Vertical Foliage Retention in Douglas-Fir Across Environmental Gradients of the Western Oregon Coast Range Influenced by Swiss Needle Cast

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Abstract

We investigated the vertical pattern of foliage retention of Douglas-fir (*Pseudotsuga menziesii*) in the western Oregon Coast Range where Swiss needle cast, a foliage disease caused by *Phaeocryptopus gaeumannii,* is causing foliage loss and growth impacts. Swiss needle cast reduced foliage retention more in the upper crown than the lower crown within the epidemic area, which is unusual as foliage diseases usually reduce foliage retention most in the lower crown. We hypothesized that as foliage retention increased across environmental gradients that it would also increase in the upper crown at a greater rate than the lower crown. We randomly selected 72 sites from a population of Douglas-fir plantations in the northwest Oregon Coast Range. We estimated foliage retention from the lower, mid and upper crown of 10 trees per plot. We fitted a two-level hierarchical model with tree and stand level predictors to model changes in foliage retention with changing environmental gradient for foliage in each of three vertical crown positions. We found that the vertical pattern of foliage retention was generally similar throughout the study area with lowest retention in the upper crown, and highest retention in the lower crown. Foliage retention increased with increasing distance from the coast, which is correlated with increased elevation and decreased temperature and site productivity. These findings are consistent with our current understanding of conifer foliage retention. No apparent shift occurs from whole crown to lower crown impacts in our study area as foliage retention increases and approaches normal.

Keywords: Douglas-fir, foliage retention, hierarchical modeling, foliage disease

Introduction

Foliage retention in determinant growth conifers, expressed as the number of years of foliage cohorts retained on a stem, varies due to environmental and biological factors. Foliage retention in conifers is known to increase with increasing elevation and decreasing site productivity (Ewers and Schmid 1981, Schoettle 1990, Reich et al. 1995, Reich et al. 1996), or increasing latitude and decreasing temperature (Xiao 2003). Fertilization with urea (N) has also been shown to reduce foliage retention (Brix 1983, Balster and Marshall 2000). Within a healthy tree crown, the upper crown typically has the lowest foliage retention and the lower crown has the highest foliage retention (Schoettle and Smith 1991, Reich et al. 1995).

Foliage diseases that affect conifers cause reductions in foliage retention, with greater reduction of foliage occurring where the spores landing on foliage have the greater chance of survival. This is typically in the lower portions of the crown (Tatter 1989, Scharpf 1993, Goheen and Willhite 2006) due to higher humidity. Foliage diseases also appear to be most prevalent in certain landscape settings, such as on north slopes and in wetter areas where humid air settles (Goheen and Willhite 2006, Shaw et al. 2009).

Swiss needle cast (Swiss needle cast), a foliage disease of Douglas-fir, (*Pseudotsuga menziesii*) caused by *Phaeocryptopus gaeumannii*, has reached epidemic proportions in the state of

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Oregon, USA along the Pacific coast and west slope of the Oregon Coast Range—referred to hereafter as the epidemic area (Shaw et al. 2011). The disease is most severe near the coast and at low elevations. The severity of Swiss needle cast has been linked to warm winter temperature and consistent spring/summer leaf wetness (Hansen et al. 2000, Rosso and Hansen 2003, Manter et al. 2005). Swiss needle cast symptoms include early loss of foliage, thinning and chlorosis of the crown, and reduced tree growth. Within the epidemic area, Douglas-fir foliage retention is thought to be directly affected by *P. gaeumannii* (Hansen et al. 2000, Manter et al. 2001, Winton et al. 2003). Tree growth has been directly linked to foliage retention (Maguire et al. 2011), and effects of foliage retention have been incorporated into the forest growth model ORGANON (Maguire et al. 2002, Garber et al. 2007).

Zhao et al. (2011) investigated the correlation of regional and annual trends in foliage retention with 85 different climatic variables. They found that average foliage retention in western Oregon Douglas-fir was correlated with a temperature-based continentality index, mean annual precipitation, winter temperature, summer temperature, and spring or summer precipitation when distance from coast and elevation were excluded. Zhao et al. (2012) then investigated the climatic influences on needle cohort survival associated with Swiss needle cast in coastal Douglas-fir. They found that needle survival was positively correlated with maximum summer temperature, and negatively associated with minimum winter temperature and spring precipitation.

Typically, Swiss needle cast causes foliage loss in the lower and inner portion of the crown, where humidity is higher (Merrill and Longenecker 1973, Chastagner and Byther 1983, Scharpf 1993). However, Hansen et al. (2000) concluded that disease severity, measured as the density of Swiss needle cast reproductive structures emerging from the stomates (pseudothecia) was greater and foliage retention was lower in the upper crown for the first three cohorts of foliage at seven Douglas-fir plantations near Tillamook, Oregon. These coastal Oregon forests have unique environmental conditions where summer precipitation and fog cause similar leaf wetness throughout the entire crown during the Swiss needle cast spore dispersal period from late May through August.

Manter et al. (2003) also studied vertical patterns of Swiss needle cast in Douglas-fir crowns in coastal Oregon. They sampled one branch each from the north-top, north-bottom, south-top, and south-bottom quadrants of the crown of three infected trees at each of five Swiss needle cast impacted sites near the coast. The highest pseudothecia density (disease severity) and greatest relative foliage loss were found on the south-top, followed by north-top quadrant. Manter et al. (2003) also compared trees from north and south aspects across three sample sites representing the gradient from the western coast to the eastern drier Willamette Valley margin. They found higher levels of infection and symptom severity on trees growing on south slopes in the western Coast Range. Weiskittel et al. (2006) investigated the influence of Swiss needle cast on foliage mass, foliage age-class structure, and vertical foliage distribution at twenty-one Douglas-fir plantations (10- to 60-year-old) across a gradient of disease severity within the Swiss needle cast epidemic area. Reduction in the total mass of foliage in each age class was associated with increasing Swiss needle cast severity. As would be expected, this resulted in an increased relative mass in the younger age classes. The older age classes (4- to 5-year-old) were skewed to the lower crown, while younger age classes (1- to 3-year-old) were proportionally more abundant in the upper crown.

Methods for estimating foliage retention vary among studies. Hansen et al. (2000) and Manter et al. (2003) used a disease assessment technique where they focused on the first three years of cohorts because impacts to these cohorts reflect disease impacts to the host. They estimated the percent of retained foliage in each cohort and found that an average of 87% of the foliage was retained in all three cohorts. Schoettle (1990) used leaf longevity, defined as the age of the oldest leaves that are firmly attached to the stem of a shoot. A leaf longevity of 10 years indicates presence of leaves in 11 annual cohorts, including the current year. Reich et al. (1996) also assessed needle longevity or retention by counting annual needle cohorts. However, a cohort was only counted if > 50% of the needles in a cohort were retained. With this technique, leaf longevity represents an average needle life span. In addition, Reich et al. (1996) recognized difference in vertical patterns and averaged needle longevity from the upper and lower crown. In contrast, Xiao (2003) defined leaf longevity as the time in years that current-year foliage of individual trees is expected to live given the observed mortality rate using a life table approach.

An understanding of foliage retention patterns is important to management of the disease. For example, thinning (density reduction) and vegetation control are suggested as management options to reduce foliage disease in conifer plantations. However, research in the Swiss needle cast epidemic area has so far shown thinning and vegetation management does not aid in control of the disease (Crane 2002, Mainwaring et al. 2005). Similar insights have been gained in studies of Swiss needle cast in New Zealand (Hood and Sandberg 1979). However, the lack of response to thinning may only be the case in the high severity area and it should still be suggested for low severity sites (higher foliage retention) if relative impacts of disease are greater in the lower crown than the upper.

The objective of our research was to examine whether the vertical pattern of foliage retention in Douglas-fir within the Swiss needle cast epidemic area on the western slope of the Oregon Coast Range varies across an environmental gradient of increasing elevation and decreasing temperature and productivity as one moves inland. We hypothesized that the change in foliage retention across environmental gradients would be greater in the upper crown than in the lower crown due to lessening of disease severity as one moves out of the coastal fog zone.

Methods

Study Sites and Data Collection

We used an existing plot system of Douglas-fir plantations in the northwest Coast Range of Oregon. This plot system was originally designed to assess tree growth impacts resulting from *P. gaeumannii* infection (Maguire et al. 2002). These plots were measured annually from 1998-2003 and have become a foundation for monitoring Swiss needle cast (Shaw et al. 2011). A single permanent 0.02 ha plot was randomly established within each of 76 Douglas-fir plantations between 10 and 30 years of age, located north of Newport (N44°35', W124°00'), south of Astoria (N46°10', 123°50'), and within 31 km of the coast and on sites ranging in elevation from 45 m to 518 m (Figure 1). These plantations were randomly selected from a large database that included all major landowners with Douglas-fir plantations within the given geographic and age constraints. Height, height to live crown base, and foliage retention was measured for 10 tallest trees per plot (dominant or co-dominant trees), and tree diameter at breast height (DBH) was measured for all trees, annually from 1998-2003 (Table 1). Estimates of foliage retention were obtained in the year 2000. Results are reported for a total of

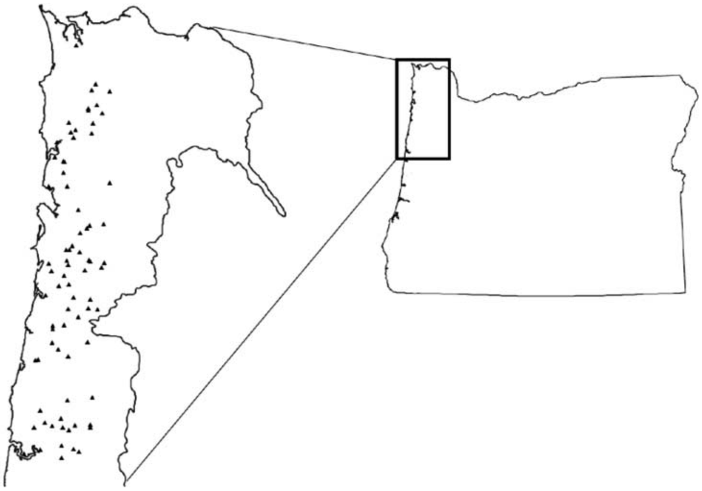

Figure 1. Map showing Growth Impact Study field sites (triangles) on which foliage retention was measured. Plots are located in the northern half of the Oregon coastal ecoregion between Newport and Astoria.

TABLE 1. Mean and range of stand attributes for 76 permanent growth impact study plots in the northern Oregon coast range mountains.

Stand Attribute	Mean	Range
DBH (cm)	25.9	11.8 – 40.0*
Douglas-fir Density (trees/ha)	688	148 – 1,927
Douglas-fir Basal Area (m^2/ha)	15.77	2.03 – 37.24
Total Basal Area (m^2/ha)	19.25	2.84 – 54.97
Site Index (Height at 50 yr, m)	41.0	24.4 – 52.1
Average Foliage retention (yr)	2.26	1.12 – 3.4*
Elevation (m)	230	45 – 518
Aspect (°)	180.8	0 – 356
Distance from Coast (km)	9.5	0.6 – 19.8

* +/- 2 standard deviations

72 stands and 676 trees. Two sites were excluded from the analysis because their elevations were well above the range of the remaining sites and were located on the east side of the Coast Range crest, beyond the scope of our study. Two sites were lost to disturbance.

The purpose of obtaining foliage retention estimates was to determine the amount of foliage present and its impact on tree growth (Maguire et al. 2011). Therefore, our estimate of foliage retention was not foliage longevity. The foliage retention estimate was made by observing the amount of foliage present and estimating the number of cohorts where a full complement would fit. For example, if year 1 and year 2 had full cohorts, year 3 had 0.8 cohort and year 4 had 0.5 cohort then foliage retention = 3.3. Foliage retention was determined in spring (April) prior to current year budbreak (early May). The live crown was divided into thirds (lower, middle, upper) with the base of the live crown defined as the lowest live branch. A single secondary, or lateral branch, off a primary branch in the center of each crown third was examined. A two person crew (rarely a third person substituting) did the needle retention estimates to maintain consistency.

Data Analysis

The relationship of foliage retention to environmental measurements (distance from coast, elevation, aspect) was modeled using a two-level hierarchical linear model (Bryk and Raudenbush 1992; Singer 1998) with both tree- and stand-level predictors. This method accounts for multi-level variation due to measurement of explanatory variables at different scales than the response variable. The tree level model assumed the relationship of foliage retention to DBH within a stand did not differ among crown positions within a tree, but allowed the mean foliage retention to change as a function of position within the tree canopy. Although DBH in general is known to impact foliage retention, the general variation in DBH among trees in our study was not great (Figure 2) and it is difficult to interpret the degree to which DBH actually

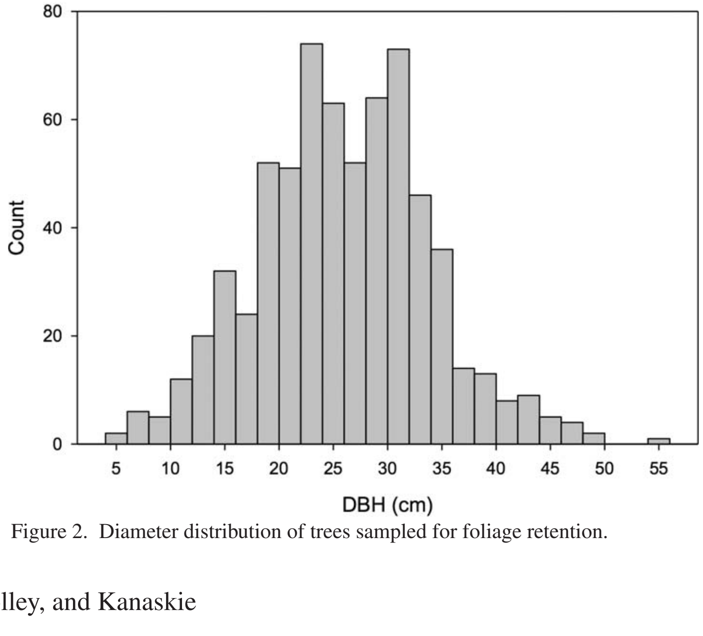

Figure 2. Diameter distribution of trees sampled for foliage retention.

influences foliage retention. Therefore we held the effect constant in our models. The model translates to a constant slope model with different intercepts for each crown position and can be written as:

$$Y_{ijk} = \beta_{0i} + \beta_{1i} I_{b,ijk} + \beta_{2i} I_{m,ijk} + \beta_3 DBH_{ijk} + \varepsilon_{ijk}$$

where Y_{ijk} is the mean foliage retention of the i^{th} position in the j^{th} tree in the k^{th} stand, and I_b is an indicator of whether the measurement was made in the bottom position and I_m is an indicator of whether the measurement was made in the middle position. By convention, the intercept, β_0 represents the mean foliage retention of the top position. In this model, each tree was repeatedly measured (at 3 positions) and residuals were assumed to be multivariate normal with an unstructured 3 by 3 variance-covariance matrix. Tree level covariates included DBH and canopy position.

The second level model represented the hypothesis that the mean foliage retention of each position was dependent on stand level variables. The second level model was

$$\begin{aligned} \beta_{0i} &= \gamma_{00} + \gamma_{01} X_i + \lambda_{0i} \\ \beta_{1i} &= \gamma_{10} + \gamma_{11} X_i + \lambda_{1i} \\ \beta_{2i} &= \gamma_{20} + \gamma_{21} X_i + \lambda_{2i} \\ \beta_{3i} &= \gamma_{30} + \gamma_{31} X_i + \lambda_{3i} \end{aligned} \quad \begin{bmatrix} \lambda_{0i} \\ \lambda_{1i} \\ \lambda_{2i} \\ \lambda_{3i} \end{bmatrix} \sim MVN \left[\begin{matrix} 0 \\ 0 \\ 0 \\ 0 \end{matrix}, \begin{bmatrix} \tau_{00}^2 & \tau_{01} & \tau_{02} & \tau_{03} \\ \tau_{01} & \tau_{11}^2 & \tau_{12} & \tau_{13} \\ \tau_{02} & \tau_{12} & \tau_{22}^2 & \tau_{23} \\ \tau_{03} & \tau_{13} & \tau_{23} & \tau_{33}^2 \end{bmatrix} \right]$$

where X_i represents a stand level variable or variables, and residuals are multivariate normal with mean 0 and in a 4 by 4 unstructured variance-covariance matrix. Stand level covariates were elevation, aspect, and distance from coastline. Aspect was measured as an azimuth (0-360°) and transformed for analysis using a cosine transformation (cosine[(aspect/360)*2π]) resulting in continuous values between 1 (0° or 360°) and -1 (180), thus removing the disjunction between 0° and 360°. Values of DBH, elevation, and distance from coast were centered to either the mean values within a stand (DBH), or the mean values across all stands (distance and elevation). This approach provides more interpretable model coefficients (Singer 1998).

Explanatory variables at the tree (canopy position and DBH) and stand (elevation, distance from coast, and cos_aspect) levels were used to develop 18 *a priori* candidate models (Table 2). Models included combinations and interactions of explanatory variables at both the tree and stand level, based on *a priori* hypotheses These models were then compared using Akaike's Information Criterion (AIC) to select the best model (Burnham and Anderson 2002). Models were ranked by the change in AIC (Δ_i). and Akaike's weight (W_i, the weight of evidence in favor of a model being the best model within the entire set being tested given the data [Burnham and Anderson 2002]). Estimated proportional reduction in variance of ($\tau_{00}^2, \tau_{11}^2, \tau_{22}^2, \tau_{33}^2$) after inclusion of tree level and/or stand level explanatory variables provided evidence of the importance of these variables in explaining variance in foliage retention.

All regression analyses were performed using the MIXED procedure with maximum likelihood estimation methods in SAS v9.2 (SAS Institute Cary, NY). The CORR procedure was also used prior to model selection to determine correlation between explanatory variables. Variables with significant correlations were not included in the same model. Because stand age and tree diameter were moderately correlated ($r = 0.57$), stand age was not used as a stand level variable in model selection.

Results

The highest ranked models of foliage retention included canopy position (lower, middle, upper), tree diameter, and distance from coast (Table 3). Foliage retention averaged 1.603 (0.038) for the upper crown, 2.37 (0.051) for the mid crown, and 2.85 (0.068) for the lower crown. The lowest foliage retention occurred in the upper third of the canopy and the highest occurred in the lower third of the canopy (Figure 3, 4). Variation in foliage retention was lowest in the upper canopy and highest in the lower canopy (Table 4). One hundred percent of cumulative weight (W_{aic}) was given to the top 10 ranked models, which all included canopy position, DBH, and distance from coast.

We chose the top-ranked model to indicate the most relevant variables explaining foliage retention due to its relative simplicity and because the interaction between canopy position and distance from coast is biologically meaningful in relation

TABLE 2. Rankings based on AIC values and explanatory variables for the 18 a priori candidate modelsand the NULL model.

Rank	Variables	AIC	Δ_{aic}	W_{aic}
1	CP, DBH, DIST, CP*DIST	2835.2	0.0	0.23
2	CP, DBH, DIST	2835.8	0.528	0.18
3	CP, DBH, DIST, ELEV	2836.4	1.156	0.13
4	CP, DBH, DIST, ASP	2836.9	1.631	0.10
5	CP, DBH, DIST, ASP, DIST*ASP	2837.0	1.807	0.09
6	CP, DBH, DIST, ELEV, DIST*ASP	2837.4	2.148	0.08
7	CP, DBH, DIST, ELEV, ASP	2837.5	2.220	0.08
8	CP, DBH, DIST, ELEV, DIST*ELEV	2838.4	3.203	0.05
9	CP, DBH, ASP DIST, ELEV, ELEV*ASP	2839.3	4.035	0.03
10	CP, DBH, ASP DIST, ELEV, DIST*ELEV	2839.5	4.265	0.03
11	CP, DBH, ELEV	2848.2	12.917	0.00
12	CP, DBH, ELEV, ASP	2849.3	14.106	0.00
13	CP, DBH, ASP, ELEV*ASP	2851.4	16.152	0.00
14	CP, DBH, ELEV, CP*ELEV	2851.5	16.302	0.00
15	CP, DBH^	2852.1	16.842	0.00
16	CP, DBH, ASP	2853.4	18.180	0.00
17	CP, DBH, ASP, DBH*ASP	2855.0	19.780	0.00
18	CP, DBH, ASP, CP*ASP	2857.3	22.027	0.00
19	NULL	3022.2	187.0	0.00

^Tree level variables only

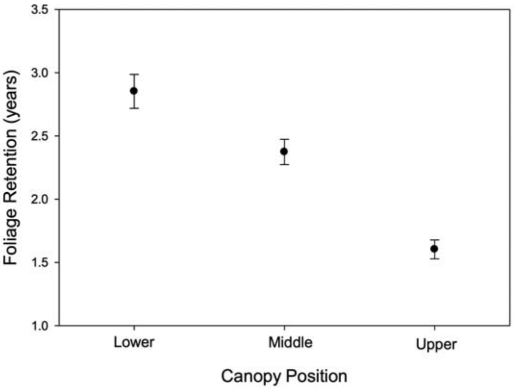

Figure 3. Mean foliage retention estimates in three canopy positions for trees of average DBH in the Swiss needle cast infected area of the western Oregon coast range. Error bars indicate 95% confidence intervals.

to our original hypotheses (Table 2). All *a priori* models with distance as an explanatory variable were included in this top 10. Delta AIC values (Δ_{aic}) showed that there was little difference among the top eight models. The second-ranked and simplest model included only canopy position, DBH, and distance from coast. The model including elevation in addition to canopy position, DBH, and distance from coast, was ranked third among the pool of possible models.

At the stand level, distance from coast was the most important of the stand variables ($F_{1,66.1}$ = 26.06, $p<0.001$), but there is some evidence that its effect differs with position in the canopy ($F_{2,70.1}$ = 2.33, p = 0.105; Figure 3).When considering trees of average DBH, foliage retention in the lower canopy was found to increase by 0.40 years (95% CI: 0.21-0.58 years) every 10 km increase in the distance from the coast. In the mid-canopy, foliage retention was found to increase by 0.33 years (95% CI: 0.19-0.46 years) for every 10 km increase in distance from the coast, and in the upper canopy, foliage retention was found to increase by 0.25 years (95% CI: 0.14-0.35 years) for every 10 km increase in distance from the coast. Foliage retention does increase at a greater rate in the upper crown than in the lower crown, but this difference does not appear meaningful across the study area.

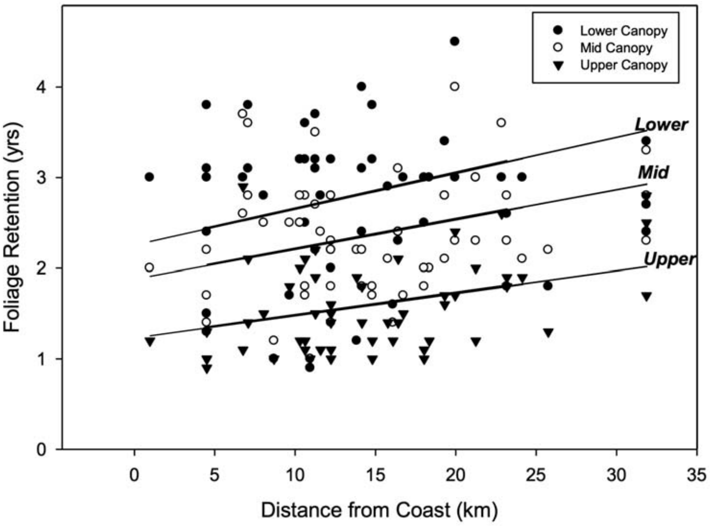

Figure 4. Foliage retention for lower, middle, and upper canopy positions illustrating the relationship of foliage retention and distance from the coastline for trees of average DBH.

In individual tree canopies (i.e., tree level factors) in 10-30 year-old Douglas-fir stands on the Oregon coast range, DBH was a significant factor explaining foliage retention patterns ($F_{1,39.5} = 9.71$, $p = 0.003$) (Table 3). Holding the other model variables constant, foliage retention increases by 0.1 years (95% CI: 0.04-0.17) for every 10 cm increase in DBH. In addition to DBH, foliage retention varies by canopy position (lower, middle, and upper positions).

Discussion

The vertical pattern of foliage retention was generally consistent throughout the study area with lowest retention in the upper crown and highest retention in the lower crown. Foliage retention in all crown positions increased with distance from the coast (Figure 4). Contrary to our hypothesis, we could detect little difference in the rate of increase in foliage retention with distance to the coast among the three crown positions. The top 10 models (all within ~4 AIC units of each other; Table 3), were similar to one another, all of them involving crown position, DBH and distance from coast, but differing either by inclusion of an additional stand level variable or by allowing the effect of distance

TABLE 3. Rankings based on AIC values for the top three hierarchical models and both the level 1 model (no stand level covariates) and the NULL model (intercept only). ***T*** = estimated variance among trees in FR in each crown position. Proportional variance reduction = $(T_1 - T_2)/T_1$.

Rank	Variables	AIC	Δ_{aic}	W_{aic}	***T***(Crown Position)	Proportional variance reduction relative to NULL	Proportional variance reduction relative to Level 1
1	CP, DBH, DIST, CP*DIST	2835.2	0.0	0.27 (Upper) 0.23 0.07 (Lower)	0.89 0.14 (Mid) 0.50	0.23 0.87 0.36	0.26
2	CP, DBH, DIST	2835.8	0.528	0.28 (Upper) 0.18 0.07 (Lower)	0.88 0.14 (Mid) 0.50	0.20 0.87 0.36	0.26
3	CP, DBH, DIST, ELEV	2836.4	1.156	0.28 (Upper) 0.13 0.07 (Lower)	0.88 0.14 (Mid) 0.50	0.20 0.87 0.36	NA
15	CP, DBH (Level 1)	2852.1	16.8	0.35 (Upper) 0.00 0.11 (Lower)	0.82 0.19 (Mid) 0.21	0.87	NA
19	NULL	3022.2	187.0	2.35 (Upper) 0.00 0.14 (Lower)	1.07 (Mid)	NA	NA

TABLE 4. Model coefficients for the top ranked model (SE in parentheses). The model is in the form of: FR= β_0 + β_1*DBH + β_2*Distance for each position. DBH is measured in cm and distance in kilometers.

Canopy Position	β_0 (Intercept)	β_1 (DBH)	β_2 (Distance)
Lower	2.852 (0.068)	0.011 (0.003)	0.040 (0.009)
Middle	2.373 (0.051)	0.011 (0.003)	0.033 (0.007)
Upper	1.603 (0.038)	0.011 (0.003)	0.025 (0.005)

to differ among crown positions. There was no clear evidence that any one of these models was the best, implying that none of the factors besides the crown position, DBH, and distance from coast appear to be important in explaining much of the variation in vertical foliage retention patterns.

Distance from the coast was clearly more closely related to foliage retention in our analysis than was elevation (Table 3). This is consistent with our understanding of disease distribution and severity relative to winter temperature and coastal fog and rain during spring and summer (Hansen et al. 2000, Rosso and Hansen 2003, Manter et al. 2005) while needle retention and longevity are related to climatic factors also (Zhao et al. 2011, 2012). In our study area, elevation increases with distance from the coast, and is slightly correlated (r =0.36) with foliage retention patterns.

Separating out the interaction among elevation, distance from coast, and other environmental factors that influence foliage retention is very difficult. Zhao et al. (2011, 2012) did not include distance from coast and elevation in their models purposely to determine the influence of climate. Perakis et al. (2005) documented a strong soil and foliar nitrogen decline from the coastline moving inland, and lower nitrogen levels have been correlated with higher foliage retention (Brix 1983, Reich et al. 1995, Balster and Marshall 2000). The high nitrogen levels near the coast combined with mild winter temperature, longer growing season, greater summer precipitation and fog all interact to reduce foliage retention. Tree size is also known to influence relative vertical foliage distribution in Douglas-fir (Maguire and Bennett 1996) as well as overall foliage retention (Xiao 2003).

We held DBH constant in our model due to the fairly narrow distribution of DBH and tree age in our sample (Figure 2). Given that tree diameter is closely related to tree height, the relationship of foliage retention and tree diameter may be reflecting changes in tree height and subsequent changes in canopy architecture and microclimate as stand structure changes through stand development. Findings from Weiskittel et al. (2006) also support this conclusion; crown size and tree social position were both factors influencing patterns of foliage retention. We accounted for tree social position by only choosing dominant or co-dominant trees.

Foliage retention and/or leaf longevity in conifers is known to increase with increasing elevation and decreasing site productivity (Reich et al. 1992, 1996). Our results support this paradigm, although we did not explicitly account for site productivity. Tree height is often used to predict site productivity and Swiss needle cast has been shown to influence tree height, making site productivity difficult to measure. However, site productivity is generally thought to decrease with distance from coast and increasing elevation in the Oregon Coast Range (Perakis et al. 2005).

Merrill and Longenecker (1973), Chastagner and Byther (1983) and Scharpf (1993) all note that Swiss needle cast symptoms were most severe in the lower crown. We hypothesized that at high elevations far from the coast, where foliage retention in Douglas-fir is highest, the largest reduction in foliage retention would occur in the lower crown. This would be manifested as a smaller difference in foliage retention between upper and lower crowns at high elevations than at low elevations. This was not the case in our study area on the western slopes of the Coast Range of northwest Oregon, where we found no evidence of this effect but some slight evidence of an opposite effect with distance (Figure 3). In our Swiss needle cast study area, the difference in foliage retention between the upper and lower crowns was greater farther from the coast than near the coast.

Our approach to estimating foliage retention differed from those more interested in foliage longevity (Ewers and Schmid 1981, Schoettle 1990, Reich et al. 1995, and Reich et al. 1996) and disease biology (Hansen et al. 2000, Manter et al. 2003). However, we feel our approach is practical for estimates of foliage retention and may not be extremely different from estimates of foliage longevity. Our technique has been used to quantify foliage retention with respect to impact on tree growth (Maguire et al. 2011) and foliage retention is the basis for estimating growth deviations from normal using models such as ORGANON (Garber et al. 2007).

Our results show that on the west slope of the Oregon Coast Range the vertical pattern of foliage retention is similar across environmental gradients and it does not appear to fit the usual paradigm applied to trees influenced by foliage disease in general, or Swiss needle cast infestations in other regions. Typical foliage disease plantation treatments, such as thinning to dry out the stand and improve airflow, do not reduce Swiss needle cast severity (Mainwaring et al. 2005). Swiss needle cast management in the Oregon Coast Range therefore involves an integrated pest management strategy that incorporates both qualitative models using disease severity estimates based on foliage retention, quantitative tools to measure growth impacts, adaptive silviculture, economic models, and alternative species where appropriate (Shaw et al. 2011, Mulvey et al. 2013).

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