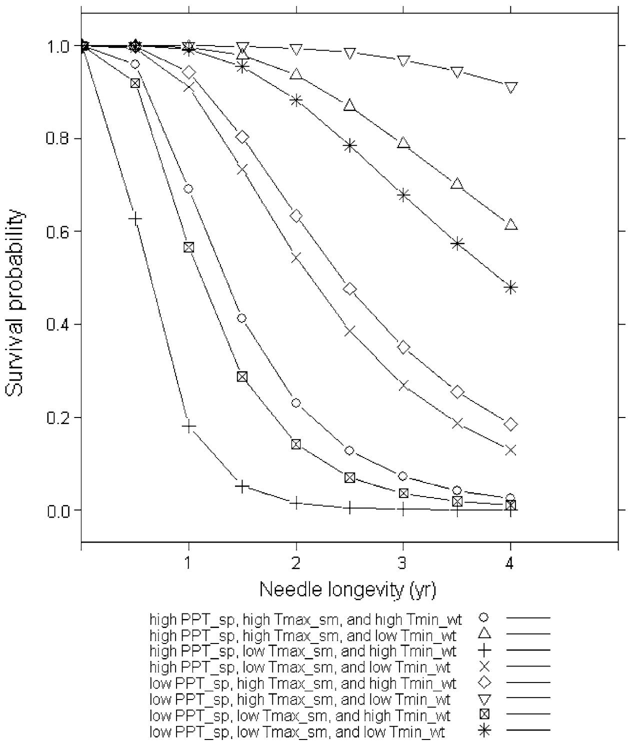


Fig. 5 Predicted survival curves for Douglas-fir needles initiated under different climatic conditions (high and low PPT_sp = 1,281 and 275 mm, respectively; high and low Tmax_sm = 25.6 and 17.1 °C, respectively; and high and low Tmin_wt = 5.8 and −2.2 °C, respectively)

become weaker under future climates. Similarly, if the distribution of precipitation within the growing season changes, MSP may become either less or more predictive of needle survival depending on whether more of the precipitation is shifted to the critical period of sporulation and infection of new foliage early in the summer.

Numerous SNC hazard maps have been developed for Douglas-fir stands in the Oregon Coast Ranges (Manter et al. 2005; Coop and Stone 2007; Latta et al. 2009, Zhao et al. in preparation). These maps were based at least in part on characterizing sites by their local climate and quantifying the link between foliage retention and local climate. The SNC hazard maps have enabled forest managers to prioritize certain zones with respect to various silvicultural strategies for ameliorating growth loses, including immediate harvest and planting of SNC-resistant families or species. With quantitative links between foliage retention and growth loss (Maguire et al. 2011), the maps can also facilitate prediction of growth losses and adjustment of harvest schedules and economic appraisal of current stands. The above hazard rating models predict foliage retention as the average number of annual needle cohorts, but do not reflect the survival rate of any specific cohort. For some applications, including refinement of growth losses and improved understanding of the climatic drivers of SNC epidemiology, it may be more important to accurately simulate the proportion of surviving foliage in each annual cohort. With respect to growth impacts, needle cohorts have been shown to experience declining net photosynthetic rates and resource use efficiency with age (Warren 2006; Ethier et al. 2006). Although the oldest foliage on an individual SNC-infected Douglas-fir tends to be lost first, this pattern is not universal. At sites experiencing moderate levels of infection, annual variation in SNC infection pressure can result in a given cohort losing foliage before an older cohort that was formed during a year that was less conducive to *Phaeocryptopus* infection (Mainwaring et al. 2008). This variability in cohort survival and associated stomatal occlusion complicates the usual patterns in photosynthetic efficiency and introduce some additional variation in growth that has not been accounted for by correlating growth with average foliation retention (e.g., Maguire et al. 2011).

The ability to predict survival rates of individual needle cohorts or age classes over time may be particularly useful for refining mechanistic or hybrid models that simulate ecophysiological processes, total carbon fixation, and stem growth and yield (e.g., Mäkelä et al. 2000; Schwalm and Ek 2004; Weiskittel et al. 2010). Such models combine conventional empirical data with mechanistic elements such as climate- and soil-driven water availability, water uptake and evapotranspiration, nutrient uptake, foliar nutrient dynamics, and net photosynthesis. This hybridization allows the models to react to changes in environmental conditions including various climatic factors, and possibly improves predicted responses of trees and stands to silvicultural treatment and foliage loss from insects or disease (Monserud 2003). Given the apparent influence of climate on foliar longevity, and obvious links between foliar longevity and carbon fixation, the ability to predict the survival of individual cohorts may prove valuable in forecasting future growth.

Care must be taken in application of the cohort survival models beyond the geographic bounds of the SNC plot network. During an earlier effort to produce a climate-based prediction model, a dataset was compiled that included the data used in this analysis and additional data collected in the southern and central Coast Ranges and in the western Cascades of Oregon. In the initial analysis, ordinary least square regression produced a model that significantly underpredicted foliage retention at nearly every site outside the geographic range of the sites used in the cohort analysis (Latta et al. 2009). Although this bias was corrected by accounting for spatial autocorrelation, such techniques do not account for the factors which cause foliage retention to vary between sites.

The data for the current analysis were distributed in and around the area that has exhibited the most severe SNC symptoms since the epidemic began over 20 years ago. The start of the epidemic may have many causes, including off-site planting of seedlings from more interior families, introduction of Douglas-fir into stands formerly supporting spruce–hemlock–alder close to the Pacific coast (Hansen et al. 2000), or changing climate conditions (Mote et al. 2003). In addressing an epidemic, the classic disease triangle depicts the balance between the causal agent (*P. gaeumannii*), the host (Douglas-fir), and the environment (McNew 1960). The fungus *P. gaeumannii* is both endemic and ubiquitous, and its sole host is Douglas-fir. Overestimation of disease severity outside north coastal Oregon suggests subtle differences in environmental conditions that are not captured as well by the variables that were effective for the north coast, but genotypic differences in the host and abundance of fungal spores also cannot be totally dismissed (e.g., Johnson 2002; Hood and Kimberley 2005). It is possible that subtle differences in climate that are not represented by the monthly, seasonal, or annual climatic variables from ClimateWNA create conditions that are not as conducive to SNC intensification, or that biases in geographic interpolation of climate variables imply predisposing climatic conditions that do not actually occur in these areas. Alternatively, stands experiencing similar climatic regimes, but much lighter spore loads than stands at the SNC epicenter in north coastal Oregon may be protected to some degree by lower disease pressure. Where this disease pressure is absent, the same climate variables may not lead to the same declines in needle longevity.

Acknowledgments 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.

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