

# 1 Climatic influences on needle cohort survival mediated by 2 Swiss needle cast in coastal Douglas-fir

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## 16 17 **Abstract**

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

30 *Key Words: cohort survival, needle longevity, climatic effects, survival probability.*

32

## 33 Introduction

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

40           Coastal stands of Douglas-fir are among the most productive native conifer forests in the world due to a  
41 long growing season, abundant nitrogen, high precipitation, and relatively warm winter temperatures (Waring and  
42 Franklin 1979). In general, conifer needle longevity is negatively correlated with site productivity (Niinemets and  
43 Lukjanova 2003); therefore, needle retention on Douglas-fir growing in coastal zones is expected to be relatively  
44 low compared to less productive interior regions. In fact, foliage retention on interior Douglas-fir trees may be as  
45 high as 20 years (Gower et al. 1992), but healthy Douglas-fir stands in the Oregon Coast Range typically retain  
46 approximately 4 years of needles (Maguire et al. 2002). Since the mid-1980s (Black et al. 2010), Douglas-fir  
47 productivity in many coastal stands has diminished significantly due to Swiss needle cast (SNC), a foliar disease that  
48 causes premature needle loss. SNC is an endemic foliar disease specific to Douglas-fir and is caused by the fungus  
49 *Phaeocryptopus gaeumannii* (Boyce 1940). In the last 25 years, this disease has reached epidemic levels along the  
50 northwestern coast of the United States, resulting in varying levels of tree defoliation and growth loss (Maguire et al.  
51 2002, Maguire et al. 2011). Although the cause of this epidemic is hypothesized to result from numerous factors  
52 (Hansen et al. 2000), epidemiological research has identified climate factors as playing a large role in intensification  
53 of SNC (Rosso and Hansen 2003). Specifically, fungal spore germination and growth of hyphae into stomates has  
54 been shown to require wet springtime conditions (Capitano 1999), and development of the fungus in intercellular  
55 spaces of the needles appears to be enhanced by relatively cool summers (Rosso and Hansen 2003) and warm  
56 winters (Manter et al. 2005).

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

63           Across the age range, management intensity, and site conditions sampled in the permanent plot network,  
64 Douglas-fir foliage retention ranged from a maximum of approximately four years in healthy stands to as low as  
65 one year in the most severely infected stands (Maguire et al. 2002, Maguire et al. 2011). Due to the significant  
66 positive correlation between tree growth and foliage retention in infected stands, foliage retention has been used to  
67 estimate regional volume growth losses from SNC (Maguire et al. 2002, Mainwaring et al. 2005, Maguire et al.  
68 2011), and has also been incorporated into regional growth models (Garber et al. 2007) and applied in financial  
69 analyses (Latta and Adams 2010).

70           In the effort to create hazard rating maps for SNC in the Coast Ranges of Oregon and Washington,  
71 quantitative links between foliage retention and climate variables have been established using varying  
72 methodologies (Rosso and Hansen 2003, Manter et al. 2005, Coop and Stone 2007, Latta et al. 2009, Zhao et al.  
73 2011). In each of these analyses, tree-level foliage retention is calculated as the summed proportions of needles

74 surviving in each annual cohort. This foliage retention is generally interpreted as number of annual cohorts with  
75 100% survival plus the surviving fraction of the oldest cohort that is experiencing needle abscission. Older foliage  
76 is generally cast before younger foliage, but this pattern is not universal because: 1) only new emerging foliage can  
77 be infected by hyphae growing across the surface of the needles and into stomates; and 2) annual variation in  
78 climatic conditions creates annual variability in infection success or intensity. As a result, some younger annual  
79 cohorts may start to lose foliage before older cohorts. [Zhao et al. \(2011\)](#) analyzed the influence of local climatic  
80 factors on spatial and temporal variation on SNC as measured by average foliage retention. Modeling the effect of  
81 climatic factors on individual needle cohorts may further advance our understanding of mechanisms behind  
82 infection and mycelial development, and subsequent intensification of SNC. The objectives of this study were: 1) to  
83 identify climate variables that account for variability in survival patterns of annual cohorts of Douglas-fir needles; 2)  
84 to develop a needle survival model that explains observed variation in needle longevity by specific climatic  
85 conditions that prevailed during year of needle formation; and 3) to explore implied survival curves for needle  
86 cohorts formed under the full range of climatic conditions observed over the last 10 years.

## 87 **Method**

### 88 **Field Work**

89 Plots were distributed across a range of SNC severity, stand density, aspect, and slope (Table 1). The study  
90 sites ranged from 44.53° to 46.23° N latitude and from 123.38° to 124.00°W longitude (Fig. 1). Elevation ranged  
91 from 48 to 914 m above sea level. Over the last 40 years, the mean January minimum temperature for this region  
92 was 1.5 °C and the mean July maximum temperature was 22.8 °C. Total annual precipitation averaged  
93 approximately 240 cm, with 80% of the total typically occurring from October to March.

### 94 **Measurements**

95 Data for this analysis were compiled from two ongoing studies established to investigate growth losses  
96 under the influence of SNC: the Growth Impact Study (GIS) and the Precommercial Thinning study (PCT). The GIS  
97 plots were established in 1998 to monitor SNC symptoms and tree growth in 77 randomly selected 10- to 30-yr-old  
98 Douglas-fir plantations within 18 miles of the Pacific coast in northwestern Oregon ([Maguire et al. 2002](#), [Maguire et al. 2011](#)). The PCT plots were established in 23 stands in 1998 and to test the effect of thinning and initial SNC  
99 severity on subsequent symptom development and tree growth ([Mainwaring et al., review](#)). Only control plots from  
100 the PCT study were included in this analysis.  
101

102 Just prior to budbreak in each spring (April-May), foliage retention was recorded **using** two different  
103 methods on ten dominant or codominant trees on each plot. The first method involved estimating the average  
104 number of annual needle cohorts held by the tree, and has been referred to in past analyses as foliage retention  
105 ([Hansen et al. 2000](#), [Maguire et al. 2002](#)). The second approach yielded the data used in this analysis and called for  
106 estimating separately the percentage of surviving needles from each of the four youngest annual cohorts.  
107 Specifically, cohort retention was scored on each of the four most recent shoot age classes on secondary laterals.  
108 This retention score was recorded as 0, 1, . . . , or 9, with 0 representing 0-10%, 1 representing 11-20%, . . . , and 9  
109 representing 91-100%. These measurements were generally repeated on the same trees on each plot from 1998-  
110 2005; however, if a tree died or was badly damaged, a tree similar in size was chosen as a replacement.

### 111 **Climate data**

112 Climate data corresponding to the year that each needle cohort emerged was calculated with the software  
113 ClimateWNA v4.60. ClimateWNA extracts and downscales PRISM ([Daly et al. 2002](#)) monthly data (2.5 x 2.5

114 arcmin) for the reference period (1961-1990), and calculates annual, seasonal and monthly climate variables for  
115 specific locations based on latitude, longitude, and elevation for western North America. This program also  
116 downscales and integrates historical climate data (1901-2009) (Mitchell and Jones 2005, Mbogga et al. 2009). The  
117 output included both measurable climate variables and derived climatic indices (Hamann and Wang 2005).

118 In total, ClimateWNA can produce 85 climate variables, including 48 monthly, 16 seasonal and 21 annual  
119 variables (Table 2 and 3). The monthly and seasonal variables included minimum, maximum, and average  
120 temperatures and precipitation. Of the 21 annual climate variables, eight were directly calculated from the monthly  
121 data including mean annual temperature (MAT), mean coldest month temperature (MCMT), mean warmest  
122 temperature (MWMT), continentality (TD, the difference between MWMT and MCMT), mean annual precipitation  
123 (MAP), mean May to September precipitation (MSP), annual heat-moisture index (AHM), and summer heat-  
124 moisture index (SHM). Calculations of other annual variables, such as growing degree-days ( $DD > 5^{\circ}\text{C}$ ), cooling  
125 degree-days ( $DD < 0^{\circ}\text{C}$ ), frost-free period (FFP), required daily weather data. ClimateWNA derived these variables  
126 using either linearly interpolated monthly data or relationships between these daily variables and monthly climate  
127 variables (Wang et al. 2006).

## 128 **Statistical Analysis**

129 Annual cohort retention scores were expressed as the midpoint of each interval of percent retention, i.e.,  
130 5%, 15%, . . . , and 95%. We first generated the observed life-table survival and hazard probabilities (Lawless 1982)  
131 to obtain descriptive information using PROC LIFETEST in SAS version 9.2 (SAS Institute Inc. 2009). A  
132 proportional hazards model (Lawless 1982) was first fitted to the data with PROC PHREG in SAS version 9.2 to  
133 select best subsets of climate variables for predicting needle longevity of individual cohorts. Climate variables at  
134 different scales (annual, seasonal and monthly climate variables) were tested as potential predictors, and only those  
135 pertaining to the year of foliage emergence and first year of foliage development were considered as predictors for  
136 each corresponding foliage cohort. The criterion to determine "best" subsets was based on the highest global score  
137 chi-square statistic (Lawless 1982).

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

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

## 154 **Results**

### 155 **Survival and hazard probabilities**

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

### 164 **Best climate predictors**

165 The climate predictors that appeared in the best proportional hazards models varied somewhat among the  
166 three temporal resolutions (Table 5). Based on variables identified in previous epidemiological research (Capitano  
167 1999, Rosso and Hansen 2003, Manter et al. 2005), and on statistical scores (global chi-square statistic), models  
168 based on seasonal climate variables (models 4-6 in table 4), were judged most suitable. Model 5 included maximum  
169 temperature in summer (Tmax\_sm), minimum temperature in winter (Tmin\_wt), and precipitation in spring  
170 (PPT\_sp), so was selected as the optimal subset because it had the best combination of few predictors and high  
171 accuracy (high score).

### 172 **Needle longevity model**

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

181 In order to view differences in the survival curve for needles formed under different climatic conditions,  
182 survival probabilities were predicted from the final model based on minimum and maximum values of the covariates  
183 represented in this dataset (maximum PPT\_sp, Tmax\_sm, and Tmin\_wt of 1281 mm, 25.6°C, and 5.8°C,  
184 respectively; minimum PPT\_sp, Tmax\_sm, and Tmin\_wt of 275 mm, 17.1°C, and -2.2°C, respectively). The highest  
185 survival probabilities occurred for a cohort formed in a year with low PPT\_sp, high Tmax\_sm, and low Tmin\_wt,  
186 with survival probabilities exceeding 90% through year four (Fig. 5). The lowest survival probabilities occurred for  
187 a cohort formed in a year with high PPT\_sp, low Tmax\_sm, and high Tmin\_wt, with survival probabilities dropping  
188 below 20% by year four.

## 189 **Discussion**

190 Swiss Needle Cast (SNC) can be sufficiently severe that foliage retention reaches slightly less than one year  
191 in populations where the maximum foliage retention would otherwise be approximately four years (Hansen et al.  
192 2000, Maguire et al. 2002). In general, needle loss progresses from the oldest to the youngest needles, but it is not

193 uncommon for a younger needle cohort to start losing needles before an older cohort. Presumably this sequence is a  
194 result of environmental conditions that are more favorable for infection of new foliage during the year that the  
195 younger cohort was formed. Survival analysis provided a methodology to describe differential rates of survival for  
196 specific needle cohorts, and to test the effects of weather conditions specific to the year in which each cohort  
197 emerged and developed. In our analysis of Douglas-fir needle dynamics, patterns in needle longevity and survival  
198 probability were first assessed by nonparametric estimation of empirical survival rates and hazard probabilities,  
199 indicating that survival probability declines rapidly after two years in the population sampled. The semi-parametric  
200 proportional hazards models illustrated that a relatively small set of climatic variables describing conditions during  
201 year of foliage emergence could explain a significant amount of variation in cohort survival. These key variables  
202 were then introduced into alternative parametric models, identifying the lognormal distribution as best and providing  
203 a model that could be compared to previous work analyzing the spatial and temporal variability in foliage retention  
204 (Manter et al. 2005, Stone et al. 2007, Zhao et al. 2011).

205 The climate variables with greatest efficacy for predicting survival of Douglas-fir needle cohorts were  
206 consistent with the strongest variables for predicting spatial and temporal patterns in average foliage retention (Zhao  
207 et al. 2011). In general both cohort survival rates and average foliage retention declined as winter temperatures and  
208 spring precipitation increased, and increased as summer temperatures increased (Zhao et al. 2011 and results  
209 presented above). Similar climatic variables have also been shown to influence indices of SNC infection intensity  
210 based on frequency of stomatal occlusion by pseudothecia (Manter et al. 2005, Stone et al. 2007).

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

224 Annual climate variables also accounted on average for a greater proportion of the variability in needle  
225 survival than did seasonal climate variables. Growing season precipitation (MSP) was probably a coarse surrogate  
226 for spring wetness, and continentality (TD) probably indicated the combined effects of low winter temperature and  
227 high summer temperature, both of which have been shown to influence spatial and temporal patterns in average  
228 foliage retention (Zhao et al. 2011). Variables representing the number of frost free days (NFFD, eFFP) likewise  
229 probably integrate the positive effect of warmer and/or shorter winters on SNC intensification. Although TD is a  
230 combination of maximum summer temperature and minimum winter temperature, the individual covariates  
231 constituting TD may be more important to represent in the model if the inherent correlations with TD and other  
232 climatic variables become weaker under future climates. Similarly, if the distribution of precipitation within the  
233 growing season changes, MSP may become either less or more predictive of needle survival depending on whether  
234 more of the precipitation is shifted to the critical period of sporulation and infection of new foliage early in the  
235 summer.



236 Numerous SNC hazard maps have been developed for Douglas-fir stands in the Oregon Coast Ranges (Manter  
237 et al. 2005, Coop and Stone 2007, Latta 2009, Zhao et al. *In prep*). These maps were based at least in part on  
238 characterizing sites by their local climate and quantifying the link between foliage retention and local climate. The  
239 SNC hazard maps have enabled forest managers to prioritize certain zones with respect to various silvicultural  
240 strategies for ameliorating growth losses, including immediate harvest and planting of SNC-resistant families or  
241 species. With quantitative links between foliage retention and growth loss (Maguire et al. 2011), the maps can also  
242 facilitate prediction of growth losses and adjustment of harvest schedules and economic appraisal of current stands.  
243 The above hazard rating models predict foliage retention as the average number of annual needle cohorts, but do not  
244 reflect the survival rate of any specific cohort. For some applications, including refinement of growth losses and  
245 improved understanding of the climatic drivers of SNC epidemiology, it may be more important to accurately  
246 simulate the proportion of surviving foliage in each annual cohort. With respect to growth impacts, needle cohorts  
247 have been shown to experience declining net photosynthetic rates and resource use efficiency with age (Warren  
248 2006, Ethier 2006). Although the oldest foliage on an individual SNC-infected Douglas-fir tends to be lost first, this  
249 pattern is not universal. At sites experiencing moderate levels of infection, annual variation in SNC infection  
250 pressure can result in a given cohort losing foliage before an older cohort that was formed during a year that was less  
251 conducive to *Phaeocryptopus* infection (Mainwaring et al. 2008). This variability in cohort survival and associated  
252 stomatal occlusion complicate the usual patterns in photosynthetic efficiency and introduce some additional  
253 variation in growth that has not been accounted for by correlating growth with average foliation retention (e.g.,  
254 Maguire et al. 2011).

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

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

272 The data for the current analysis were distributed in and around the area that has exhibited the most severe  
273 SNC symptoms since the epidemic began over 20 years ago. The start of the epidemic may have many causes,  
274 including off-site planting of seedlings from more interior families, introduction of Douglas-fir into stands formerly  
275 supporting spruce-hemlock-alder close to the Pacific coast (Hansen et al. 2000), or changing climate conditions  
276 (Mote et al. 2003). In addressing an epidemic, the classic disease triangle depicts the balance between the causal  
277 agent (*P. gaeumannii*), the host (Douglas-fir), and the environment (McNew 1960). The fungus *P. gaeumannii* is  
278 both endemic and ubiquitous, and its sole host is Douglas-fir. Overestimation of disease severity outside north  
279 coastal Oregon suggests subtle differences in environmental conditions that are not captured as well by the variables  
280 that were effective for the north coast, but genotypic differences in the host and abundance of fungal spores also

281 cannot be totally dismissed (e.g., Johnson 2002, Hood and Kimberly 2005). It is possible that subtle differences in  
282 climate that are not represented by the monthly, seasonal, or annual climatic variables from ClimateWNA create  
283 conditions that are not as conducive to SNC intensification, or that biases in geographic interpolation of  
284 climatevariables imply predisposing climatic conditions that do not actually occur in these areas. Alternatively,  
285 stands experiencing similar climatic regimes but much lighter spore loads than stands at the SNC epicenter in north  
286 coastal Oregon may be protected to some degree by lower disease pressure. Where this disease pressure is absent,  
287 the same climate variables may not lead to the same declines in needle longevity.

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294 **Literature Cited:**

- 295 Allison PD (2010) Survival analysis using SAS: A practical guide (2nd edition) Cary, NC: SAS Institute.
- 296 Balster NJ and Marshall JD (2000) Decreased needle longevity of fertilized Douglas-fir and grand fir in the northern  
297 Rockies. *Tree Physiol.* 20:1191–1197.
- 298 Black BA, Shaw DC, and Stone JK (2010) Impacts of Swiss needle cast on overstory Douglas-fir forests of the  
299 western Oregon Coast Range. *For. Ecol. and Man.* 259: 1673-1680.
- 300 Boyce JS (1940) A needle cast of Douglas-fir associated with *Adelopus gaeumannii*. *Phytopathol* 30:649–59.
- 301 Chastagner GA and Byther RS (1983) Infection period of *Phaeocryptopus gaeumannii* on Douglas-fir needles in  
302 western Washington. *Plant Dis* 67:811–813.
- 303 Capitano B (1999) The infection and colonization of Douglas-fir by *P. gaeumannii*. MS thesis, Oregon State  
304 University, Corvallis, OR, USA.
- 305 Coop LB and Stone JK (2007) Prediction maps of Swiss needle case needle retention based on climate factors.  
306 Pages 15-21, in: D. Shaw, ed., 2007 Swiss Needle Cast Cooperative Annual Report.
- 307 Daly C, Gibson WP, Taylor GH, Johnson GL, and Pasteris P (2002) A knowledge-based approach to the statistical  
308 mapping of climate. *Climate Research* 22:99–113.
- 309 Ethier GJ, Livingston NJ, Harrison DL, Black TA & Moran JA (2006) Low stomatal and internal conductance to  
310 CO<sub>2</sub> versus Rubisco deactivation as determinants of the photosynthetic decline of ageing evergreen leaves. *Plant,*  
311 *Cell & Environment* **29**, 2168–2184.
- 312 Garber S, Maguire D, Mainwaring D, and Hann D (2007) Swiss Needle Cast ORGANON module update. Pages  
313 63-66, in: D. Shaw, ed., 2007 Swiss Needle Cast Cooperative Annual Report.
- 314 Gower ST, Vogt KA, and Grier CG. 1992. Carbon dynamics of Rocky Mountain Douglas-fir: Influence of water  
315 and nutrient availability. *Ecol. Monogr.* 62:43-65.
- 316 Hamann, A., and T. L. Wang. 2005. Models of climatic normals for genecology and climate change studies in  
317 British Columbia. *Agricultural and Forest Meteorology* 128:211–221.
- 318 Hansen EM, Stone JK, Capitano BR, Rosso P, Sutton W, Winton L, Kanaskie A, and McWilliams M (2000)  
319 Incidence and impact of Swiss needle cast in forest plantations of Douglas-fir in coastal Oregon. *Plant. Dis.* 84: 773–  
320 778.
- 321 Hood IA, Kimberley MO (2005) Douglas-fir provenance susceptibility to Swiss needle cast in New Zealand.  
322 *Australasian Plant Pathology* 34:57-62.
- 323 Johnson R (2002) Genetic variation in tolerance of Douglas-fir to Swiss needle cast as assessed by symptom  
324 expression. *Silvae Genetica* 51:80-86.
- 325 Kurkela T, Aalto T, Varama M & Jalkanen R (2005) Defoliation by the common pine sawfly (*Diprion pini*) and  
326 subsequent growth reduction in Scots pine: a retrospective approach. *Silva Fennica* 39: 467–480.

- 327 Latta G, Adams D, and Shaw D (2009) Mapping western Oregon Douglas-fir foliage retention with a simultaneous  
328 autoregressive model. Pages 37-51, in: D. Shaw and T. Woolley, eds., 2009 Swiss Needle Cast Cooperative Annual  
329 Report.
- 330 Latta G, and Adams D (2010) The economic and market impacts of Swiss needle cast in western Oregon. Available  
331 online at [http://sncc.forestry.oregonstate.edu/sites/default/files/2010Workshop\\_Latta\\_Adams.pdf](http://sncc.forestry.oregonstate.edu/sites/default/files/2010Workshop_Latta_Adams.pdf). Last accessed Feb  
332 11, 2011.
- 333 Lawless JF (1982) Statistical models and methods for lifetime data. John Wiley & Sons, New York.
- 334 Maguire DA, Kanaskie A, Voelker W, Johnson R, and Johnson G (2002) Growth of young Douglas-fir plantations  
335 across a gradient in Swiss needle cast severity. *Western Journal of Applied Forestry*. 17: 86-95.
- 336 Maguire DA, Mainwaring DB, and Kanaskie A (2011) Ten-year growth and mortality in young Douglas-fir stands  
337 experiencing a range in Swiss needle cast severity. *Canadian Journal of Forest Research* 41:2064-2076.
- 338 Mäkelä A, Landsberg J, Ek AR, Burk TE, Ter-Mikaelian M, Agren GI, Oliver CD, Puttonen P (2000) Process-  
339 based models for forest ecosystem management: current state of the art and challenges for practical implementation.  
340 *Tree Physiology* 20:289–298
- 341 Mainwaring D, Maguire D, Kanaskie A, and Brandt J (2005) Growth responses to commercial thinning in Douglas-  
342 fir stands with varying severity of Swiss needle cast in Oregon, USA. *Can. J. For. Res* 35: 2394–2402.
- 343 Mainwaring D, Maguire D, and DeRoss J (2008) Seasonal Adjustment of Foliage Retention for Swiss Needle Cast  
344 Infected Stands. Pages 25-31, in: D. Shaw, ed., 2008 Swiss Needle Cast Cooperative Annual Report.
- 345 Manter DK, Reeser PD, and Stone JK (2005) A Climate-Based Model for Predicting Geographic Variation in Swiss  
346 Needle Cast Severity in the Oregon Coast Range. *Phytopathology*. 95:1256-1265.
- 347 Mbogga MS, Hamann A, Wang TL (2009) Historical and projected climate data for natural resource management in  
348 western Canada. *Agricultural and Forest Meteorology* 149: 881–890.
- 349 McNew GL (1960) The nature, origin, and evolution of parasitism. In *Plant Pathology: An Advanced Treatise* (eds  
350 Horsfall, J. G. & Dimond, A. E.) 19–69 (Academic Press, New York, 1960).
- 351 Mitchell RG (1974) Estimation of needle populations on young, open-grown Douglas-fir by regression and life  
352 table analysis. USDA-FS Pacific Northwest Research Station, Portland, OR, USA. Research Paper PNW-181. 14  
353 p.
- 354 Mitchell T, and Jones P (2005) An improved method of constructing a database of monthly climate observations and  
355 associated high-resolution grids, *Int. J. Climatol.*, 25, 693– 712.
- 356 Monserud RA (2003) Evaluating forest models in a sustainable forest management context. *Forest Biometry,*  
357 *Modelling and Information Sciences* 1, 35-47.
- 358 Mote PW, Parson EA, Hamlet AF, Keeton WS, Lettenmaier D, Mantua N, Miles EL, Peterson DW, Peterson DL,  
359 Slaughter R, and Snover AK (2003) Preparing for climatic change, the water, salmon, and forests of the Pacific  
360 Northwest. *Clim. Change*, 61: 45–88.
- 361 Niinemets Ü and Lukjanova A (2003) Needle longevity, shoot growth and branching frequency in relation to site  
362 fertility and within-canopy light conditions in *Pinus sylvestris*. *Annals of Forest Science* 60:195–208.

- 363 Reich PB, Koike T, Gower ST and Schoettle AW (1994) Causes and consequences of variation in conifer leaf life  
364 span. Pp. 225-254 in W.K. Smith and T.M. Hinckley (eds). *Ecophysiology of Coniferous Forests*. Academic Press,  
365 San Diego, CA, USA.
- 366 Reich PB, Oleksyn J, Modrzynski J, and Tjoelker MG (1996) Evidence that longer needle retention of spruce and  
367 pine populations at high elevations and high latitudes is largely a phenotypic response. *Tree Physiology* 16: 643–647.
- 368 Rosso PH, and Hansen EM (2003) Predicting Swiss Needle Cast Disease Distribution and Severity in Young  
369 Douglas-Fir Plantations in Coastal Oregon *Phytopathology* 93:790-798.
- 370 SAS Institute (2009) *SAS/STAT(R) 9.2 User's Guide, Second Edition*. SAS Institute Inc., Cary,NC.
- 371 Schwalm CR, Ek AR (2004) A process-based model of forest ecosystems driven by meteorology. *Ecological*  
372 *Modeling* 179:317–348
- 373 Silver GT (1962) The distribution of Douglas-fir foliage by age. *For. Chron.* 38:433–438.
- 374 Stone JK, Hood IA, Watt MS, and Kerrigan JL (2007) Distribution of Swiss needle cast in New Zealand in relation  
375 to winter temperature. *Australasian Plant Pathology* 36: 445-454.
- 376 Wang, T., A. Hamann, D. L. Spittlehouse, and S. N. Aitken. 2006. Development of scale-free climate data for  
377 western Canada for use in resource management. *Intl. J. Climatol.* 26:383-397.
- 378 Waring RH, and Franklin JF (1979) Evergreen coniferous forests of the Pacific Northwest. *Science* 204:1380–1386.
- 379 Warren CR (2006) Why does photosynthesis decrease with needle age in *Pinus pinaster*? *Trees* 20: 157–164.
- 380 Weiskittel AR, Maguire DA, Monserud RA, Johnson GP (2010) A hybrid model for intensively managed Douglas-  
381 Fir plantations in the Pacific Northwest, USA. *European Journal of Forest Research* 129:325-338.
- 382 Xiao Y (2003) Variation in needle longevity of *Pinus tabulaeformis* forests at different geographic scales. *Tree*  
383 *Physiology*, 23, 463–471.
- 384 Zhao J, Mainwaring DB, Maguire DA, Kanaskie A (2011) Regional and annual trends in Douglas-fir foliage  
385 retention: Correlations with climatic variables. *Forest Ecology & Management* 262:1872-1886

Table 1. Initial (1998) attributes of Douglas-fir control plots included in the SNCC pre-commercial thinning (PCT) study and Growth Impact (GIS) Study.

Variable	Units	<i>PCT Study</i>			<i>GIS Study</i>		
		mean (stdev)	Minimum	Maximum	Mean (stdev)	Minimum	Maximum
<b>Douglas-fir tree density</b>	trees ha <sup>-1</sup>	1020.8 (313.3)	629.9	2001.0	628.1 (290.7)	86.5	1630.2
<b>Douglas-fir basal area</b>	m <sup>2</sup> ha <sup>-1</sup>	15.76 (6.32)	3.92	27.05	17.62 (8.59)	0.62	38.71
<b>Douglas-fir breast height age</b>	yrs	10.9 (2.4)	5.0	15.5	20.0 (5.6)	11.0	32.0
<b>Douglas-fir QMD</b>	cm	14.1 (3.1)	7.2	19.7	18.6 (6.2)	3.8	34.0
<b>Douglas-fir top height</b>	m	11.7 (2.1)	7.8	15.6	26.2 (8.4)	5.8	44.6
<b>Douglas-fir site index</b>	m at 50 yrs	43.0 (6.7)	32.1	62.5	44.9 (7.6)	14.6	61.7
<b>Basal area of other conifers</b>	m <sup>2</sup> ha <sup>-1</sup>	1.75 (6.14)	0.00	29.62	2.76 (5.24)	0.00	24.03
<b>Basal area of broadleaved species</b>	m <sup>2</sup> ha <sup>-1</sup>	1.21 (1.14)	0.00	3.97	1.05 (2.03)	0.00	13.40
<b>Total tree density</b>	trees ha <sup>-1</sup>	1496.6 (950.2)	629.9	5101.0	848.4 (413.7)	259.4	2037.8
<b>Total plot basal area</b>	m <sup>2</sup> ha <sup>-1</sup>	18.72 (8.79)	3.92	60.64	21.43 (10.17)	0.66	48.65
<b>Foliage retention</b>	years	2.4 (0.5)	1.3	3.3	2.3 (0.4)	1.1	3.1

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

<i>Group</i>	<i>Predictor</i>	<i>Definition</i>
<b>Annual variables</b>	<i>Direct variables</i>	
	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 Sept.) precipitation (mm)
	AHM	annual heat:moisture index $(MAT+10)/(MAP/1000)$
SHM	summer heat:moisture index $((MWMT)/(MSP/1000))$	
<i>Derived variables</i>	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., $E_{ref} = E_{Har}(1.18 - 0.0067\text{latitude})$ , $n=56$ , $R^2=0.734$ , $se_{xy}=0.039E_{Har}$ and the latitude is in degrees.
	CMD	Hargreaves climatic moisture deficit, sum of the monthly difference between a reference evaporation (Eref) and precipitation.
<b>Seasonal variables</b>	Tave_wt, Tave_sp, Tave_sm, Tave_at.	mean temperature(°C) of winter (Dec.(prev. yr) - Feb.), spring (Mar. - May), summer (Jun. - Aug.), and autumn (Sep. - Nov.).
	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.
<b>Monthly variables</b>	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)



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

	Unit	mean (stdev)	Minimum	Maximum
<b>Longevity</b>	years	2.5(1.2)	0.5	4.0
<b>Latitude</b>	° N	45.3(0.4)	44.5	46.2
<b>Longitude</b>	° W	-123.7(0.1)	-124.0	-123.4
<b>Elevation</b>	m	243.5(156.8)	48.0	914.0
<b>Slope</b>	°	8.7(6.9)	0.0	24.0
<b>Aspect</b>	°	166.1(110.2)	-1.0	358.0
<b>Tave02</b>	°C	6.7(1.3)	1.2	9.5
<b>Tave09</b>	°C	15.6(1.4)	11.1	18.9
<b>Tmax03</b>	°C	12.3(1.5)	6.2	16.2
<b>PPT03</b>	mm	299.7(109.8)	95.0	752.0
<b>PPT10</b>	mm	229.3(79.3)	40.0	533.0
<b>Tmax_sm</b>	°C	21.3(1.4)	17.1	25.6
<b>Tmin_wt</b>	°C	2.6(1.3)	-2.2	5.8
<b>Tmin_sm</b>	°C	10.2(0.7)	7.2	12.2
<b>Tave_wt</b>	°C	6.2(1.2)	1.6	9.0

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<b>Tave_sp</b>	°C	9.9(1.1)	5.1	12.5
<b>PPT_sp</b>	mm	633.1(148.3)	275.0	1281.0
<b>TD</b>	°C	11.1(1.4)	6.8	15.9
<b>MSP</b>	mm	416.0(134.2)	136.0	892.0
<b>NFFD</b>	days	317.2(18.0)	232.0	349.0
<b>eFFP</b>		319.0(14.2)	267.0	350.0

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

<i>Age Interval</i>	<i>Number Failed</i>	<i>Number Censored</i>	<i>Effective Sample Size</i>	<i>Survival</i>		<i>Hazard</i>	
				<i>probability</i>	<i>(SE)</i>	<i>probability</i>	<i>(SE)</i>
0-1	625	0	60661	1.0000	0.0000	0.0104	0.0004
1-2	15644	0	60036	0.9897	0.0004	0.2996	0.0024
2-3	17766	6651	41066.5	0.7318	0.0018	0.5520	0.0040
3-4	9180	5690	17130	0.4152	0.0021	0.7321	0.0071
4-	0	5105	2552.5	0.1927	0.0019		

Table 5. Selected models for predicting Douglas-fir needle cohort survival from climatic variables. Bold type indicates negative effects and regular type indicates positive effects.

<i>No</i>	<i>Climate variables</i>	<i>Number of predictors</i>	<i>Predictors</i>	<i>Score</i>
1	Annual	2	<b>TD</b> MSP	6131.7829
2	Annual	3	MSP NFFD <b>eFFP</b>	7631.4501
3	Annual	4	<b>TD</b> MSP NFFD <b>eFFP</b>	8428.1364
4	Seasonal	2	Tmin_wt PPT_sp	5929.6470
5	Seasonal	3	Tmin_wt <b>Tmax_sm</b> PPT_sp	6780.4181
6	Seasonal	4	Tave_wt Tmin_sm <b>Tave_sp</b> PPT_sp	7680.2884
7	Monthly	2	Tave02 <b>Tmax03</b>	9123.6956
8	Monthly	3	PPT03 Tave02 <b>Tave09</b>	9828.2675
9	Monthly	4	Tave02 <b>Tave09</b> <b>Tmax03</b> PPT10	10469.6083

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

<i>Distribution</i>	<i>2 Log Likelihood</i>	<i>AIC</i>	<i>AICC</i>	<i>BIC</i>
<b>Exponential</b>	132023.9	132031.9	132031.9	132054.7
<b>Normal</b>	157245.0	157255.0	157255.0	157283.5
<b>Lognormal</b>	99508.83	99518.83	99518.86	99547.36
<b>LLogistic</b>	100475.4	100485.4	100485.4	100513.9
<b>Logistic</b>	157402.6	157412.6	157412.6	157441.1
<b>Weibull</b>	105373.5	105383.5	105383.5	105412.0
<b>Gamma</b>	99358.9	99370.9	99370.9	99405.1

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

<i>Parameter</i>	<i>DF</i>	<i>Estimate</i>	<i>Standard Error</i>	<i>95% Confidence Limits</i>		<i>Chi-Square</i>	<i>Pr &gt; ChiSq</i>
<b>Intercept</b>	1	-0.4170	0.0371	-0.4898	-0.3442	126.13	<.0001
<b>Tmin_wt</b>	1	-0.1582	0.0020	-0.1621	-0.1543	6327.82	<.0001
<b>Tmax_sm</b>	1	0.0931	0.0016	0.0899	0.0964	3211.51	<.0001
<b>PPT_sp</b>	1	-0.0006	0.0000	-0.0007	-0.0006	1548.46	<.0001
<b>Scale</b>	1	0.5591	0.0020	0.5552	0.5630		



## Figure Captions

- Figure 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.
- Figure 2. Empirical needle survival curves for two average plots (2 and 7), a relatively healthy plot (107), and a severely impacted plot (99).
- Figure 2. Survival probability of Douglas-fir needles by age class.
- Figure 3. Lognormal probability plot for Douglas-fir needle longevity data.
- Figure 4. Predicted survival curves for Douglas-fir needles initiated under different climatic conditions (high and low PPT<sub>sp</sub>=1281 mm and 275 mm, respectively; high and low Tmax<sub>sm</sub>=25.6°C and 17.1°C, respectively; and high and low Tmin<sub>wt</sub>=5.8°C and -2.2°C, respectively).

Fig. 1

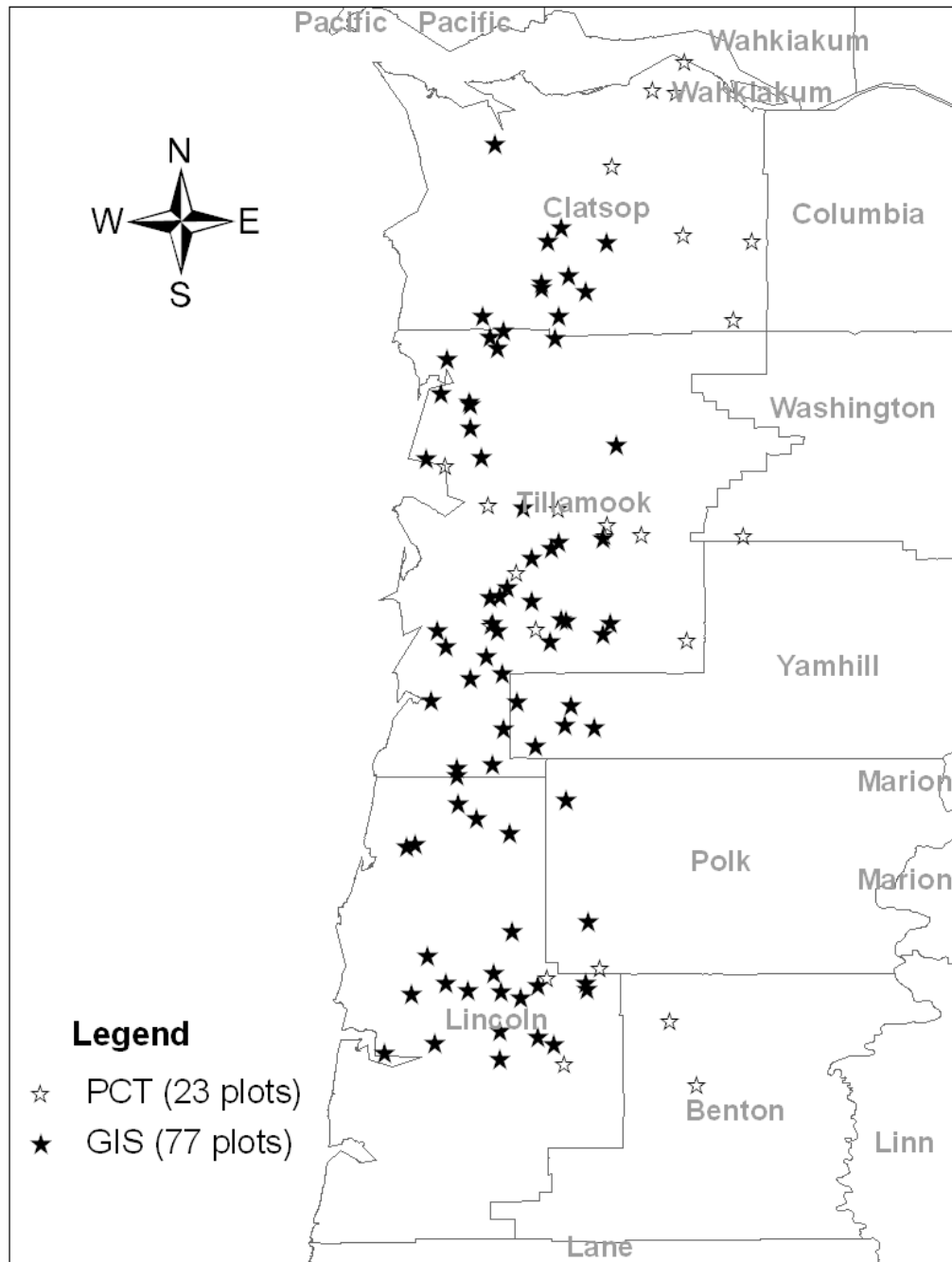


Fig. 2

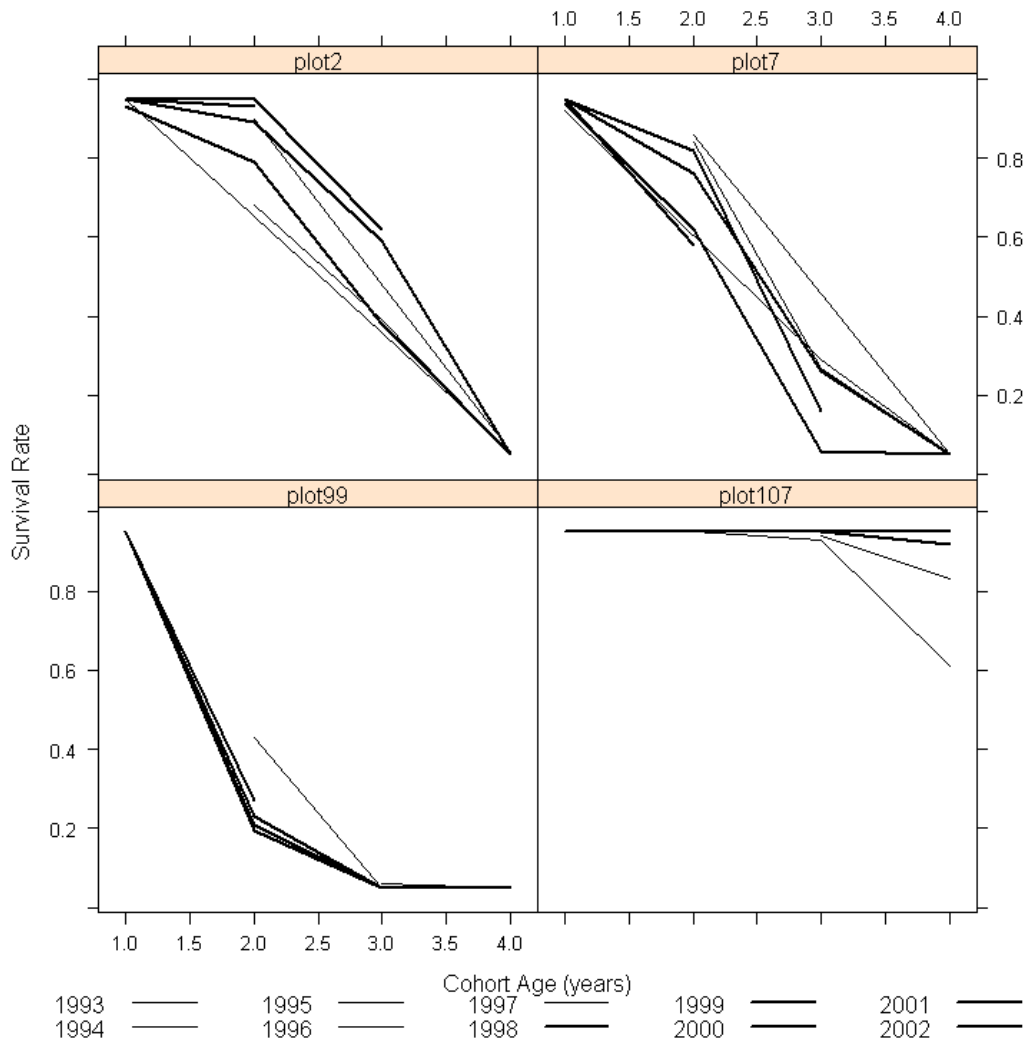


Fig. 3

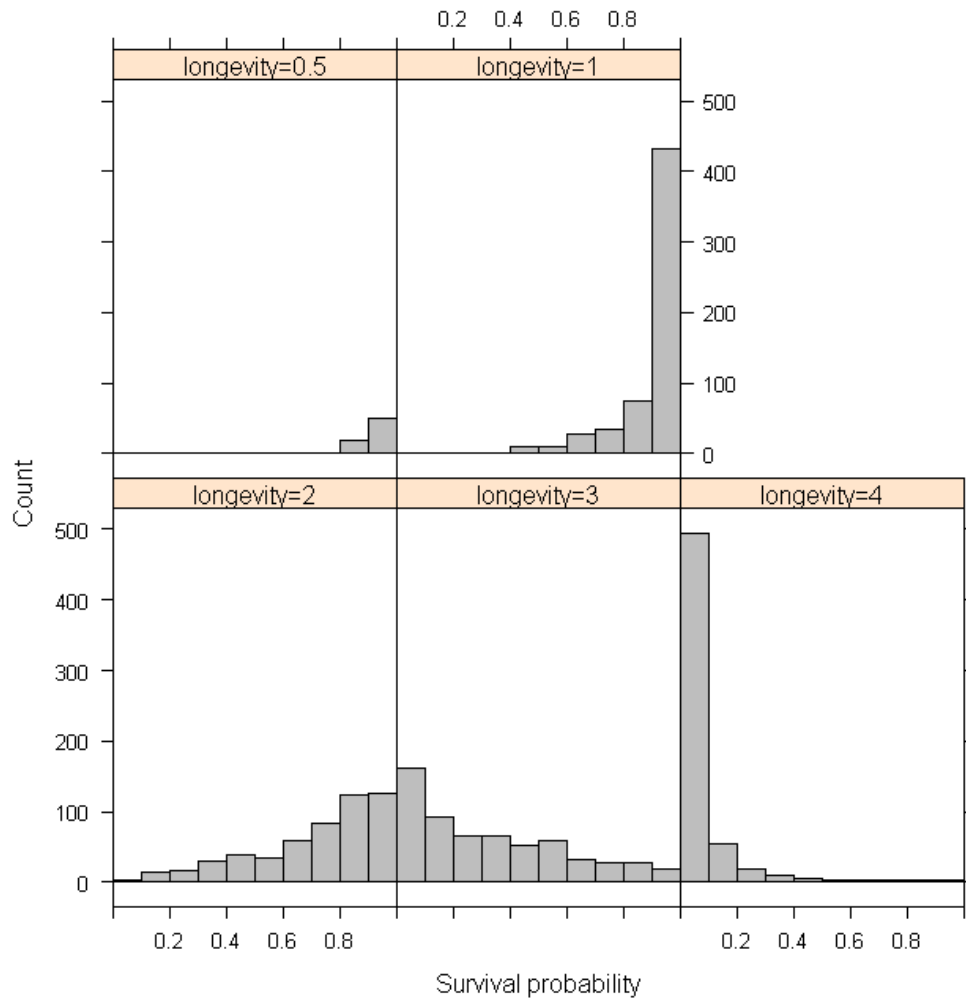


Fig. 4

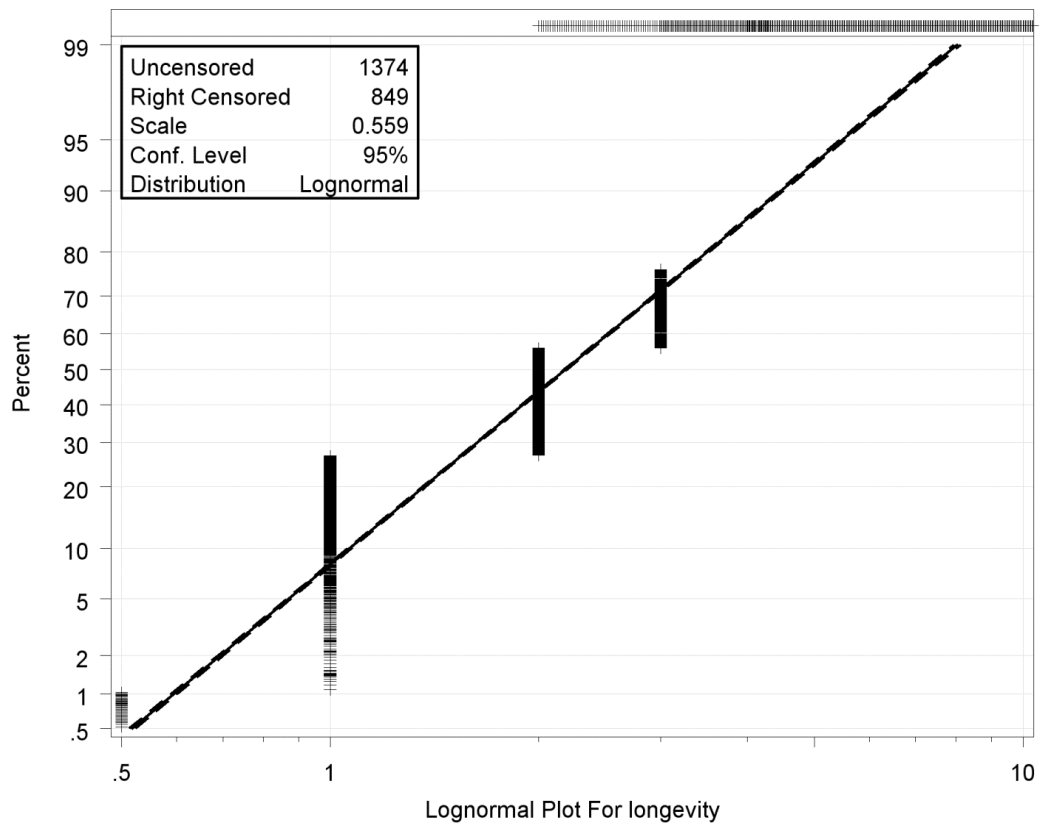


Fig. 5

