

Climate of seed source affects susceptibility of coastal Douglas-fir to foliage diseases

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Abstract. Seed-source movement trials using common garden experiments are needed to understand climate, tree (host), and pathogen interactions. Douglas-fir (*Pseudotsuga menziesii* var *menziesii*) is an important tree species native to western North America influenced by the foliar fungi *Phaeocryptopus gaeumannii*, a biotroph and causal agent of Swiss needle cast (SNC), and *Rhabdocline* species, necrotrophs that cause *Rhabdocline* needle cast. We used the Douglas-fir Seed-Source Movement Trial, a large provenance study of Douglas-fir that consists of populations and test sites chosen to represent the range of climate conditions experienced by Douglas-fir west of the Cascade and northern Sierra Nevada Mountains, USA, to assess disease severity and symptom expression in Douglas-fir in relation to climatic differences between test sites and population sources. Using generalized linear mixed models, probability of disease severity/expression was modeled with respect to the climate variables May through September precipitation (MSP), mean winter temperature (MWT), and continentality. Stark differences in disease expression were observed in trees from different regions, especially in relation to resistance to *Rhabdocline* spp. and tolerance to *P. gaeumannii*. There were no major differences across seed-source regions at any particular site in infection levels of *P. gaeumannii* assessed by fruiting body abundance, yet disease tolerance followed similar geographic patterns as resistance to *Rhabdocline* spp. Transfers of populations from low to high MSP, and/or cool to warm MWT, increased the probability of moderate to severe *Rhabdocline* spp. infection and SNC disease symptoms. Our results suggest that local seed sources are adapted to local climate and pathogen pressures and that seed sources from regions with high foliage disease pressure are most resistant/tolerant to those foliage diseases. We also confirm that temperature and precipitation are important epidemiological factors in forest disease and that assisted migration must take into account trophic interactions of trees. Movement of seed sources from dry spring and summer and/or cool winter conditions to mild, mesic environments is likely to lead to increased probability of losses due to these foliage diseases.

Key words: adaptation; assisted migration; climate change; climate transfer distance; coastal Douglas-fir; *Rhabdocline* needle cast; seed-source movement trials; Swiss needle cast.

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INTRODUCTION

Forest and tree health have emerged as major forest conservation and management concerns due to changing climates and human-driven resource extraction needs (Trumbore and Brando 2015). How trees are adapted to climate and their interactions/coevolution with pests and pathogens under certain climate regimes is a potential challenge to forest health management. Assisted migration is now being widely considered as a management option to maintain tree health in a changing climate (St. Clair and Howe 2007, Ste-Marie et al. 2011), and trophic interactions of forest tree pathogens and insects must be included in models and planning efforts. Climate envelope models, for example, rarely include pathogen and insect pest interactions in recommendations for assisted migration movements even though climate is a driver of host pathogen/insect interactions (Hill and Thomson 2015). Seed-source movement studies using common garden trials are needed for major trees species where assisted migration is proposed so that pest/host interactions can be evaluated under different climate scenarios. Foliage diseases are particularly responsive to both climate and host genetics (Woods et al. 2005) and therefore lend themselves well to evaluation in seed-source movement studies.

Phaeocryptopus gaeumannii ((T. Rohde) Petrak), causal agent of Swiss needle cast (SNC), and *Rhabdocline* spp., causal agents of Rhabdocline needle cast (Rhabdocline), are foliar pathogens responsible for major growth reductions and economic loss in Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) forests in the Pacific Northwest of the United States (Parker and Reid 1969, Kurkela 1981, Stone 1997, Maguire et al. 2002, Shaw et al. 2011). Swiss needle cast, in particular, has intensified in coastal Oregon over the past 20 yr (Ritokova et al. 2016), likely due to a complex interaction of management actions, changes in climate (Black et al. 2010), and specific site conditions (Shaw et al. 2011). While off-site planting of Douglas-fir is thought to increase impacts of SNC (Hood 1982), disease symptoms have intensified in plantations comprising local seed sources, causing significant alarm (Kastner et al. 2001, Jayawickrama et al. 2012, Ritokova et al. 2016). Rhabdocline has been considered exclusively an

issue of off-site plantings, with adherence to seed zones largely solving the Rhabdocline problem in Douglas-fir plantations (Stone 1997). However, predicted and observed changes in climate have led to an increased interest in revising Douglas-fir seed transfer guidelines (St. Clair and Howe 2007, Abatzoglou et al. 2014). How changes in climate and changes to seed transfer guidelines might influence the incidence and impacts of Rhabdocline and SNC across the range of west-side Douglas-fir has not been explored.

Climate change and seed transfer have the potential to alter the relationship between host, pathogen, and climate conditions (Agrios 2005). Climate is an important determinant of pathogen pressure experienced by host populations and is one of the key limiting factors to outbreaks of foliage diseases in particular (Agrios 2005). Under conditions within the natural range of variation, it is believed that native pathogens and their hosts coevolve to reach a pathological balance in which both are able to maintain reproductive capacity and severe epidemics are largely absent (Bingham et al. 1971). Exposing populations to major changes in climate, whether through climate change or through seed transfer, can alter this relationship resulting in exposure of populations or species to increased disease pressure that may overcome evolved host defenses, likely resulting in large economic and ecological losses (Bingham et al. 1971, Kastner et al. 2001). Understanding the influence of climate on susceptibility to these diseases is necessary to better predict the impacts of climate change on west-side Douglas-fir and to better refine seed transfer recommendations.

The epidemiology of foliage micro-fungi is governed by climate at the time of spore dispersal, or by the ability of the fungi to respond to optimal climate conditions by producing spores (Agrios 2005). In many fungi, asexual reproduction allows them to sporulate whenever conditions are suitable. *Phaeocryptopus gaeumannii* and most *Rhabdocline* species are restricted to sexual reproduction, fruiting once a year with conditions during sporulation (May–August) largely dictating the level of disease severity (Brandt 1960, Chastagner and Byther 1983). Both *P. gaeumannii* and *Rhabdocline* spp. require leaf wetness and humidity in late spring/early summer, soon after budburst and elongation of new growth, for

successful dispersal, germination, and infection (Parker 1970, Capitano 1999, Stone et al. 2008a). Thus, greater spring and summer precipitation facilitates high disease pressure (Hansen et al. 2000, Rosso and Hansen 2003, Manter et al. 2005, Shaw et al. 2011). Warmer winter temperatures, which may promote development of the fungi during the winter, have also been associated with high disease pressure (Stone et al. 2007, Black et al. 2010). In contrast, seasonal temperature extremes, such as those experienced in continental climates, as well as dry conditions in the spring and early summer, negatively affect the ability of *P. gaeumannii* and *Rhabdocline* spp. to infect and colonize host tissue at a rate sufficient to cause severe disease (Capitano 1999, Zhao et al. 2011).

Winter temperatures and spring/summer precipitation have increased in the Pacific Northwest during the last century (Mote 2003, Abatzoglou et al. 2014, Mildrexler et al. 2016). Spring precipitation (March through May) has increased at a rate of 2–5% per decade from 1901 to 2012, with average spring precipitation from 2009 to 2012 30% above twentieth-century normals (30-yr averages). Annual mean temperature in the Pacific Northwest has increased by approximately 0.6–0.8°C from 1901 to 2012, with the majority of the observed warming occurring in the winter (Mote 2003, Abatzoglou et al. 2014). The observed increases in spring precipitation coupled with increasing temperatures have created increasingly conducive conditions for *Rhabdocline* and SNC in the Pacific Northwest (Stone et al. 2008b, Black et al. 2010). The observed changes in these conditions coincide with the increase in the geographic range and severity of the current SNC epidemic, affecting Douglas-fir plantations regardless of seed source in the most heavily infected areas (Ritokova et al. 2016).

Projected increases in temperature are predicted to expose coastal Douglas-fir populations to hotter and drier conditions, possibly resulting in populations with drought hardiness that is sub-optimal to their current geographic seed zone by the end of the century (St. Clair and Howe 2007). Assisted migration has been proposed to facilitate the rapid rate of migration needed to maintain adaptation of Douglas-fir populations in the face of the current rates of

climate change (St. Clair and Howe 2007, Rehfeldt et al. 2014, Coops et al. 2016). Many proponents of assisted migration have recommended the movement of seed from south to north and from low to high elevation in order to match climate projections (Rehfeldt et al. 2001, 2014, St. Clair and Howe 2007, Aitken et al. 2008, Coops et al. 2016). These transfers may, under current climate conditions, result in the movement of seed from dry to wet climates and/or from cool to warm climates, likely exposing these seed sources to levels of pathogen pressure that is higher than that experienced in their natural seed zones. How these transfers will be influenced by foliage diseases has not been investigated.

Differences among Douglas-fir populations have been observed for both resistance and tolerance to *Rhabdocline* and SNC (Hood 1982, Hoff 1987, McDermott and Robinson 1989, Chastagner 2001, Johnson 2002). Resistance is defined as the ability of an organism to exclude or overcome the effects of a pathogen, whereas tolerance is defined as the ability of an organism to sustain the effects of a pathogen without dying or suffering serious losses in productivity (Agrios 2005). In addition, susceptibility refers to the likelihood of displaying disease symptoms whether due to a lack of tolerance or resistance (Agrios 2005). Population differences in susceptibility to these foliage diseases are influenced by climate conditions at the seed source location, with tolerant or resistant populations generally evolving under conditions conducive to foliar pathogens and, thus, higher disease pressure conducive to natural selection for resistance and/or tolerance (Hood 1982, Hoff 1987, McDermott and Robinson 1989).

Studies have identified inland Douglas-fir populations that are resistant to *Rhabdocline* spp. (Catal et al. 2010), and lack of disease in coastal Douglas-fir has suggested resistance. However, little is known about variation in resistance across the geographic range of coastal Douglas-fir. Whether susceptibility to *P. gaeumannii* is driven by tolerance or resistance has proven to be more nuanced. Hood (1982) suggested resistance to infection, as populations displayed differing levels of infection. In contrast, studies by Temel et al. (2004) and Kastner (2001) observed a lack of resistance as all populations displayed similar levels of infection, indicating tolerance to infection rather

than resistance. The fundamental difference between the two pathogens is that *P. gaeumannii* is a biotroph that enters its host passively through the stomata (Manter et al. 2005, Stone et al. 2008a). This passive mode of entry does not seem to elicit a host response. *Phaeocryptopus gaeumannii* functions largely as an endophyte within its host and does not cause visible symptoms in the foliage until reproductive structures (pseudothecia) plug the stomata causing carbon starvation (Manter et al. 2005, Stone et al. 2008a). While some *Rhabdocline* species may also be endophytic (Sherwood-Pike et al. 1986), the pathogenic species are necrotrophic, feeding on and killing host cells, causing symptoms to develop within months (Brandt 1960). *Rhabdocline* spp. enter host tissue directly through the cuticle and cell death is noticeable shortly after infection (Brandt 1960). These key differences in infection method and life strategy may be influential in determining host defense strategies, specifically whether or not a host is tolerant or resistant to these foliar pathogens.

Progress has been made in tree improvement programs for the selection of SNC-tolerant populations in coastal Douglas-fir, contributing to significant gains in growth over unimproved stock in SNC-affected areas (Jayawickrama et al. 2012). These studies are restricted in terms of the populations and geographic range of test sites, yet demonstrate the potential to select tolerant individuals within local breeding programs to offset losses due to SNC. No definitive studies have been conducted on resistance of coastal Douglas-fir to *Rhabdocline* spp. on the west side of the Cascade Mountains and northern Sierra Nevada.

Reciprocal transplant provenance studies examine variation in adaptive traits and are critical to the study of pathogen epidemiology (Kawecki and Ebert 2004, Enderle et al. 2013, Bansal et al. 2015a) because they enable the use of climate transfer distance. Climate transfer distance is the difference in climate between the seed source and where the plant is grown (Rehfeldt et al. 1999, 2003, Bansal et al. 2015b). Climate transfer distances are effective in the identification of genetic variation in relation to climate and, therefore, can provide insight into climate transfers which are most influential on the productivity and health of different populations of trees (Gould et al. 2012, Bansal et al. 2015b, Ford et al. 2016).

Our study used the Douglas-fir Seed-Source Movement Trial (SSMT) to evaluate population variation in susceptibility to foliar pathogens of coastal Douglas-fir. The SSMT is a large common garden, reciprocal transplant provenance study of coastal Douglas-fir including populations from northwestern California through western Oregon and southwestern Washington State, USA (Ford et al. 2016). The SSMT provides an ideal platform from which to study population variation in susceptibility to foliage diseases and the consequences of moving populations between different growing conditions. We assessed the relationship between resistance/tolerance to *Rhabdocline* and SNC in Douglas-fir using the climate transfer distance between the population source and the test site. We hypothesized that:

1. There are differences in the levels of resistance/tolerance to *Rhabdocline* spp. and *P. gaeumannii* among populations planted at these test sites.
2. Consistent with our knowledge of plant pathosystems, host populations that evolve under high levels of inoculum from disease agents will be less susceptible to disease than those that do not.
3. Differences in the levels of resistance/tolerance are a function of differences in climate between the population source climate and the climate of the test site.
 - a. Movement of seed sources from climates which are not conducive to these pathogens such as from drier to wetter regions, or cooler to warmer regions, will result in increased disease symptoms and severity.
 - b. Climate variables that are influential to the epidemiology of *P. gaeumannii* and *Rhabdocline* spp., specifically May through September precipitation (MSP), mean winter temperature (MWT), and continentality index (TD), are influential to the susceptibility of populations to SNC and *Rhabdocline*.
4. Locally adapted populations, those from source climates most similar to that of the test site, are the least susceptible to *Rhabdocline* and SNC.

METHODS

Test sites and experimental design

Resistance and tolerance to SNC and Rhabdoclone were evaluated in a reciprocal transplant study (SSMT) in which 60 Douglas-fir populations from 12 geographic regions in northern California, western Oregon, and southwestern Washington were tested at nine planting sites in each region of Oregon and Washington (Fig. 1; Ford et al. 2016).

Each region was represented by five populations, and each population was represented by open-pollinated seed collected from two naturally regenerated parent trees within a stand. Parent trees were located at least 100 m from each other at a similar elevation and aspect in order to reduce the probability of relatedness but still represent the same climate. Populations and test sites were chosen to represent the range of climate conditions experienced by Douglas-fir in the study area

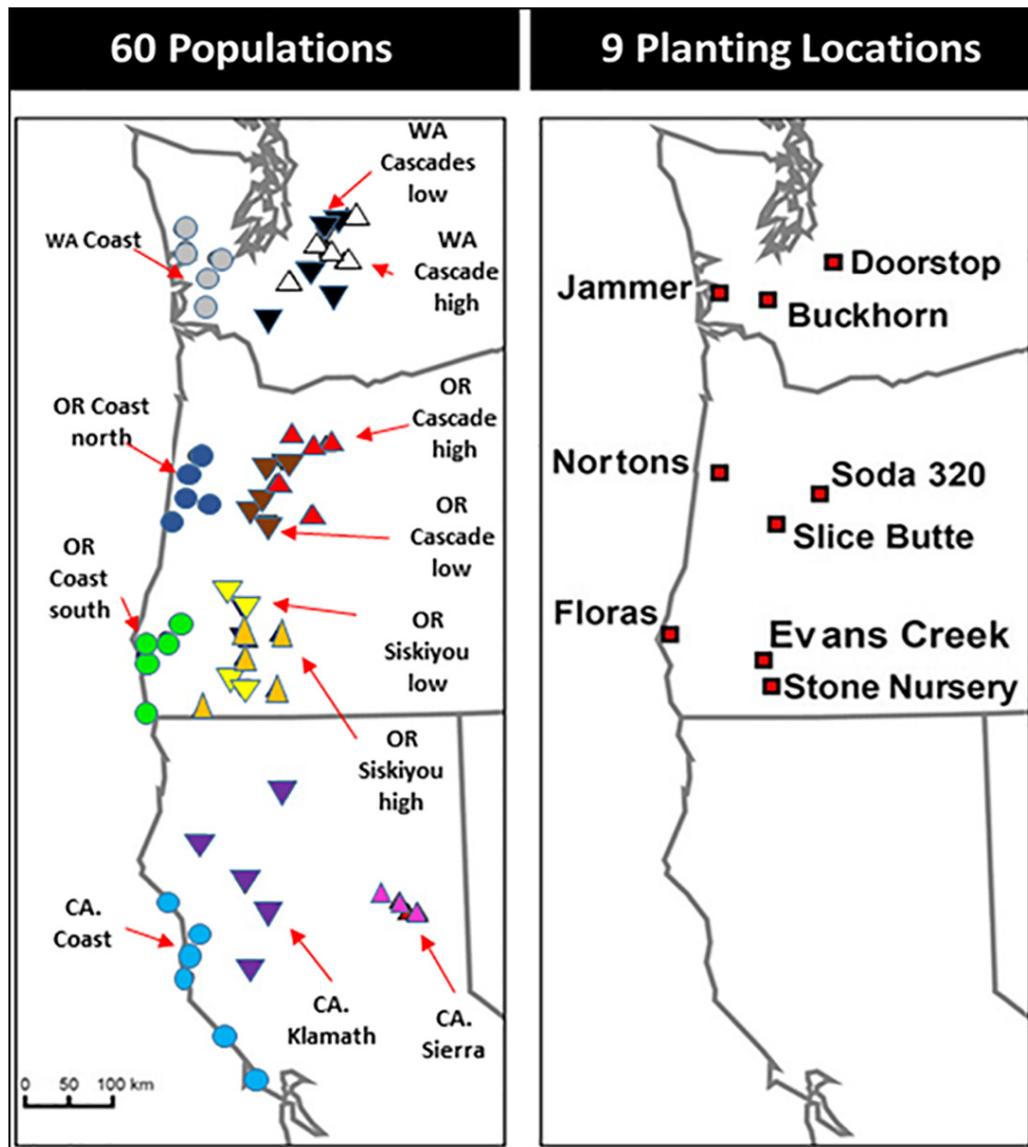


Fig. 1. Locations of seed sources (left) and test sites (right) of the Douglas-fir Seed-Source Movement Trial.

(Fig. 1). The study area includes large climate gradients resulting from topography, latitude, and distance from the ocean.

Each test site included four blocks to control for topographic variation within a site. Within each site, each block included 12 plots with one region randomly assigned to each plot. Within each plot, two seedlings from each of the ten families of each region were planted. A total of 960 study seedlings plus additional buffer trees were planted at each site. Within a plot, seedlings were planted at a 3.6×3.6 m spacing and family location was randomly assigned. Vegetation was operationally controlled. Sites were fenced to exclude animal damage from deer and elk. The test sites were planted in the winter of 2008–2009.

Regional climate and ecological setting

The seed sources and test sites were chosen to capture the climate variation experienced by coastal Douglas-fir (Table 1). The northern portion of this region, as described by the northern

Oregon and southern Washington populations and test sites, is largely characterized by a maritime climate of mild, wet winters with long frost-free periods and relatively mild, dry summers. The southern portion of the represented region, as represented by the southern Oregon and northern California populations, is characterized by arid, continental climates of warm dry summer and cool winter conditions. There are large north–south climate gradients related to southerly changes in latitude most evident from the Willamette Valley and Oregon Coast Range to the Klamath Mountains. Movement in this direction is characterized by decreases in precipitation and increased continentality, with exceptions due to elevation and distance from coast (Franklin and Dyrness 1973, Wang et al. 2012).

Measurements

All trees at all sites were assessed for infection levels and symptoms associated with SNC and Rhabdocline (8960 trees in total). Surveys were conducted from 23 March to 29 May of 2015.

Table 1. Climate variables associated with the regions (top) and test sites (bottom) of the Douglas-fir Seed-Source Movement Trial.

Location	Latitude	Longitude	Elevation (m)	MSP (mm)	MAP (mm)	MAT (C°)	TD (C°)	MWT (C°)
Region								
CA.coast	39.01	–123.49	156	71	1122	12	8	9
CA.Klamath	40.26	–122.91	1389	119	1472	11	17	4
CA.Sierra	39.87	–120.74	1469	107	1172	9	19	1
OR.coast (south)	42.72	–124.19	308	313	2528	11	11	7
OR.Siskiyou (low)	43.01	–123.08	462	162	1067	11	16	4
OR.Siskiyou (high)	42.54	–122.88	1062	173	1254	9	17	3
OR.coast (north)	44.48	–123.76	312	301	2260	10	13	5
OR.Cascades (low)	44.48	–122.64	437	291	1628	10	15	4
OR.Cascades (high)	44.74	–122.11	1005	345	2055	8	15	1
WA.coast	46.94	–123.65	179	415	2530	10	13	4
WA.Cascades (low)	46.91	–121.92	442	391	1926	8	15	2
WA.Cascades (high)	47.06	–121.74	1053	388	2068	6	16	–1
Site								
Floras	42.90	–124.36	400	352	2484	10	11	6
Evans Creek	42.63	–123.05	700	111	610	12	20	4
Stone Nursery	42.35	–122.94	415	103	613	12	19	4
Nortons	44.66	–123.69	185	265	1663	10	14	5
Slice Butte	44.11	–122.87	380	266	1360	11	16	5
Soda320	44.43	–122.24	850	351	1936	9	17	3
Jammer3	46.62	–123.71	177	405	2481	9	13	4
Buckhorn2	46.55	–122.99	240	286	1419	10	15	4
Doorstop	46.95	–122.01	860	506	1841	7	16	1

Note: Climate variables: MSP, May through September precipitation; MAP, mean annual precipitation; MAT, mean annual temperature; TD, continentality; MWT, mean winter temperature.

Survey dates were chosen to correspond with the date at which 50% of trees at a site had undergone vegetative budburst based on assessments done in past years. This is the period when the infection and symptoms associated with both diseases are most visible.

Infection severity ratings were estimated based on the presence of fruiting bodies of each fungal pathogen. Severity of *Phaeocryptopus gaeumannii* infection, as assessed by pseudothecia (*P. gaeumannii* fruiting bodies) density, was rated on both the north and south side of each tree on the two-year-old needles of a secondary lateral branch on the fourth whorl down from the top of the tree. Ratings were scored on a scale of 0–3, where 0 = no pseudothecia present on the underside of the needle, 1 = 1–33% stomata occluded, 2 = 33–66% stomata occluded, and 3 = >66% of stomata occluded by pseudothecia. A 15–25 × hand lens was used to see occlusion of stomata. A minimum of 15 needles were assessed on both the north and south sides of each tree. *Rhabdocline* spp. infection level was estimated over the entire crown of the tree on both the north and south sides. Ratings for *Rhabdocline* spp. ranged from 0 to 3 and were based on the same percentages as SNC though in relation to infection levels over the entire crown of the tree. In order to get an infection level for the entire tree, we averaged the north and south values for infection levels of *Rhabdocline* spp. and *P. gaeumannii* to obtain one value per tree for each fungal species.

We used crown density to evaluate disease tolerance. Crown density was rated on a scale ranging from 1 to 4, where 1 represents a sparse crown lacking in needle retention and 4 represents a full healthy crown. Although crown color and needle retention were also used to assess disease symptoms, these attributes proved to be difficult to assess in eight-year-old trees, and field assessment was inconsistent. Results for these predictor variables are presented in Appendix S1.

Climate data

Climate measures of population sources and test sites were obtained using ClimateWNA (Wang et al. 2012). ClimateWNA is a program that uses bilinear interpolation and local elevation adjustment approaches to downscale ~4 KM² PRISM data (Daly et al. 2008) into a continuous

surface rather than reporting the mid-point value for each grid cell. We selected variables identified in past literature as influential on SNC and *Rhabdocline* disease occurrence and severity including spring/summer precipitation which is defined in ClimateWNA as May through September precipitation (ClimateWNA abbreviation = MSP), mean winter temperature (ClimateWNA abbreviation = Tave_wt), and difference between the mean temperature of the warmest month and the mean temperature of the coldest month, referred to as continentality (ClimateWNA abbreviation = TD; Parker 1970, Michaels and Chastagner 1984, Rosso and Hansen 2003, Manter et al. 2005, Stone et al. 2007, 2008b, Zhao et al. 2011, Lee et al. 2013). Climate data for source locations were the 30-yr average from 1961 to 1991, while climate data for the test sites were the average from 2008 to 2013. Climate data for sites were assumed to represent the conditions under which the test trees had grown. Transfer distance was calculated by subtracting the climate value at the population source from the climate value at the test site. Due to differences in the scale of the climate transfer distances, each climate transfer distance was standardized by subtracting its mean and dividing by the standard deviation.

Analysis

The counts of seedlings for each infection rating (0, 1, 2, 3) were not well distributed among the levels. Specifically, most trees were either not or severely infected, making the distinction between none and light infection, or moderate and severe infection, not meaningful. In addition, models failed to converge under multinomial analysis also due to few trees with light or moderate infection levels. Therefore, infection and crown density ratings were condensed into binomial responses. The response variables for our analyses were calculated as follows: *Rhabdocline* spp. and *P. gaeumannii* infection ratings of 1 and 0 were recoded as 0 reflecting low infection levels and ratings of 2 and 3 were recoded as 1 reflecting moderate to severe infection levels. Crown density was coded similarly: Ratings of 1 and 2 were recoded as 1 reflecting sparse unhealthy crown density, and 3 and 4 were recoded as 0 indicating healthy full crown density. No signs of infection by either pathogen were present at Evans Creek or Stone Nursery, and therefore,

these test sites were removed from the analysis. Trees that were not assigned to a population were also removed from the analysis. This resulted in the removal of 263 test trees.

We analyzed three datasets. The full dataset was used to obtain probability related to all predictor variables in the presence of all diseases. This dataset was used to analyze susceptibility to infection by *Rhabdocline* species. Severe impacts associated with trees susceptible to *Rhabdocline* spp. prevented accurate assessments of *P. gaeumannii* infection and associated damage. Therefore, two subsets of the full dataset were created to assess the variation in crown density related to SNC and the variation in level of infection by *P. gaeumannii*.

Subsets:

1. *Crown density in relation to SNC*: Trees with moderate to severe *Rhabdocline* spp. rating were removed from this subset. This enabled better assessment of crown density impacts related to SNC as *Rhabdocline* spp. infection prevented this assessment.
2. *Variation in the infection levels of *P. gaeumannii**: Trees were removed from this subset for either of two reasons: (1) They did not retain more than one year of needles; assessment of *P. gaeumannii* fruiting bodies was made on second-year needles, and therefore, trees lacking two-year-old needles could not be assessed, or (2) they were rated as having moderate to severe *Rhabdocline* spp. infection, as *Rhabdocline* fruiting bodies prevented accurate assessment of infection levels.

The removal of trees from these subsets most heavily impacted the presence of California and inland southern Oregon regions. Therefore, the sample size of these regions is reduced in these datasets. The influence and dominance of *Rhabdocline* and the need to remove these trees to analyze SNC impacts likely reduced the strength of the results related to SNC. However, due to the similarities of the pathogens, it is likely that patterns in susceptibility are very similar.

The effects of climate transfer distance on the probability of low crown density and high infection severity were analyzed using generalized

linear mixed models with the probit link function for our Bernoulli-distributed responses (*P. gaeumannii* infection severity, crown density, and *Rhabdocline* spp. infection severity; Stroup 2012). The analysis was conducted using R version 3.2.3 (RStudio Team 2015).

The models presented in this paper include random effects for population, family (nested in population), and site. The random effect of site is included to account for the random variation present from site to site. The random effects of population and family, with family nested in population, were included to account for the genetic variation within each of these levels of relatedness. The random effect for variation due to combinations of population and site was also included in the models. However, most models failed to converge if this combination was included, and in these cases, it was omitted.

The statistical models (Appendix S1: Table S1) tested included fixed effects for the climate transfer distance variables representing MSP, MWT, and continentality index. Past analysis of provenance studies has revealed quadratic relationships between the transfer distance of climate variables and response variables. Based on this, quadratic relationships for all variables were also considered as fixed effects. The model for each response variable was chosen using Akaike Information Criterion (AIC; Akaike 1974). The model with the lowest score was selected as the best supported model (Akaike 1974, Burnham et al. 2010): However, models that differed by <2 AIC units were considered equally supported, and in these cases, the simplest model was selected based on the principle of parsimony.

We evaluated the effect of transfer distance for each climate variable in the selected model individually with the other climate transfer distances set to their mean value. The value of the climate variable in question was allowed to vary across its range in the dataset. This process enabled us to evaluate the relative effect of each climate transfer distance on the populations. We also obtained the distribution of predicted probability of moderate to severe disease symptoms or infection over all the transfer distances in question without holding any variables constant.

Transfer distance risk

We estimated climate transfer distance risk to examine the implications of population movement. Low-risk transfer distances are those beyond which unacceptably high probability of disease symptoms or infection is estimated to occur. We chose 25% as a threshold for modeling. May through September precipitation and mean winter temperatures displayed the largest variation in probability of moderate to severe *Rhabdocline* spp. infection and low crown density, and therefore, those climate variables were used to assess low-risk transfer distances. Since confidence intervals identify plausible values for the probability of infection or symptom, we identified the boundary of low-risk transfer distance as that point where the confidence interval for the estimated probability of infection/symptom was completely below 25% probability. This 25% threshold is arbitrary and is meant to demonstrate how these models may be used by land managers. Managers are urged to choose a threshold which they feel is acceptable and apply the models accordingly.

No variation was observed in relation to the probability of moderate to severe *P. gaeumannii* infection at any given site; thus, low-risk transfer distances were not identified for *P. gaeumannii* infection. Low-risk transfer distances were calculated for the probability of moderate to severe *Rhabdocline* spp. infection and susceptibility to SNC (disease expression) as measured by crown density. The probability of moderate to severe *Rhabdocline* spp. infection follows the same pattern as the probability of low crown density in the presence of all diseases (Appendix S1: Figs. S1, S2, Table S6). Therefore, low-risk transfers in relation to crown density in the presence of all diseases can be inferred based on the estimated probability of moderate to severe *Rhabdocline* spp. infection.

Mapping probability of *Rhabdocline* infection and lack of tolerance to Swiss needle cast

Maps illustrate the effects of moving three California and three Washington regions across the landscape in the Pacific Northwest. Two sets of maps were created based on what we predict will happen with foliage diseases if seed is moved from a given location—one set showing the estimated probability of low crown density associated

with SNC and the other set showing the estimated probability of moderate to severe *Rhabdocline* spp. infection. Transfer distances were calculated by subtracting the average value of each climate variable for each region from the value of that climate variable in each grid cell across the study area (Wang et al. 2012, 2016). These transfer distances were then scaled by subtracting the global mean and dividing by the global standard deviation as done in the original model. Scaled transfer distance variables were used in the models selected for crown density and *Rhabdocline* spp. infection along with the model coefficients to estimate the corresponding probability in relation to the current climate and projected climate of 2080 under moderate (4.5 RCP) and high (8.5 RCP) emissions scenarios. Random effects were not included in the models used to create these maps. This may affect the variation associated with the point estimates of probability but will not affect the values of the point estimates of probability. Projected climate values were obtained using HadGEM2 climate scenarios (Jones et al. 2011) projected to year 2080 and were obtained from ClimateNA v5.10 software package as described by Wang et al. (2016). Each grid cell was colored according to the estimated probability.

RESULTS

Phaeocryptopus gaeumannii infection

Infection severity as assessed by pseudothecia density was generally similar among all tree populations within a given site, although crown density, or disease expression, did vary, supporting the idea of tolerance. Moderate to severe *Phaeocryptopus gaeumannii* infection was observed at every site except Stone Nursery and Evans Creek, where no infection was observed (Table 2). Evans Creek and Stone Nursery have the lowest levels of MSP and mean annual precipitation among all the test sites in the SSMT. These sites are also characterized by cool winters and hot summer conditions (high continentality).

The chosen model for *P. gaeumannii* infection severity included MWT transfer distance as the only fixed effect (Appendix S1: Table S1). The variance due to random effects did not change with the addition of MWT transfer distance as a fixed effect. Site accounts for the majority of variance due to random effects in both models

Table 2. Percentage of trees in each of the 12 regions in the Douglas-fir Seed-Source Movement Trial (SSMT) rated as having moderate to severe *Phaeocryptopus gaeumannii* infection at each test site in the SSMT.

Region	Floras	Stone Nursery	Evans Creek	Nortons	Slice Butte	Soda320	Jammer3	Buckhorn2	Doorstop	All sites
CA.coast	67	0	0	79	96	85	77	87	81	64
CA.Klamath	89	0	0	90	100	88	93	85	78	69
CA.Sierra	90	0	0	79	58	52	65	59	38	49
OR.coast (south)	86	0	0	82	97	92	95	98	92	71
OR.Siskiyou (low)	85	0	0	81	90	86	99	88	86	68
OR.Siskiyou (high)	85	0	0	77	84	91	92	93	85	67
OR.coast (north)	83	0	0	79	83	92	100	91	96	69
OR.Cascades (low)	85	0	0	86	94	90	100	94	95	72
OR.Cascades (high)	96	0	0	94	99	97	98	98	96	75
WA.coast	73	0	0	81	95	97	99	98	94	71
WA.Cascades (low)	81	0	0	85	94	95	96	98	98	72
WA.Cascades (high)	95	0	0	85	96	100	98	99	94	74
Site average	85	0	0	83	91	89	93	91	86	68

Notes: Regions are ordered by latitudinal transect (three regions per transect) from south to north and from coast to high elevation within each transect. Sites are ordered in the same manner.

(Table 3), indicating that the site conditions were influential on the level of infection by *P. gaeumannii*. Relatively little variation was observed among populations or families within populations.

Climate transfer distance did not influence the probability of infection by *P. gaeumannii* (Fig. 2A). The probability of infection was close to one at all sites in which infection occurred.

The furthest transfers in either direction, increasing or decreasing in MWT, displayed similar probability of moderate to severe *P. gaeumannii* infection (Table 4). Populations transferred from source climates of warm MWT to test sites of cool MWT were estimated to have lower probability of moderate to severe infection relative to populations transferred from cool to warm MWT (Fig. 2B). These differences are minor and can be

Table 3. Variance components associated with the random effects-only model (no fixed effects) and the selected models.

Random effect	Random effects-only model			Selected model		
	Variance	SD	Variance explained (%)	Variance	SD	Variance explained (%)
<i>P. gaeumannii</i> infection						
Family	0.03	0.12	7	0.01	0.12	2
Population	0.06	0.24	15	0.05	0.23	12
Site	0.32	0.56	78	0.35	0.59	85
Total	0.41		100	0.41		100
Crown density						
Family	0.05	0.22	7	0.05	0.23	16
Population	0.24	0.49	37	0.08	0.28	23
Site	0.37	0.61	56	0.21	0.46	61
Total	0.67		100	0.34		100
<i>Rhabdocline</i> spp. infection						
Family	0.02	0.14	2	0.019	0.14	4
Population	0.91	0.96	92	0.24	0.49	51
Site	0.07	0.26	6	0.21	0.46	45
Total	1		100	0.469		100

Note: Data are from all test trees at the seven test sites that displayed signs of *Phaeocryptopus gaeumannii* and *Rhabdocline* spp. in the Douglas-fir Seed-Source Movement Trial.

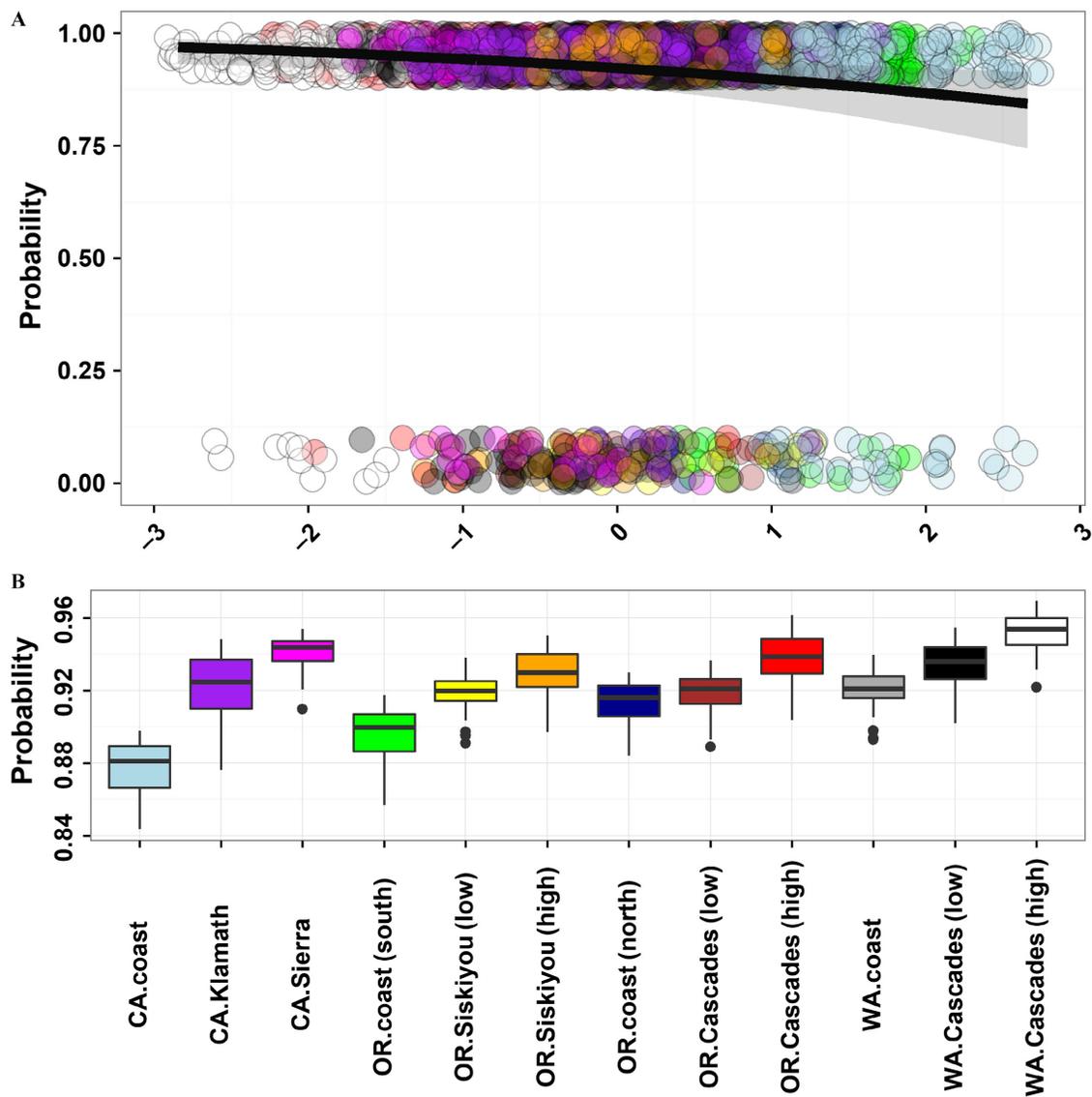


Fig. 2. (A) Estimated probability of moderate to severe *Phaeocryptopus gaeumannii* infection vs. mean winter temperature transfer distance (population – site) and 95% confidence intervals with raw data. Data are from all trees in the Douglas-fir Seed-Source Movement Trial (SSMT) at the seven sites that displayed signs of *P. gaeumannii* and *Rhabdocline* spp. (B) Distributions of the estimated probability of moderate to severe *P. gaeumannii* infection in relation to each region in the seven sites of the SSMT that displayed signs of *P. gaeumannii* and *Rhabdocline* spp. Probability scale ranges from 0.84 to 1.0. The x-axis displays the regions and is labeled by latitudinal transect (three regions per transect) in order from south to north and from coast to high elevation within each latitudinal transect.

considered to be biologically insignificant. Populations from coastal regions had only slightly lower probability of infection than populations from further inland or from higher-elevation regions (Fig. 2B).

Crown density

Populations from the southern Oregon and northern California regions had low percentages of trees with healthy crown density. These regions are characterized by arid climates of cool winter

Table 4. Furthest climate transfer distances and the transfer distance closest to zero (local) with associated probability of each prediction variable and 95% confidence intervals.

Prediction and climate variable	Direction of transfer	Distance	Probability of low crown density (%) (95% CI)
<i>P. gaumannii</i> infection			
MWT (°C)	Low to High	8.75	99 (96–99)
	Local	0	97 (93–99)
	High to Low	7.93	95 (87–99)
Crown density			
MSP (mm)	Low to high	472.83	52 (29–73)
	Local	0.33	4 (2–8)
	High to low	282.99	0.3 (1–8)
MWT (°C)	Low to high	8.75	57 (34–78)
	Local	0	5 (2–10)
	High to low	7.93	8 (2–22)
<i>Rhabdocline</i> spp.			
MSP (mm)	Low to high	472.83	62 (38–82)
	Local	–0.33	4 (2–9)
	High to low	282.99	0.0014 (0.0002–0.9)
MWT (°C)	Low to high	8.75	27 (7–60)
	Local	0	8 (4–15)
	High to low	7.93	2 (0.1–10)
Continentality (°C)	Low to high	10	0.6 (0.0003–6)
	Local	0	8 (4–15)
	High to low	7.68	29 (10–57)

Notes: Data are from all test trees at the seven test sites that displayed signs of *Phaeocryptopus gaumannii* and *Rhabdocline* spp. infection in the Douglas-fir Seed-Source Movement Trial. Climate variables: MSP, May through September precipitation; MWT, mean winter temperature, and continentality.

temperatures (Table 1). Populations from coastal and low-elevation regions of northern Oregon and southern Washington had the highest percentage of trees with healthy crown density and represent mild maritime climates (Tables 1, 5).

Within each latitudinal transect, high-elevation populations had the lowest percentage of trees with healthy crown density (Table 5). High-elevation populations are from regions characterized by cool winter temperatures (Table 1).

Table 5. Percentage of trees in each of the 12 regions of the Douglas-fir Seed-Source Movement Trial (SSMT) rated as having healthy crown density at each test site of the SSMT (trees susceptible to *Rhabdocline* spp. removed).

Region	Floras	Stone Nursery	Evans Creek	Nortons	Slice Butte	Soda320	Jammer3	Buckhorn2	Doorstop	All sites
CA.coast	82	96	98	89	95	68	82	95	33	82
CA.Klamath	43	98	100	100	96	66	67	93	72	82
CA.Sierra	53	100	99	78	83	63	48	61	64	72
OR.coast (south)	90	95	97	100	99	92	95	99	76	94
OR.Siskiyou (low)	87	100	99	97	98	98	91	95	84	94
OR.Siskiyou (high)	60	100	97	98	90	83	70	96	74	85
OR.coast (north)	81	99	98	100	100	95	94	100	91	95
OR.Cascades (low)	72	96	98	100	96	97	98	100	94	95
OR.Cascades (high)	54	97	100	100	96	91	87	94	85	89
WA.coast	70	93	99	100	99	97	97	98	87	93
WA.Cascades (low)	58	98	100	99	100	94	85	96	84	90
WA.Cascades (high)	66	92	95	97	96	81	78	92	91	88
Site average	68	97	98	97	96	85	83	93	78	88

Note: Regions are ordered by latitudinal transect (three regions per transect) from south to north and from coast to high elevation within each transect. Sites are ordered in the same manner.

Our chosen model for crown density included a linear and quadratic term for MSP, and a linear and quadratic term for MWT (Appendix S1: Table S1). Inclusion of the selected covariates reduced the variance of the population and site random effects but had little to no effect on family variance (Table 3). Variation among sites accounted for the majority of variance. The small proportion of variance due to random effects explained by family indicates that there is little additional variation from within populations (Table 3).

Transfers of populations from low to high summer precipitation (MSP) and from cool to

warm winter temperatures (MWT) resulted in increased probability of low crown density (Table 4, Fig. 3). Populations transferred more than 243 mm (from low to high values) in MSP resulted in >25% probability of low crown density (95% CI: 7–24.5 probability; Fig. 3). Additionally, transfer of populations beyond 4°C (cool to warm) in MWT resulted in >25% probability of low crown density (95% CI: 7–24.8 probability; Fig. 3). Local populations, however, had low probability of poor crown density, well below the threshold limit of a 25% probability.

The probability of low crown density associated with MSP transfer displays a strong geographic

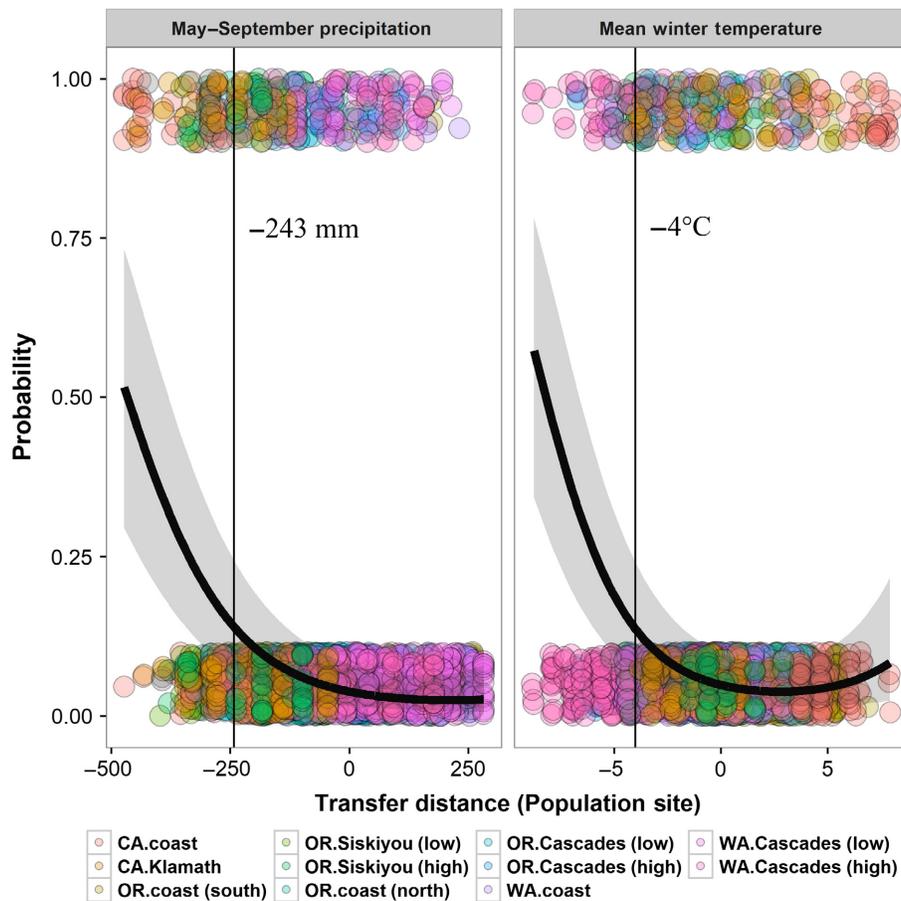


Fig. 3. Estimated probability of low crown density vs. climate transfer distances (population – site) and 95% confidence intervals with the raw data; confidence intervals include random effects. Each plot holds the other climate transfer distance to its mean. Probability of low crown density is hypothesized to be due to Swiss needle cast (trees susceptible to *Rhabdocline* spp. removed). Data are from all trees in the Douglas-fir Seed-Source Movement Trial at the seven sites where *Phaeocryptopus gaumannii* and *Rhabdocline* spp. were identified as present. The vertical line indicates the threshold below which probability is estimated to be >25%.

trend as populations from northern regions had low probability and populations from southern regions had high probability (Fig. 4A). Populations from southern regions have low values for MSP (Table 1). Probability of low crown density in relation to MWT increases from coastal populations to low elevation populations and is greatest for high elevation populations. These populations

had the highest probability of low crown density within each latitudinal transect represented in the study (Fig. 4A). Populations from high-elevation regions have low values for MWT (Table 1).

The spatial distributions of the estimated probability of low crown density, allowing all variables to vary across their range in the dataset, also follow strong geographic patterns as populations from

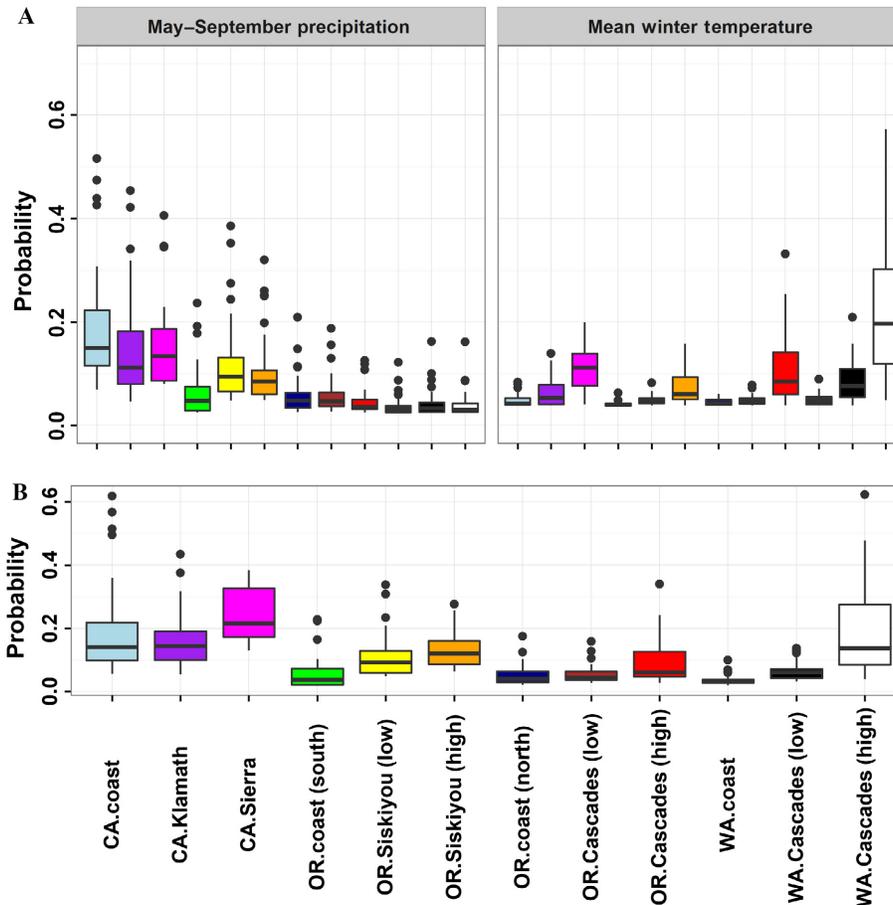


Fig. 4. (A) Estimated distribution of probability of low crown density in relation to each climate transfer distance (population – site) holding the other climate transfer distance to its mean. Data are in relation to all 12 regions at all seven sites of the Douglas-fir Seed-Source Movement Trial (SSMT) that displayed signs of *Phaeocryptopus gaeumannii* and *Rhabdocline* spp. The *x*-axes display the regions and are in order from south to north and from coast to high elevation within each latitudinal transect (three regions per transect). Colors correspond to the same region in each figure. (B) Distribution of the estimated probability of low crown density with all explanatory variables varying over their entire range in the dataset. Probability of low crown density is hypothesized to be due to Swiss needle cast (trees susceptible to *Rhabdocline* spp. removed). Data are in relation to all 12 regions at all seven sites of the Douglas-fir SSMT that displayed signs of *P. gaeumannii* and *Rhabdocline* spp. The *x*-axes display the regions and are labeled by latitudinal transect (three regions per transect) in order from south to north and from coast to high elevation within each latitudinal transect. Colors correspond to the same region in each figure.

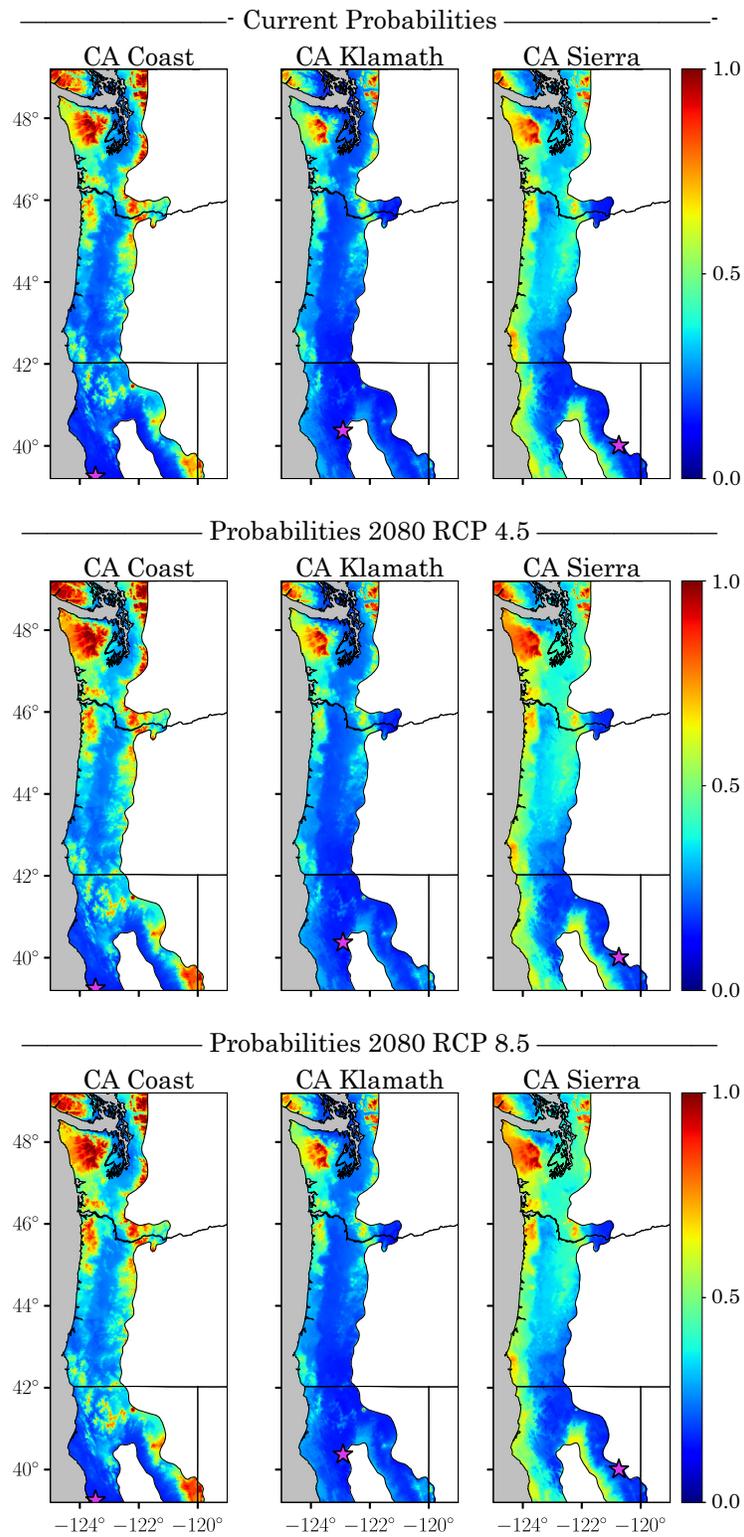


Fig. 5. Geographic distribution of estimated probability of low crown density in relation to the transfer of the

(Fig. 5. *Continued*)

California regions of the Douglas-fir Seed-Source Movement Trial (SSMT). Probability was estimated with the model selected using data from these regions in relation to the seven sites of the SSMT that displayed signs of *Phaeocryptopus gaeumannii* and *Rhabdocline* spp. (trees susceptible to *Rhabdocline* spp. removed). Climate predictions were made using the HadGEM2 climate projections under RCP 4.5 (moderate) and RCP 8.5 (high) emissions (Jones et al. 2011, Wang et al. 2016). Magenta star indicates seed-source location.

southern regions exhibit higher probability than those from northern regions, and high-elevation regions exhibit higher probability than low-elevation or coastal regions (Fig. 4B). Populations from southern regions are most influenced by MSP transfer distance, while high-elevation regions are most influenced by MWT transfer distance (Fig. 4A).

Geographic distributions of low crown density

Movement of populations from northern California regions into areas of higher precipitation, such as the areas west of the Coast Range Mountains of Oregon and Washington and the western slopes of the Cascade Mountains, resulted in high probability of low crown density (Fig. 5). The highest probabilities are characterized by the movement from low MSP to high MSP and/or from low to high MWT (Fig. 5). Populations from the California Coast exhibited high probability of low crown density when moved to higher elevations; the increased probabilities may have been influenced by cold damage rather than foliage diseases. These populations did not have high probabilities of low crown density at most test sites including those with severe disease based on pseudothecia density.

High-elevation Washington Cascades populations displayed the highest probability of low crown density associated with SNC within the Washington regions (Fig. 6). Disease expression due to movement of populations from Washington Cascades high-elevation region is associated with the transfer of trees from higher to lower elevations and, therefore, lower to higher winter temperatures. The highest probabilities are associated with movement into areas west of the Coast Range Mountains of Oregon and Washington (Fig. 6). Populations from the coastal and low-elevation regions of Washington exhibit low probability of low crown density in relation to transfers across the Pacific Northwest.

The probability of low crown density based on projected climate conditions in 2080, under both

RCP 4.5 and RCP 8.5 scenarios, did not result in large changes to the maps of probability of low crown density (Figs. 5, 6). May through September precipitation is projected to decrease by 61 mm (RCP 4.5) and 46 mm (RCP 8.5) and MWT is projected to increase by 2°C (RCP 4.5) and 4°C (RCP 8.5) by 2080. These changes in climate are well below those that would lead to large increases in the probability of low crown density as predicted by our models (Fig. 3). Winter temperature, shown to be most influential across the study on infection by *P. gaeumannii*, is predicted to increase creating conducive conditions in areas where precipitation is not a limiting factor.

Rhabdocline spp. infection

Percentage of trees displaying moderate to severe *Rhabdocline* spp. infection varied by site (0–23%) and region (1–60%; Table 6). The Washington test sites had a higher percentage of trees displaying moderate to severe *Rhabdocline* spp. infection than test sites further south. Doorstop, Buckhorn2, and Soda320 had the highest percentage of *Rhabdocline* spp. infection (Table 6). The two inland southern Oregon sites, Evans Creek and Stone Nursery, which are characterized by arid, warm summer conditions and cool winter conditions, displayed no signs of *Rhabdocline* spp. infection (Tables 1, 6). Within each latitudinal transect, the high-elevation populations had the highest percentage of trees with moderate to severe infection. The populations from the coastal regions and low-elevation Cascades regions had small percentages of trees displaying moderate to severe disease symptoms. The populations from the region local to each site generally had low percentages of trees displaying moderate to severe *Rhabdocline* infection. The only exceptions were the local sources at the high-elevation sites of northern Oregon (Soda320) and southern Washington (Doorstop). Populations from regions local to these test sites exhibited higher

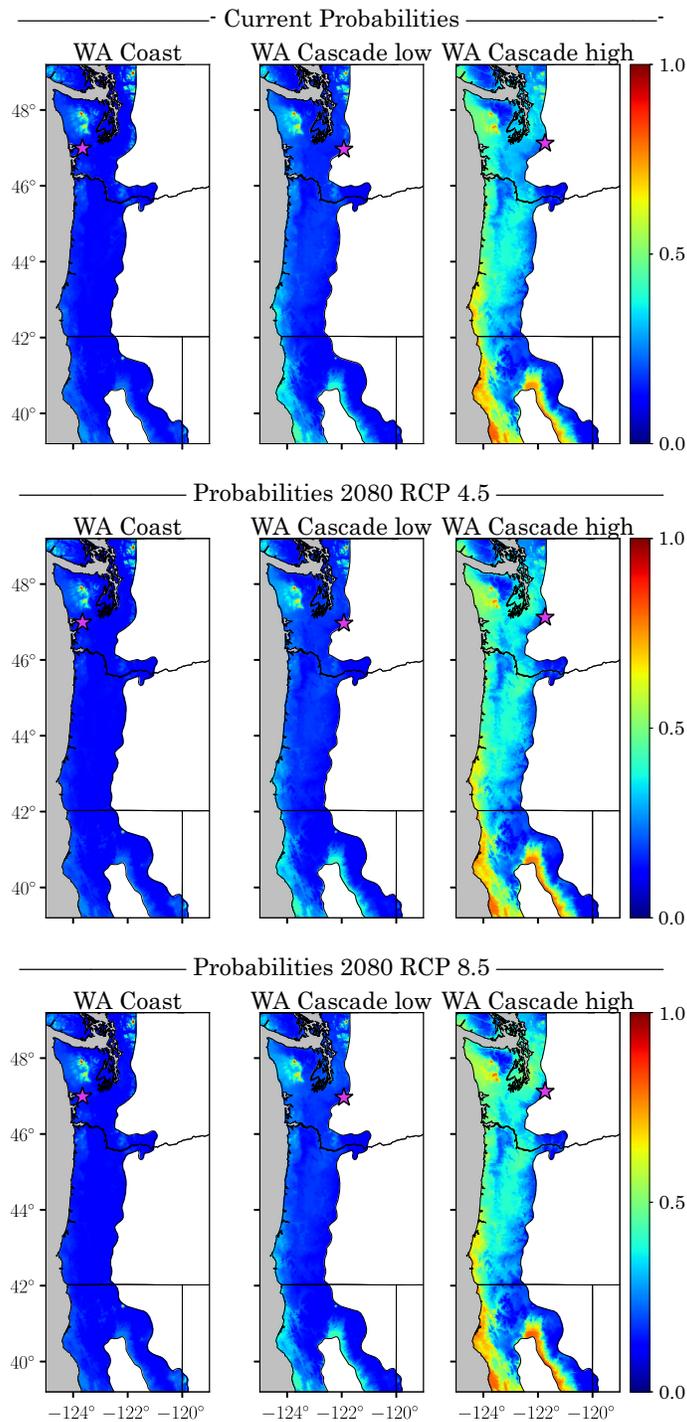


Fig. 6. Geographic distribution of estimated probability of low crown density in relation to the transfer of the Washington regions of the Douglas-fir Seed-Source Movement Trial (SSMT). Probability was estimated with the model selected using data from these regions in relation to the seven sites of the SSMT that displayed signs of *Phaeocryptopus gaumanni* and *Rhabdocline* spp. (trees susceptible to *Rhabdocline* spp. removed). Climate predictions were made using the HadGEM2 climate projections under RCP 4.5 (moderate) and RCP 8.5 (high) emissions (Jones et al. 2011, Wang et al. 2016). Magenta star indicates seed-source locations.

Table 6. Percentage of trees in each of the 12 regions of the Douglas-fir Seed-Source Movement Trial (SSMT) with moderate to severe *Rhabdocline* spp. infection at each test site of the SSMT.

Region	Floras	Stone Nursery	Evans Creek	Nortons	Slice Butte	Soda320	Jammer3	Buckhorn2	Doorstop	All sites
CA.coast	3	0	0	9	1	6	5	13	5	5
CA.Klamath	28	0	1	23	34	36	29	48	51	28
CA.Sierra	75	0	0	52	92	90	67	77	83	60
OR.coast (south)	1	0	0	3	0	3	3	1	9	2
OR.Siskiyou (low)	14	0	0	7	11	15	9	12	32	11
OR.Siskiyou (high)	11	0	0	18	8	22	21	32	32	16
OR.coast (north)	4	0	0	1	1	3	3	4	4	2
OR.Cascades (low)	3	0	0	4	0	4	0	4	10	3
OR.Cascades (high)	4	0	0	9	5	11	5	18	18	8
WA.coast	0	0	0	0	1	3	3	0	5	1
WA.Cascades (low)	4	0	0	3	3	3	0	3	8	3
WA.Cascades (high)	1	0	0	8	4	9	14	3	16	6
Site average	12	0	0	11	13	17	13	18	23	12

Notes: Regions are ordered by latitudinal transect (three regions per transect) from south to north and from coast to high elevation within each transect. Sites are ordered in the same manner.

infection levels at these test sites than many of the other regions (Table 6).

The *Rhabdocline* model included linear terms for the climate transfer distances of MSP, MWT, and continentality. The inclusion of the selected covariates reduced total variance and was most influential on population and site random effects, with little to no effect on the random effect for family (Table 3). Variation among populations accounts for the majority of variance. The small proportion of variance due to random effects explained by family indicates that there is little additional variation from within populations (Table 3).

Transferring populations from low to high MSP resulted in the highest probability of moderate to severe *Rhabdocline* spp. infection (Table 4, Fig. 7). Mean winter temperature and continentality transfer distances displayed weaker relationships with the probability of moderate to severe *Rhabdocline* spp. infection, but are estimated to increase with transfers of populations from cool to warm MWT and high to low continentality (Fig. 7). Transfers of populations beyond a 159 mm increase in MSP are estimated to result in >25% probability (95% CI: 7–24.9) of moderate to severe *Rhabdocline* spp. infection (Fig. 7). Transfers beyond a 3°C increase in MWT and a 3°C decrease in continentality are also estimated to result in >25% probability (95% CI: 5–24 and 6–24, respectively) of moderate to

severe *Rhabdocline* spp. infection (Fig. 7). Local populations had low probabilities of moderate to severe *Rhabdocline* spp. infection, well below the threshold limit of a 25% probability (Table 4).

The probability of moderate to severe *Rhabdocline* infection associated with MSP transfer displays a strong geographic trend as populations from northern regions had low probability and populations from southern regions had high probability of moderate to severe *Rhabdocline* spp. infection (Fig. 8A). These populations have low values for MSP (Table 1). Probability of moderate to severe infection in relation to MWT increases from coastal populations to low-elevation populations and is greatest for the populations from high-elevation regions (Fig. 8A). Populations from high-elevation regions have low values for MWT (Table 1). The estimated effect of continentality is similar to that of MWT though there is little difference between populations from low-elevation inland regions and high-elevation regions.

The spatial distributions of the estimated probability of moderate to severe *Rhabdocline* spp. infection, allowing all variables to vary across their range in the dataset, also follow strong geographic patterns as populations from high-elevation regions exhibit higher probability than those from low-elevation or coastal regions, and populations from southern regions exhibit higher probability than those from northern regions (Fig. 8B). Populations from high-elevation

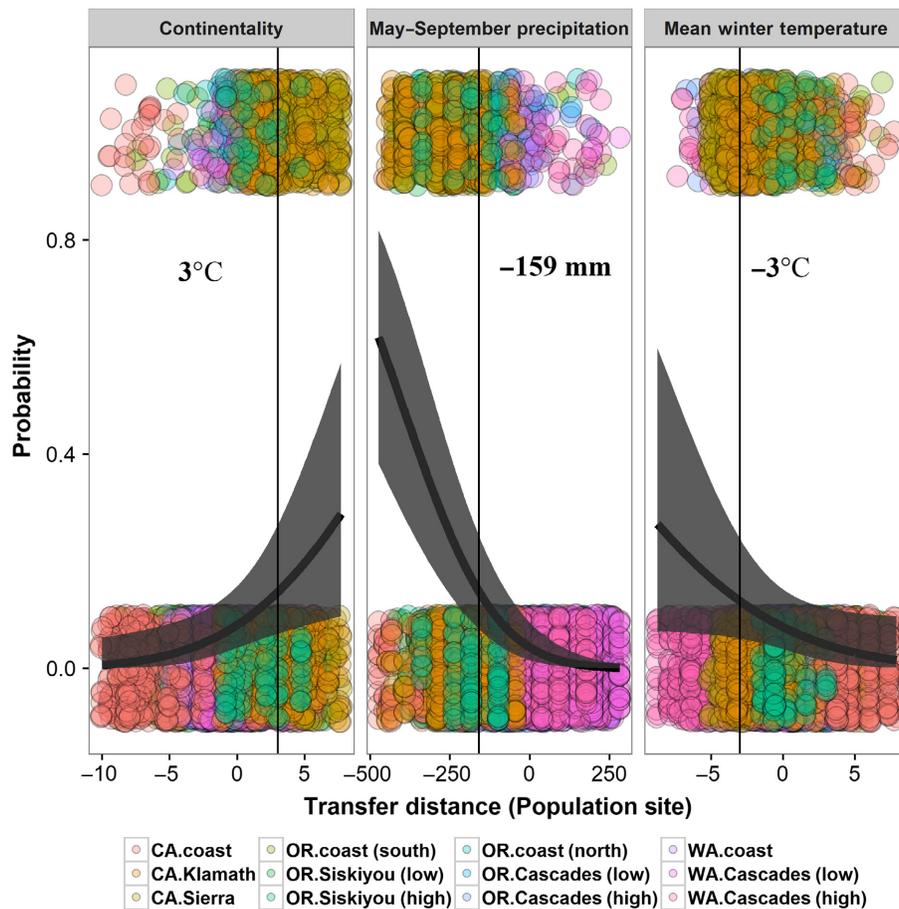


Fig. 7. Estimated probability of moderate to severe *Rhabdocline* spp. infection vs. climate transfer distance (population – site) and 95% confidence intervals with raw data; confidence intervals include random effects. Data are from all trees in the Douglas-fir Seed-Source Movement Trial at the seven sites where *Phaeocryptopus gaeumannii* and *Rhabdocline* spp. were identified as present. Each predicted line holds the other climate transfer distances to their mean. The vertical line indicates the threshold above which (continentality) or below which (May through September precipitation and mean winter temperature) probability of infection is estimated to be >25%.

regions had the highest probability of moderate to severe *Rhabdocline* infection within each latitudinal transect. High probability of *Rhabdocline* spp. infection in high-elevation regions is most strongly influenced by MWT, while the high probability in southern regions is influenced by MSP (Fig. 8A).

Geographic distribution—*Rhabdocline* spp. infection

California Sierra and Klamath populations had high probability of infection when transferred north and west to more maritime areas with milder winters and higher spring and summer

precipitation. Transfers to the coastal areas of Washington and Oregon, west of the Coast Range, are associated with the highest probability of infection. High probability of infection is characterized by the movement from low MSP to high MSP and/or from cool to warm MWT (Fig. 9).

Populations from Washington regions could be transferred throughout the Pacific Northwest with low probability of infection by *Rhabdocline* spp. Populations from the Washington Cascades high-elevation region were associated with the highest probability of moderate to severe infection specifically when transferred west of the coastal mountain ranges of Washington and

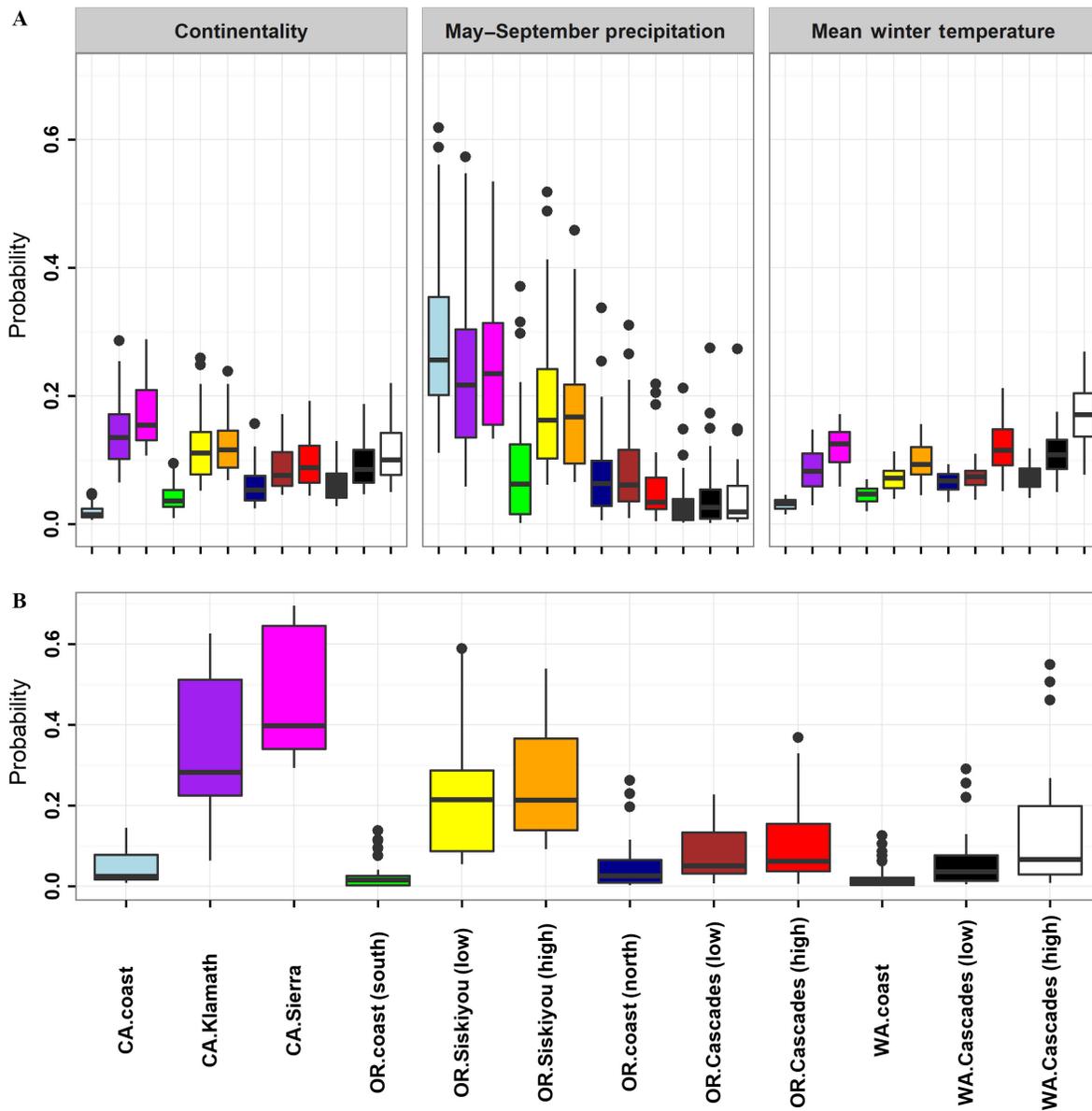


Fig. 8. (A) Estimated distribution of probability of moderate to severe *Rhabdocline* spp. infection in relation to each climate variable transfer distance (population – site), holding the other climate transfer distances to their mean. Probability of infection is in relation to all 12 regions at all seven sites of the Douglas-fir Seed-Source Movement Trial (SSMT) that displayed signs of *Phaeocryptopus gaeumannii* and *Rhabdocline* spp. The x-axes represent the regions and are in order from south to north and from coast to high elevation within each latitudinal transect (three regions per transect). Colors correspond to the same region in each figure. (B) Distribution of the estimated probability of moderate to severe *Rhabdocline* spp. infection with all explanatory variables varying over their entire range in the dataset. Probability of infection is in relation to all 12 regions at all seven sites of the Douglas-fir SSMT that displayed signs of *P. gaeumannii* and *Rhabdocline* spp. The x-axes represent the regions and are labeled by latitudinal transect (three regions per transect) in order from south to north and from coast to high elevation within each latitudinal transect. Colors correspond to the same region in each figure.

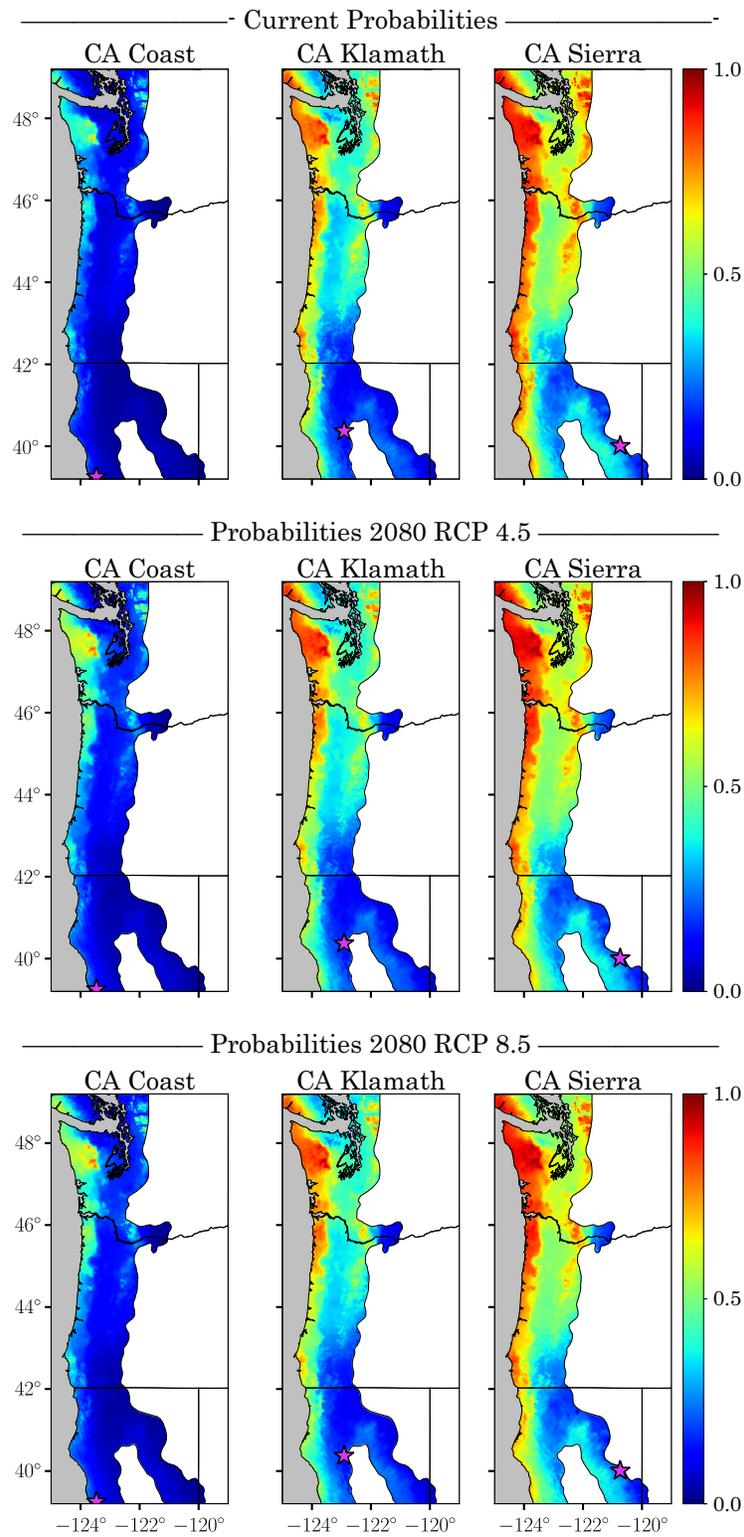


Fig. 9. Geographic distribution of estimated probability of moderate to severe *Rhabdocline* spp. infection in

(Fig. 9. Continued)

relation to the transfer of the California regions of the Douglas-fir Seed-Source Movement Trial (SSMT). Probability of infection was estimated with the model selected using data from these regions in relation to the seven sites of the SSMT that displayed signs of *Phaeocryptopus gaeumannii* and *Rhabdocline* spp. Climate predictions were made using the HadGEM2 climate projections under RCP 4.5 (moderate) and RCP 8.5 (high) emissions scenarios (Jones et al. 2011, Wang et al. 2016). Magenta star indicates seed-source location.

Oregon. Probability is highest when transferred to the coastal areas of the Olympic Peninsula (Fig. 10). These transfers are characterized by transfers from cool to warm MWT.

The probability of moderate to severe *Rhabdocline* spp. infection for source populations based on climate conditions in 2080 (Jones et al. 2011) for RCP 4.5 and RCP 8.5 emissions scenarios did not result in large changes to the estimated probability of severe *Rhabdocline* spp. infection (Figs. 9, 10). Projected changes include decreases in MSP, 61 mm (RCP 4.5) and 46 mm (8.5) and increased continentality, 2°C (RCP 4.5) and 4°C (RCP 8.5), both of which will likely reduce the prevalence of *Rhabdocline* needle cast. However, winter temperature is predicted to increase creating increasingly conducive conditions for infection in areas where precipitation is not a limiting factor. Large changes in the probability of *Rhabdocline* spp. infection were not observed in our model.

DISCUSSION

We confirmed that strong geographic patterns occur in the susceptibility and symptom development of foliage diseases within coastal Douglas-fir, implying that disease pressure increases the resistance and/or tolerance for a pathogen within a host population. Douglas-fir populations from environments not conducive to fungi that cause disease were the most susceptible to disease when grown in sites conducive to these fungi, while local populations, or populations from areas with environment conducive to foliar fungi, were generally among the most tolerant and resistant. Key climate variables that were associated with disease response changes, such as winter temperature and summer precipitation, are well-known epidemiological factors in plant pathology models, as well as forest foliage disease models because they influence fungal growth rates, spore dispersal, and host colonization success.

Though it is possible to select populations resistant to *Rhabdocline* spp., there was no evidence to suggest that populations may be selected for resistance to *Phaeocryptopus gaeumannii*. All populations had similar pseudothecia densities (infection levels) at a given site. However, there was tolerance to infection by *P. gaeumannii*, evidenced by variation in crown density. Populations from many regions in the current study, especially those from coastal regions, had healthy crown color and high crown density despite having high infection levels. This further validates findings by Temel et al. (2004) who attributed variation in susceptibility to SNC disease symptoms to tolerance rather than resistance to the pathogen.

The difference between these two pathogens—one is associated with resistance, while the other is associated with tolerance—is hypothesized to be due to infection method and life strategy. *Rhabdocline* spp., a necrotroph, forcibly enters its host killing and consuming host cells as it progresses (Brandt 1960). This strategy is likely to induce host defense mechanisms leading to selection for resistance because host cells are actively killed. *Phaeocryptopus gaeumannii*, a biotroph, enters the leaf via stomata and lives as an endophyte, apparently killing no cells (Capitani 1999). The endophytic lifestyle may not induce a host response. Therefore, tolerance to clogged stomata may be an evolutionary adaptive trait associated with high fungal infection levels.

Natural selection for resistance/tolerance, or adaptive co-evolutionary traits in relation to a pathogen, is commonly observed in trees under disease pressure over long periods of time (Kawecki and Ebert 2004, Ennos 2015). Resistance or tolerance, which provides benefits that outweigh the costs of such traits, may exert strong selection pressure (Telford et al. 2014, Ennos 2015). This trend has been noted in relation to many foliage diseases and blights including but not limited to SNC and *Rhabdocline*

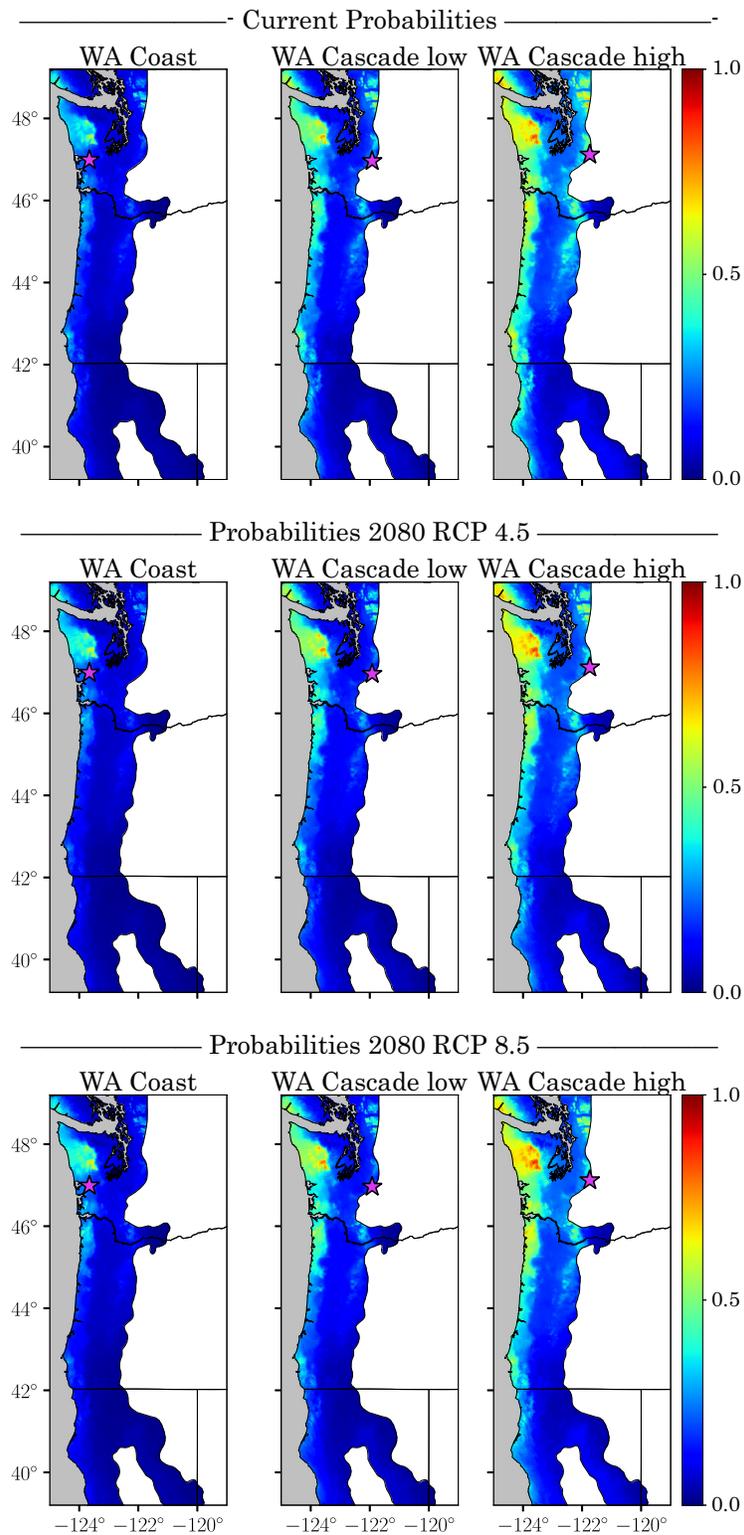


Fig. 10. Geographic distribution of estimated probability of moderate to severe *Rhabdocline* spp. infection in

(Fig. 10. *Continued*)

relation to the transfer of the Washington regions of the Douglas-fir Seed-Source Movement Trial (SSMT). Probability of infection was estimated with the model selected using data from these regions in relation to the seven sites of the SSMT that displayed signs of *Phaeocryptopus gaeumannii* and *Rhabdocline* spp. Climate predictions were made using the HadGEM2 climate projections under RCP 4.5 (moderate) and RCP 8.5 (high) emissions (Jones et al. 2011, Wang et al. 2016). Magenta star indicates seed-source location.

(Hood 1982, Hoff 1987, McDermott and Robinson 1989, Rehfeldt 1995, Zhang et al. 1997, Russell et al. 2007). Ennos (2015) suggested that species, such as Douglas-fir, which dominate large portions of the forested landscape and are associated with high levels of genetic diversity, have selected individuals for the resistance/tolerance to pathogens that are common and influential to the productivity of the species; our findings support these hypotheses. A general paradigm has emerged under which populations are suited to the disease pressure experienced at their source climate (Hood 1982, Hoff 1987, McDermott and Robinson 1989, Rehfeldt 1995).

The differences in susceptibility and symptom development among populations to these two major foliage diseases are related to source climate characteristics which dictate the level of disease pressure. Populations from source climates limiting to the development of *P. gaeumannii* and *Rhabdocline* spp., low MSP and/or low winter temperatures, had the highest probability of low crown density and *Rhabdocline* spp. infection, while populations from climates conducive to the development of these pathogens, high MSP and/or mild winter temperatures, had the lowest probability of low crown density and *Rhabdocline* spp. infection. Past studies have observed similar results noting a relationship between precipitation and/or winter temperatures of seed-source climate and susceptibility to SNC (Hood 1982, McDermott and Robinson 1989). Results from the current study agree with these findings and further refine them, revealing the importance of spring and summer precipitation.

Decreasing disease pressure has been observed with movement inland from the coast and has been attributed to climate factors that limit the development of *P. gaeumannii*, mainly low winter temperatures and dry spring and summer conditions (Rosso and Hansen 2003, Manter et al. 2005, Stone et al. 2008b, Lee et al. 2013, Ritokova et al. 2016). Interestingly, the test sites chosen to

represent arid climates of low winter temperatures, Evans Creek and Stone Nursery, displayed no signs of *P. gaeumannii* or *Rhabdocline* spp., providing further evidence that these climate variables are limiting to the development of these pathogens.

Our results displayed interesting trends in relation to the timing of spring budburst and the level of susceptibility of populations. Populations associated with early budburst were highly susceptible to *Rhabdocline* and SNC. Although the mechanisms behind the levels of susceptibility of each population can only be hypothesized, similarities in the timing of budburst and level of susceptibility to *Rhabdocline* spp. and tolerance to *P. gaeumannii* are very strong. Highly susceptible populations from the dry regions of northern California and southern Oregon as well as high-elevation populations exhibit early budburst, while highly resistant/tolerant populations from coastal regions exhibit late budburst (Gould et al. 2011).

Date of budburst may influence the level of inoculum to which a population is exposed, with new foliage associated with late budburst being exposed to a lower level of inoculum than foliage from populations which burst bud earlier in the spring. Both early budburst and late budburst have been implicated in mitigating and promoting damage due to insect and fungal pathogens (Desprez-Loustau et al. 2015, Sampaio et al. 2016). Climate conditions related to the timing of budburst in Douglas-fir are similar to those that affect disease pressure from both *Rhabdocline* spp. and *P. gaeumannii*. For example, early budburst is associated with Douglas-fir populations which experience low winter temperatures and the early onset of drought, climate conditions that are not conducive to *P. gaeumannii* or *Rhabdocline* spp. and thus limit the exposure of these populations to foliage diseases (Harrington et al. 2010, Gould et al. 2011, Harrington and Gould 2015, Ford et al. 2016). Therefore, it is difficult to discern adaptation to climate from adaptation to pathogen pressure.

Changes in future climates may alter the budburst phenology of Douglas-fir (Ford et al. 2016), which may in turn alter the species susceptibility to *Rhabdocline* and SNC. Studies focused on the modeling of budburst in much of the range of coastal Douglas-fir have predicted that future budburst may occur substantially earlier in much of the range of Douglas-fir. However, in the southern portion of the species range, budburst may remain unchanged or may be delayed due to a lack of chilling hours needed to satisfy bud dormancy requirements (Harrington and Gould 2015). Changes in host phenology may result in desynchronization of host and pathogen and thus reduce or enhance the impact of pathogens (Baltensweiler 1993, Ramsfield et al. 2016). The phenology of Douglas-fir is well studied, and models can provide relatively accurate estimates of growth initiation and cessation based on variables such as forcing and chilling hours (Campbell and Sorensen 1973, Harrington et al. 2010, Gould et al. 2011, Ford et al. 2016); however, insufficient information is available to model the phenology of spore dispersal for *P. gaumannii* and *Rhabdocline* spp. Therefore, it is unclear as to whether changes in climate and subsequent changes in host phenology will influence the impacts of these pathogens on the productivity of Douglas-fir.

Probability of SNC disease symptoms and moderate to severe *Rhabdocline* spp. infection associated with transfers are not predicted to significantly change, as projected climate conditions in 2080 did not result in significant increases or decreases in probability. In contrast, Zhao et al. (2011) hypothesized that future climates in the Pacific Northwest would be more continental, reducing disease pressure from SNC. The timing of leaf wetness and therefore precipitation is key for successful infection by these foliar pathogens. Large-scale climate models cannot currently predict localized seasonal patterns of precipitation as accurately as temperature. S. T. Tysor, P. L. Heinrich, and A. V. Wipple, *unpublished manuscript*, found that ClimateWNA was relatively accurate in its predictions of temperature but performed rather poorly in its prediction of precipitation. Therefore, it is difficult to predict the influence of climate change on these foliar pathogens, and results should be interpreted with these caveats. It also should be noted that climate

models vary in their predictions and results may differ using a different climate projection model.

Winter temperatures are predicted to increase in the PNW, likely leading to the increased success of foliar pathogens such as *Rhabdocline* spp. and *P. gaumannii* in areas where low winter temperatures had restricted the development of pathogens (Stone et al. 2007, 2008b, Mote and Salathé 2010, Lee et al. 2013). A study by Lee et al. (2013) predicts that SNC disease pressure will increase in areas where pathogen development is currently only limited by low winter temperatures, such as in high-elevation inland stands. Populations from high-elevation regions displayed high susceptibility to these foliage diseases. The movement of tolerant/resistant coastal or low-elevation populations further inland or up in elevation may mitigate these losses. It is recommended that tools such as the Seedlot Selection Tool (Howe et al. 2016), which have been developed to aid land managers in the identification of proper seed sources, be consulted in conjunction with the results presented in this study.

Adaptation to warmer, drier climates is a desirable characteristic which many view as important in the adaptation to future climates and, thus, influences assisted migration recommendations (St. Clair and Howe 2007, Aitken et al. 2008, Coops et al. 2016). Research as part of the SSMT, utilizing many of the same populations as the current study, has suggested that populations from source climates of cool winters and dry summers have high drought tolerance and this tolerance could be used to select seed sources for future reforestation (Bansal et al. 2015a). Results from the current study urge caution in the transfer of drought-tolerant populations from areas of cool winters and dry summers to locations of higher MSP and MWT. It may be possible, however, to select sources with higher drought tolerance from within populations with good resistance or tolerance to foliage diseases.

Our results provide evidence that (1) local seed sources are generally among the best adapted to local pathogen pressures when compared to other sources from throughout the range of a widely distributed tree species, (2) seed sources from regions with high foliage disease pressure are most resistant/tolerant to those foliage diseases, (3) seasonal temperature and precipitation are important epidemiological factors in forest disease, and (4)

assisted migration must take into account trophic interactions. Knowledge of transfer distances that are influential to the incidence and impacts of SNC and Rhabdocline is critical to proper recommendations for Douglas-fir seed transfer. Well-organized and deployed common garden studies such as the Douglas-fir SSMT are necessary to elucidate the relationship between host, pathogen, and climate.

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