

AN ABSTRACT OF THE THESIS OF

Nicholas Wilhelmi for the degree of Master of Science in Sustainable Forest Management presented on June 7, 2016

Title: The Effects of Seed Source and Planting Environment on Douglas-fir (*Pseudotsuga menziesii*) Foliage Diseases.

Abstract approved: _____

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Douglas-fir (*Pseudotsuga menziesii*) is a commercially and ecologically important tree species native to western North America. The foliar pathogens *Phaeocryptopus gaeumannii*, the causal agent of Swiss Needle Cast, and *Rhabdocline* species, the causal agents of Rhabdocline needle cast, are two important pathogens specific to Douglas-fir. These pathogens are highly influenced by climatic conditions and have been shown to disproportionately affect genetically maladapted populations, causing decreased productivity and sometimes mortality. The relationship between the levels of resistance/tolerance to these foliar pathogens and climate of the population source is a key component in the identification of proper seed sources for reforestation. The Douglas-fir Seed Source Movement Trials (SSMT) is a large provenance study of Westside Douglas-fir which consists of populations and test sites chosen to represent the range of climatic conditions experienced by Douglas-fir west of the Cascade and Sierra Nevada Mountains. We used the SSMT to assess variation in the probability of moderate to severe infection by *Rhabdocline* spp. and *P. gaeumannii*, as well as expression of disease symptoms, in relation

to climatic differences between test sites and population sources. Using generalized linear mixed models and the probit link function, probabilities were calculated using differences between population source and test sites with respect to the climate variables May through September precipitation (MSP), continentality and mean winter temperature (MWT). Stark differences were observed in side-by-side trees from different seed zones, especially in relation to the resistance to *Rhadoocone* needle cast. No patterns were observed in the infection levels of *P. gaeumannii* based on number of stomates occluded by fungal reproductive structures. However, there was variation in disease symptom expression such as crown density which was used as a surrogate for Swiss needle cast impacts in this analysis. The transfers of populations from regions of low MSP to test sites of high MSP, cool to warm MWT and high to low continentality are associated with high probabilities of moderate to severe *Rhadoocone* spp. infection and SNC disease symptoms (low crown density). Trends in high probabilities of disease symptoms and *Rhadoocone* spp. infection were associated with the movement of populations from south to north. Predictions of disease occurrence based on climate-disease-host seed source interaction indicates danger in choosing trees for assisted migration from drier regions and moving them to wetter areas in anticipation of climate change. This project exemplifies the importance of seed source movement trials in understanding trophic interactions as well as environmental controls on tree growth and adaptation

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The Effects of Seed Source and Planting Environment on Douglas-fir (*Pseudotsuga menziesii*) Foliage Diseases.

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Nicholas Wilhelmi, Author

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Chapter 1 : General Introduction

Anthropogenic climate change is predicted to have serious implications for forests and forest management (Rehfeldt 2001, St Clair and Howe 2007, Aitken et al. 2008, Littell et al. 2010, Woods et al. 2010, Sturrock 2012, Coops et al. 2016). Temperatures are estimated to rise from 0.3-4.8 °C by the end of the 21st century depending on the model and emission scenario being used (IPCC 2014). The period from 1983-2012 was estimated to be the warmest 30 year period in the last 1400 years by the Intergovernmental Panel on Climate Change (2014). These changes in climate are predicted to have serious impacts on forest productivity and management, thus, impacting the human and ecological communities that depend on them. It is estimated that most long lived trees species will not be able to keep pace with the current rates of climate change and will therefore be exposed to climatic conditions to which they are not adapted (Rehfeldt et al. 2001, Aitken et al. 2008, Ste. Marie et al. 2011, Rehfeldt et al. 2014). These changes may lead to increased drought stress in the summer months as well as changes in the growing season length, which have already been observed over the past 30 years (Mote and Salathé 2010, Abatzoglou et al. 2014, Mildrexler et al. 2016) . In addition to abiotic stressors, climate change may also alter host pathogen relationships increasing susceptibility to pathogens or increased pressure (Mueller and Hellmann 2008; Stone et al. 2008b, Sturrock 2012, Woods et al. 2005, Woods et al. 2010).

Foliar diseases are responsible for serious losses in productivity in many forest trees across the world. Foliar diseases are highly sensitive to changes in climate and have been associated with severe economic and ecological impacts in relation to changes in climate (Agrios 2005, Woods et al. 2005). *Phaeocryptopus gaeumannii* and *Rhabdocline*

spp are foliar pathogens specific to Douglas-fir (*Pseudotsuga menziesii* (Mirb.)Franco), the most prevalent and economically important conifer species of the Pacific Northwest (Franklin and Dyrness 1973, Lavender and Hermann 2014). These pathogens are responsible for causing the foliage diseases Swiss Needle Cast (SNC) and Rhabdocline needle cast (Rhabdocline), respectively. These foliage disease have been responsible for major growth reductions and significant economic loss in Douglas-fir forests (Kurkela 1981, Maguire et al. 2002, Black 2010). SNC and Rhabdocline needle cast have been shown to disproportionately affect maladapted seed sources (Stone 1997). Severe outbreaks are associated with specific climatic conditions including high spring/summer precipitation, especially May through June, and mild winter temperatures (Hansen et al. 2000; Rosso and Hansen 2003, Manter et al. 2005, Stone et al. 2008b, Lee et al. 2013).

Swiss needle cast (SNC) is a disease caused by the ascomycete fungus *Phaeocryptopus gaeumannii* which infects and colonizes Douglas fir foliage (*Pseudotsuga menziesii* (Mirb.) Franco). This pathogen was first described by Robert Gaeumann around 1925 as was responsible serious losses in European Douglas-fir plantations where Douglas-fir was grown as an exotic (Boyce 1940). *P. gaeumannii* was considered an innocuous fungal associate of Douglas-fir within its native range until the 1980s when foresters began to notice symptoms and increased impacts (Boyce 1961, Hansen et al. 2000). Since then the acreage affected by this foliar disease has continued to expand, affecting nearly 238,595 acres in Oregon and 141,520 in Washington in 2015, and resulting in total volume reductions in plantations ranging from 23% to 52% (

Hansen et al. 2000, Maguire 2002, Black et al. 2010, Shaw et al. 2011, Nordlander and Kanaskie 2015).

Swiss needle cast is associated with specific climate conditions characterized by relatively warm mild winters and moist conditions in the spring/early summer when Douglas-fir bud burst is occurring (Boyce 1940, Hansen et al. 2000, Stone 2007, Stone et al. 2008a, Lee et al. 2013). The dispersal, germination and infection of Douglas-fir by *P. gaeumannii* is highly dependent on temperature and moisture. Optimal temperatures for dispersal and germination of spores are estimated to be in the range of 18-20 °C. Successful infection of Douglas-fir tissue requires a minimum of 24 hours of needle surface moisture (Capitano 1999, Stone et al. 2008a). Therefore, this process is very sensitive to dry conditions (Capitano 1999, Stone et al. 2008a). Michaels and Chastagner (1984) have observed the release of spores by *P. gaeumannii* as late as September. However, peak sporulation coincides with conducive weather conditions in the spring/early summer during after bud burst and shoot elongation of Douglas-fir. This is thought to be when Douglas-fir tissue is most susceptible to infection. Capitano (1999) showed decreasing amounts of spores being released as the summer progresses with very few observed in August. The conditions most conducive to infection are most prevalent in the coastal areas of northern Oregon and Washington where the disease has become most severe (Hansen et al. 2000, Shaw et al. 2011).

Infection of the needle takes place through the stomata. This is the exclusive mode of infection by this pathogen (Capitano 1999, Stone et al. 2008a). Neither direct penetration of host cell walls nor penetration between epidermal cells has been observed. Germ-hyphae

from one spore has the ability to continue to grow epiphytically after the infection of one stomate producing multiple appressoria to then infect multiple stomata. This enables rapid colonization of host tissue (Capitano 1999, Stone et al. 2008a). Following the infection of the Douglas fir needle, hyphae colonize the interior of the needle, mainly inhabiting the intercellular spaces but never penetrating the epidermis. The fruiting bodies of *P.gaeumannii* (pseudothecia) can be visible emerging from stomata in early fall depending on the environment (Hansen et al. 2000).

The plugging of the stomata by pseudothecia inhibits stomatal conductance and limits CO₂ assimilation (Manter et al. 2000). This reduces the productivity of the needle, leading to pre-mature abscission (Manter et al. 2000). Fruiting bodies increase with the age of the needle as the pathogen continues to colonize the needle. Older needle cohorts consistently have a higher percentage of stomata occluded (Hansen et al. 2000). The plugging of stomata by the fruiting bodies of *P. gaeumannii* results in chlorotic crown color, low needle retention, low crown density and subsequent losses in growth (Boyce 1940, Maguire et al. 2002).

Variation in the resistance and or tolerance to SNC has been noted in many past studies, with increased susceptibility being associated with seed sources from inland areas characterized by low precipitation and cold winters (Hood 1982, McDermott and Robinson 1989, Johnson 2002). Genetics has proven to be a valuable tool in the management of this notoriously difficult disease and significant gains have been made through tree improvement programs resulting in significant growth increases over the unimproved seed sources (Jayawickrama et al. 2012). However, these gains are only seen

on sites with moderate to low disease severity. Severe disease pressure as experienced in the Tillamook area of northern Oregon has been observed to overcome any level of resistance/tolerance (Kastner et al. 2001).

Rhabdocline needle cast was first noted by Weir in 1911 and has been responsible for major losses where Douglas-fir is grown as an exotic (Boyce 1961, Kurkela 1981) Lavender and Hermann 2014). Within the natural range of Douglas-fir where *Rhabdocline* spp. is considered native, disease is associated with the planting of maladapted seed sources as well as with years in which spring and summer conditions are abnormally wet and cool (Brandt 1960, Hagle et al. 2003, Goheen and Willhite 2006). This pathogen requires conditions very similar to SNC for infection and colonization, but is usually completed with spore dispersal by July. *Rhabdocline* spp. also infects newly emerging foliage immediately following bud burst, and requires moist conditions, ideally 100% humidity, during this period for successful infection and colonization (Parker 1970).

Infection of Douglas fir needles by *Rhabdocline* spp is initiated by the germination of mature ascospores which germinate and forcibly enter through the needle epidermis (Brandt 1960). Ascospore release takes place during shoot elongation of Douglas fir, when host tissue is most susceptible (Brandt 1960, Chastagner et al. 1990). According to work by Chastagner et al. (1990) the highest concentrations of mature ascospores were found in May through June; by late June less than 20% of asci contained mature ascospores. As summer progressed needles released fewer ascospores with only

10% of needles collected in late July releasing ascospores and zero needles collected in mid-August releasing ascospores.

Humidity and rain are driving forces of spore release and severity of outbreak. Conducive conditions for *Rhabdocline* spp. during shoot elongation can lead to large scale outbreaks (Brandt 1960, Chastagner et al. 1990). Brandt (1960) observed increases in spore release coinciding with spikes in the relative humidity.

The variation in genetic resistance of different Douglas-fir populations to *Rhabdocline* was noted early on by Boyce (1961) as well as in early European provenance studies, identifying the coastal variety (var. *menziesii*) as more resistant than the inland variety (var. *glauca*) (Lavender and Hermann, 2014). Much effort, due to the preferences of Christmas tree industry, has gone into studying the variation in resistance of the *glauca* variety. Research has identified geographic and climatic factors which influence the respective levels of susceptibility of different populations within the intermountain variety (Hoff 1987, Merrill 1990, Chastagner 2001). Variation in resistance within the coastal variety has been noted but no studies have directly addressed this variation or the geographic and climatic factors that may influence it (Boyce 1961). Due to the high level of variation in resistance, *Rhabdocline* has been influential in the selection of seed sources where Douglas-fir is grown as an exotic (Lavender and Herman 2014). Since the formation of seed zones in the 1960s, *Rhabdocline* needle cast has become a disease of minor concern within the native range of Douglas-fir (Stone 1997). Seed zones establish restricted geographic or climatic areas in which seed can be safely transferred. This system was established to ensure the planting of proper seed sources and

reduce losses due the planting of maladapted trees (Randall and Berrang 2002, Johnson et al. 2004, Ying and Yanchuk, 2006)

Outbreaks of foliar pathogens such as these are associated with specific climatic conditions as well as with the planting of maladapted trees (Stone 1997, Stone et al. 2008a, Stone et al. 2008b, Woods et al. 2005). Trends in climate change have been predicted to lead to Douglas-fir populations that are maladapted to their current seed zones (St Clair and Howe 2007, Littell et al. 2010, Rehfeldt et al. 2014). These changes, depending on how patterns of precipitation and temperature are affected, may also lead to an increase in disease pressure and increased geographic range of foliage diseases such as SNC and Rhabdocline, thereby exposing populations of trees to pathogens or to accustomed disease pressure (Woods et al. 2005, Stone et al. 2008b). Changes in climate have also been shown to influence host defense mechanisms, affecting the relative tolerance or resistance of a population or species to pathogens or insects and possibly leading to increased impacts (Telford 2014, Ennos 2015). It is also possible that changes in climate will lead to reduced impacts related to foliage diseases. Zhou et al (2011) predicted reduced impacts associated with SNC due to increased continentality in climate models.

It is estimated that spring precipitation, March through May, has increased at a rate of 2%-5% a decade, with average spring precipitation from 2009 to 2012 estimated to be 30% above the twentieth century normals (30 year averages). Temperatures in the Pacific Northwest have increased at an estimated rate of 0.2 ° C per decade (Abatzoglou et al. 2014). Changes such as this will likely lead to an increased presence and severity of

SNC and Rhabdocline. The rise of the current SNC epidemic has coincided with the rise in temperatures and precipitation observed by Abatzoglou et al. (2014).

Climate change is predicted to have serious impacts on the growth and productivity of economically and ecologically important Douglas-fir (St Clair and Howe 2007). Douglas-fir is widely recognized as a specialist species, with regard to genetic adaptation because populations are closely adapted to their source climate, displaying large genetic variation over steep clines in climatic conditions (Campbell and Sorensen 1973, St.Clair 2005). Research on the impacts of climate change on Douglas-fir has largely focused on the responses of Douglas fir to various changes in climate and climate-related stressors such as drought and cold hardiness (Bansal et al. 2015a, Bansal et al. 2015b, Rehfeldt et al. 2014, St.Clair et al. 2005).

The large range of geographic and climatic conditions from hot and dry to cool and wet inhabited by Douglas-fir has likely resulted in wide variation in the pathogens and disease pressure to which populations are exposed (Franklin and Dyrness, 1973, Manter et al. 2005). The influence of climate change on the incidence and impacts of pathogens is a relatively large knowledge gap.

The large degree of genetic variability exhibited by Douglas-fir has proven to be a valuable tool in the management of both Rhabdocline and SNC. The use of genetic traits through the identification and deployment of populations predicted to be adapted to future climates is among the most widely discussed adaptive management strategies aimed at mitigating the negative impacts of climate change (McDermott and Robinson 1989, Johnson et al. 2002, Spittlehouse and Stewart, 2004, Sturrock et al. 2011,

Jayawickrama et al. 2012). However, the mechanisms that influence the successful movement of Douglas-fir populations to novel locations are not well understood.

Long term reciprocal transplant provenance studies spanning diverse geographic and climatic conditions provide insight in to the relative impacts that changes in climate will have on different populations of trees. The exposure of populations to different growing environments has been valuable in the identification of resistance/tolerance to different forest diseases and insects as disease an insect pressure may vary according to the climatic condition of the site (McDermott and Robinson 1989, Hood and Kimberley 2005, Enderle et al. 2013). Long term reciprocal transplant provenance studies provide the most appropriate platform from which to examine the responses of different populations to various climate change scenarios and thus offer valuable information to incorporate in adaptive management strategies (Randall and Berrang 2002, Johnson et al. 2004, Kaweki and Ebert 2004, St Clair and Howe 2007, Gould et al. 2011, Gould et al. 2012, Bansal et al. 2015a, Bansal et al. 2015b).

This study utilizes a large reciprocal transplant provenance study, the Seed Source Movement Trials (SSMT) (Gould et al. 2011, Gould et al. 2012, Bansal et al.2015a, Bansal et al. 2015b), to assess variation in the incidence and impacts of Rhabdocline and Swiss needle cast on Douglas-fir populations. The test sites and populations used in this study were chosen to represent the range of growing conditions experienced by west side Douglas-fir and can therefore be assumed to represent a wide range in disease severity. This study will help to elucidate the impacts that SNC and Rhabdocline will have on a diverse range of Douglas-fir populations when planted in a diverse range of

environments. This will establish a base of knowledge from which to better understand the range in disease susceptibility of west side Douglas-fir populations.

The information fills a large knowledge gap which will improve current reforestation practices by providing low risk transfer distances related to the two most influential Douglas-fir foliar pathogens in the Pacific Northwest. An understanding of the distribution of the variation in resistance/tolerance to these pathogens and the climatic factors that influence this variation is important to the formation of effective adaptive management strategies to mitigate the impacts of climate change.

Literature Cited

Abatzoglou, J., D. Rupp , and P. Mote. 2014. “Seasonal Climate Variability and Change in the Pacific Northwest of the United States.” *Journal of Climate* 27 (5): 2125–2142. doi:10.1175/JCLI-D-13-00218.1.

Agrios, G.N. 2005. *Plant Pathology*. Academic Press.

Aitken, S. N., S. Yeaman, J.A. Holliday, T.Wang, and S. C. McLane. 2008. “Adaptation, Migration or Extirpation: Climate Change Outcomes for Tree Populations.” *Evolutionary Applications* 1 (1): 95–111. doi:10.1111/j.1752-4571.2007.00013.x.

Bansal, S., C. A. Harrington, P.J. Gould, and J. B. St. Clair. 2015a. “Climate-Related Genetic Variation in Drought-Resistance of Douglas-Fir (*Pseudotsuga menziesii*). (Report)” 21 (2): 947.

Bansal, S., J. B. St. Clair, C.A. Harrington, and P. J. Gould. 2015b. “Impact of Climate Change on Cold Hardiness of Douglas-Fir (*Pseudotsuga Menziesii*): Environmental and Genetic Considerations.” *Global Change Biology* 21 (10): 3814–26. doi:10.1111/gcb.12958.

Black B.A., D.C. Shaw, J.K. Stone. 2010. Impacts of Swiss needle cast on overstory Douglas-fir forests of the western Oregon Coast Range. *For. Ecol. Manag.* 259: 1673-1680

Boyce, J. S. 1940. “A needle - cast of Douglas Fir associated with *Adelopus gaumanni*.” *Phytopathology*. 30 (8): 649–655 .

- Boyce, J. S. 1961. Forest Pathology. 1961 Third Edition edition. N.Y.; Toronto: McGraw. pp 157-162.
- Brandt, R. W. 1960a. The Rhabdocone Needle Cast of Douglas Fir /. Syracuse : State University College of Forestry,. <http://www.biodiversitylibrary.org/item/126103>.
- Campbell, R.K., and F. C. Sorensen. 1973. "Cold-Acclimation in Seedling Douglas-Fir Related to Phenology and Provenance." Ecology 54 (5): 1148–51.
doi:10.2307/1935582.
- Capitano, B. 1999. "The Infection and Colonization of Douglas-Fir by *Phaeocryptopus Gaeumannii*" Corvallis, Oregon: Oregon State University.
- Chastagner, G. A., R.S. Byther, and K.L. Riley. 1990a. Recent Research on Foliage Diseases :conference Proceedings : Carlisle, Pennsylvania, May 29-June 2, 1989 /. Washington, D.C. : <http://hdl.handle.net/2027/umn.31951d02988383q>.
- Chastagner, G. A. 2001. "Susceptibility of Intermountain Douglas-Fir to Rhabdocone Needle Cast When Grown in the Pacific Northwest." Plant Health Progress.
doi:10.1094/PHP-2001-1029-01-RS.
- Coops, N. C., R. H. Waring, A. Plowright, J. Lee, and T. E. Dilts. 2016. "Using Remotely-Sensed Land Cover and Distribution Modeling to Estimate Tree Species Migration in the Pacific Northwest Region of North America." Remote Sensing 8 (1): 65. doi:10.3390/rs8010065.

- Ennos, R. A. 2015. "Resilience of Forests to Pathogens: An Evolutionary Ecology Perspective." *Forestry* 88 (1): 41–52. doi:10.1093/forestry/cpu048.
- Franklin, J.F., and C. T. ; Dyrness. 1973. *Natural Vegetation of Oregon and Washington*. <http://www.treesearch.fs.fed.us/pubs/26203>.
- Goheen, E. M., and E. A. Willhite. 2006. *Field Guide to the Common Diseases and Insect Pests of Oregon and Washington Conifers* /. [Portland, Or.] : USDA Forest Service, Pacific Northwest Region ; <http://www.biodiversitylibrary.org/bibliography/80321>.
- Gould, P.J., C. A. Harrington, and B. J. St Clair. 2011. "Incorporating Genetic Variation into a Model of Budburst Phenology of Coast Douglas-Fir (*Pseudotsuga Menziesii* var. *menziesii*)" *Canadian Journal of Forest Research* 41: 139–50.
- Gould, P. J., C. A. Harrington, J. B. St Clair, and S. Thomas. 2012. "Growth Phenology of Coast Douglas-Fir Seed Sources Planted in Diverse Environments." *Tree Physiology* 32 (12): 1482–1496. doi:10.1093/treephys/tps106.
- Hagle, S. K., S. Tunnock, and K. E. Gibson. 2003. *Field Guide to Diseases and Insect Pests of Northern and Central Rocky Mountain Conifers*. Diseases and Insect Pests of Northern and Central Rocky Mountain Conifers. Missoula, Mont.: U.S. Dept. of Agriculture, Forest Service, State and Private Forestry, Northern Region. <http://catalog.hathitrust.org/Record/007425449>.
- Hansen, E. M., J. K. Stone, B. R. Capitano, P. Rosso, W. Sutton, L. Winton, A. Kanaskie, and M. G. McWilliams. 2000. "Incidence and Impact of Swiss Needle Cast in

- Forest Plantations of Douglas-Fir in Coastal Oregon.” *Plant Disease* 84 (7): 773–778. doi:10.1094/PDIS.2000.84.7.773.
- Hoff, R. J. 1987. *Susceptibility of Inland Douglas-Fir to Rhabdocline Needle Cast*. U.S. Dept. of Agriculture, Forest Service, Intermountain Research Station.
- Hood, I. A. 1982. “Phaeocryptopus Gaeumannii on Pseudotsuga Menziesii in Southern British Columbia.” *New Zealand Journal of Forestry Science* 12 (3): 415–424.
- Hood, I. A., and M. O. Kimberley. 2005. “Douglas Fir Provenance Susceptibility to Swiss Needle Cast in New Zealand.” *Australasian Plant Pathology* 34 (1): 57–62. doi:10.1071/AP04080.
- IPCC, 2014: *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp
- Jayawickrama K., D. C. Shaw, and T. Z. YE. 2012. “Genetic Selection in Coastal Douglas-Fir for Tolerance to Swiss Needle Cast Disease”. *Proceedings of the fourth international workshop on the genetics of host-parasite interactions in forestry: Disease and insect resistance in forest trees*. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. 372 pp.
- Johnson, G. R., 2002. “Genetic Variation of Douglas-Fir to Swiss Needle Cast as Assessed by Symptom Expression.” *Silvae Genetica* 51: 80–86.

- Johnson, G. R., F. C. Sorensen, J. B. St Clair, and R. C. Cronn. 2004. "Pacific Northwest Forest Tree Seed Zones A Template for Native Plants?" *Native Plants Journal* 5 (2): 131–40. doi:10.2979/NPJ.2004.5.2.131.
- Johnson, R., F. Temel, K. Jayawickrama, and others. 2002. "Genetic Studies Involving Swiss Needle Cast." *Swiss Needle Cast Cooperative Annual Report*, 38–43.
- Kastner, W. W., S.M. Dutton, D.M. Roche. 2001. "Effects of Swiss Needle Cast on Three Douglas-Fir Seed Sources on a Low-Elevation Site in the Northern Oregon Coast Range: Results after Five Growing Seasons." *Western Journal of Applied Forestry* 16: 31–34.
- Kawecki, T. J., and D. Ebert. 2004. "Conceptual Issues in Local Adaptation." *Ecology Letters* 7 (12): 1225–41. doi:10.1111/j.1461-0248.2004.00684.x.
- Kurkela, T.. 1981. *Growth Reduction in Douglas Fir Caused by Rhabdocline Needle Cast*. Communicationes Instituti Forestalis Fenniae. Helsinki: Finnish Forest Research Institute.
- Lavender, D. P., and R. K. Hermann. 2014. *Douglas-Fir: The Genus Pseudotsuga*. Corvallis, OR : Forest Research Publications Office, Oregon State University. pp 73-115 <http://ir.library.oregonstate.edu/xmlui/handle/1957/47168>.
- Lee, E. H., P. A. Beedlow, R. S. Waschmann, C.A. Burdick, and D.C. Shaw. 2013. "Tree-Ring Analysis of the Fungal Disease Swiss Needle Cast in Western Oregon Coastal Forests." *Canadian Journal of Forest Research* 43 (8): 677–90. doi:10.1139/cjfr-2013-0062.

- Littell, J. S., E. E. Oneil, D. McKenzie, J. A. Hicke, J. A. Lutz, R. A. Norheim, and M. M. Elsner. 2010. "Forest Ecosystems, Disturbance, and Climatic Change in Washington State, USA." *Climatic Change* 102 (1–2): 129–58.
doi:10.1007/s10584-010-9858-x.
- Maguire, D. A., A. Kanaskie, W. Voelker, R. Johnson, and G. Johnson. 2002. "Growth of Young Douglas-Fir Plantations across a Gradient in Swiss Needle Cast Severity." *Western Journal of Applied Forestry* 17 (2): 86–95.
- Manter, D. K., B. J. Bond, K. L. Kavanagh, P. H. Rosso, and G. M. Filip. 2000. "Pseudothecia of Swiss Needle Cast Fungus, *Phaeocryptopus Gaeumannii*, Physically Block Stomata of Douglas Fir, Reducing CO₂ Assimilation." *New Phytologist* 148 (3): 481–491. doi:10.1046/j.1469-8137.2000.00779.x.
- Manter, D. K., P. W. Reeser, and J. K. Stone. 2005. "A Climate-Based Model for Predicting Geographic Variation in Swiss Needle Cast Severity in the Oregon Coast Range." *Phytopathology* 95 (11): 1256–1265.
doi:http://dx.doi.org.ezproxy.proxy.library.oregonstate.edu/10.1094/PHYTO-95-1256.
- McDermott, J. M., and R. A. Robinson. 1989. "Provenance Variation for Disease Resistance in *Pseudotsugamenziesii* to the Swiss Needle-Cast Pathogen, *Phaeocryptopusgaeumannii*." *Canadian Journal of Forest Research* 19 (2): 244–246. doi:10.1139/x89-034.

- Merrill, W. 1990. "Rhabdocline Needlecast Resistance in Douglas-Fir Seed Sources from the Southwestern United States." Recent Research on Foliage Diseases : Conference Proceedings, Carlisle, Pennsylvania, May 29-June 2, 1989.
- Michaels, E., and G. A. Chastagner. 1984. "Seasonal Availability of *Phaeocryptopus Gaeumannii* Ascospores and Conditions That Influence Their Release." Plant Disease 68 (11): 942–944.
- Mildrexler, D., Zhiqiang Y., W. B. Cohen, and D. M. Bell. 2016. "A Forest Vulnerability Index Based on Drought and High Temperatures," February.
doi:10.1016/j.rse.2015.11.024.
- Mote, P. W., and Salathé. 2010. "Future Climate in the Pacific Northwest." Climatic Change 102 (1–2): 29–50. doi:10.1007/s10584-010-9848-z.
- Norlander D., A. Kanaski. (2014). 2014 Swiss Needle Cast Aerial Survey. Oregon Department of Forestry.
- Parker, A. K. 1970. "Effect of Relative Humidity and Temperature on Needle Cast Disease of Douglas-Fir." Phytopathology 60 (August): 1270.
- Randall, W. K., and Berrang, P. (2002). Washington Tree Seed Transfer Zones. Washington State Department of Natural Resources. n.d.
- Rehfeldt, G., W. Wykoff, and C. Ying. 2001. "Physiologic Plasticity, Evolution, and Impacts of a Changing Climate on *Pinus Contorta*." Climatic Change 50 (3): 355–376. doi:10.1023/A:1010614216256.

- Rehfeldt, G. E., B. C. Jaquish, C. S. Romero, D.G. Joyce, L. P. Leites, J. B. St Clair, and J.López-Upton. 2014. “Comparative Genetic Responses to Climate in the Varieties of *Pinus Ponderosa* and *Pseudotsuga Menziesii*: Reforestation.” *Forest Ecology and Management* 324 (July): 147–57. doi:10.1016/j.foreco.2014.02.040.
- Rosso, P. H., and E. M. Hansen. 2003. “Predicting Swiss Needle Cast Disease Distribution and Severity in Young Douglas-Fir Plantations in Coastal Oregon.” *Phytopathology* 93 (7): 790–798.
- Shaw, D. C., G. M. Filip, A. Kanaskie, D. A. Maguire, and W. A. Littke. 2011. “Managing an Epidemic of Swiss Needle Cast in the Douglas-Fir Region of Oregon: The Role of the Swiss Needle Cast Cooperative.” *Journal of Forestry* 109 (2): 109–119.
- Spittlehouse, D., and R. Stewart. 2004. “Adaptation to Climate Change in Forest Management.” *Journal of Ecosystems and Management* 4 (1).
- St.Clair, J. B., N. L. Mandel, and K. W. Vance-Borland. 2005. “Genecology of Douglas Fir in Western Oregon and Washington.” *Annals of Botany* 96 (7): 1199–1214. doi:10.1093/aob/mci278.
- St Clair, B., and G.T. Howe. 2007. “Genetic Maladaptation of Coastal Douglas-fir Seedlings to Future Climates.” *Global Change Biology* 13 (7): 1441–1454. doi:10.1111/j.1365-2486.2007.01385.x.

- Ste-Marie, C., E.A. Nelson, A. Dabros, and M. Bonneau. 2011. "Assisted Migration: Introduction to a Multifaceted Concept." *The Forestry Chronicle* 87 (6): 724–30. doi:10.5558/tfc2011-089.
- Stone, J. 1997. Rhabdocone needle cast. Pages 54-55 in: *Compendium of Conifer Diseases*. E. M. Hansen and K. J. Lewis, eds. The American Phytopathological Society, St. Paul, MN
- Stone, J. K., I. A. Hood, M. S. Watt, and J. L. Kerrigan. 2007. "Distribution of Swiss Needle Cast in New Zealand in Relation to Winter Temperature." *Australasian Plant Pathology* 36 (5): 445–54. doi:10.1071/AP07049.
- Stone, J. K., B. R. Capitano, and J. L. Kerrigan. 2008a. "The Histopathology of *Phaeocryptopus Gaeumannii* on Douglas-Fir Needles." *Mycologia* 100 (3): 431–444.
- Stone, J. K., L. B. Coop, and D. K. Manter. 2008b. "Predicting Effects of Climate Change on Swiss Needle Cast Disease Severity in Pacific Northwest Forests." *Canadian Journal of Plant Pathology* 30 (2): 169–176. doi:10.1080/07060661.2008.10540533.
- Sturrock, R. 2012. "Climate Change and Forest Diseases: Using Today's Knowledge to Address Future Challenges." *Forest Systems* 21 (2): 329–36. doi:10.5424/fs/2012212-02230.

- Telford, A., S. Cavers, R. A. Ennos, and J. E. Cottrell. 2014. "Can We Protect Forests by Harnessing Variation in Resistance to Pests and Pathogens?" *Forestry*, April, cpu012. doi:10.1093/forestry/cpu012.
- Temel, F., G. R. Johnson, and W. T. Adams. 2005. "Early Genetic Testing of Coastal Douglas-Fir for Swiss Needle Cast Tolerance." *Canadian Journal of Forest Research/Revue Canadienne de Recherche Forestiere* 35 (3): 521–529.
- Wang, T., A. Hamann, A. Yanchuk, G. A. O'neill, and S. N. Aitken. 2006. "Use of Response Functions in Selecting Lodgepole Pine Populations for Future Climates." *Global Change Biology* 12 (12): 2404–16. doi:10.1111/j.1365-2486.2006.01271.x.
- Weir, J. R. 1917. "A Needle Blight of Douglas Fir." *J. Agr. Res.* 10 (2), 99–103.
- Winder, R., E. Nelson, and T. Beardmore. 2011. "Ecological Implications for Assisted Migration in Canadian Forests." *The Forestry Chronicle* 87 (6): 731–44. doi:10.5558/tfc2011-090.
- Woods, A., K., D. Coates, and A. Hamann. 2005. "Is an Unprecedented Dothistroma Needle Blight Epidemic Related to Climate Change?" *BioScience* 55 (9): 761–69. doi:10.1641/0006-3568(2005)055[0761:IAUDNB]2.0.CO;2.
- Woods, A. J., D. Heppner, H. H. Kope, J. Burleigh, and L. Maclauchlan. 2010. "Forest Health and Climate Change: A British Columbia Perspective." *The Forestry Chronicle* 86 (4): 412–22. doi:10.5558/tfc86412-4.

- Ying, C.C., and A. D. Yanchuk. 2006. "The Development of British Columbia's Tree Seed Transfer Guidelines: Purpose, Concept, Methodology, and Implementation." *Forest Ecology and Management, Perspectives on Site Productivity of Loblolly Pine Plantations in the Southern United States*, 227 (1–2): 1–13.
doi:10.1016/j.foreco.2006.02.028.
- Zhao, J., D. B. Mainwaring, D. A. Maguire, and A. Kanaskie. 2011. "Regional and Annual Trends in Douglas-Fir Foliage Retention: Correlations with Climatic Variables." *Forest Ecology and Management* 262 (9): 1872–86.
doi:10.1016/j.foreco.2011.08.00

**Chapter 2: The Effects of Seed Source and Planting Environment on Douglas-fir
(*Pseudotsuga menziesii*) Foliage Diseases**

Abstract

Douglas-fir (*Pseudotsuga menziesii*) is a commercially and ecologically important tree species native to western North America. The foliar pathogens *Phaeocryptopus gaeumannii*, the causal agent of Swiss Needle Cast, and *Rhabdocline* species, the causal agents of Rhabdocline needle cast, are two important pathogens specific to Douglas-fir. These pathogens are highly influenced by climatic conditions and have been shown to disproportionately affect genetically maladapted populations, causing decreased productivity and sometimes mortality. The relationship between the levels of resistance/tolerance to these foliar pathogens and climate of the population source is a key component in the identification of proper seed sources for reforestation. The Douglas-fir Seed Source Movement Trials (SSMT) is a large provenance study of Westside Douglas-fir which consists of populations and test sites chosen to represent the range of climatic conditions experienced by Douglas-fir west of the Cascade and Sierra Nevada Mountains. We used the SSMT to assess variation in the probability of moderate to severe infection by *Rhabdocline* spp. and *P. gaeumannii*, as well as expression of disease symptoms, in relation to climatic differences between test sites and population sources. Using generalized linear mixed models and the probit link function, probabilities were calculated using differences between population source and test sites with respect to the climate variables May through September precipitation (MSP), continentality and mean winter temperature (MWT). Stark differences were observed in side-by-side trees from different seed zones, especially in relation to resistance to Rhabdocline needle cast. No patterns were observed in the infection levels of *P. gaeumannii* based on number of stomates occluded by fungal reproductive structures. However, there was variation in disease symptom expression, such as crown

density which was used as a surrogate for Swiss needle cast impacts in this analysis. The transfers of populations from regions of low MSP to test sites of high MSP, cool to warm MWT and high to low continentality are associated with high probabilities of moderate to severe *Rhabdocline* spp. infection and SNC disease symptoms (low crown density). Trends in high probabilities of disease symptoms and *Rhabdocline* spp. infection were associated with the movement of populations from south to north. Predictions of disease occurrence based on climate-disease-host seed source interaction indicates danger in choosing trees for assisted migration from drier regions and moving them to wetter areas in anticipation of climate change. This project exemplifies the importance of seed source movement trials in understanding trophic interactions as well as environmental controls on tree growth and adaptation

Introduction

Phaeocryptopus gaeumannii and *Rhabdocline* spp. (Figure 2.1) are Ascomycete foliar pathogens specific to Douglas-fir (*Pseudotsuga menziesii* (Mirb.)Franco), the most prevalent and economically valuable conifer species of the Pacific Northwest (Lavender and Hermann 2014). These pathogens are responsible for causing the diseases Swiss Needle Cast (SNC) and Rhabdocline needle cast (Rhabdocline), respectively, and have been responsible for major growth reductions and economic loss in Douglas-fir forests (Stone 1997, Maguire et al. 2002). Outbreaks of these foliar pathogens are associated with specific climatic conditions and the planting of maladapted or off-site trees (Stone 1997, Hansen et al. 2000, Manter et al. 2005, Black 2010).

Current trends in climate change may lead to maladapted Douglas-fir populations by the end of the century (St Clair and Howe 2007). These changes may also lead to an increase in disease pressure and geographic range of foliage diseases such as SNC and Rhabdocline, possibly resulting in increased economic and ecological impacts (Woods et al. 2005, Stone et al. 2008b). The acreage affected by SNC has steadily increased since the 1990s and is now estimated to affect nearly 237,145 plus hectares (Figure 2.2) (Nordlander and Kanaskie 2015). This observed rise in the acreage affected by SNC coincides with steady increases in temperatures and spring precipitation in the Pacific Northwest (Mote 2003, Black et al. 2010, Stone et al. 2008b).

Long lived forest trees, such as Douglas-fir, may not be able to migrate at a rate sufficient to adequately adapt to current rates of climate change (Rehfeldt et al. 2001).

These rapid rates of climate change may render many west side Douglas-fir populations maladapted to their current seed zones resulting in large economic losses (St Clair and Howe 2007). 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 (St.Clair and Howe 2007). Warmer winter/fall/spring temperature which can lead to maladaptation due to the timing of bud burst and bud set not occurring at the proper time (St.Clair and Howe 2007, Gould et al. 2011). This may lead to increased risks of early fall and late spring frosts as well as increased susceptibility to drought (Cannell and Smith 1986)

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. (Rehfeldt et al. 2001; St Clair and Howe 2007, Aubin et al. 2011, Winder et al. 2011, Rehfeldt 2014, Coops et al. 2016) . There are varying degrees of assisted migration which include but are not limited to ; 1) Assisted population migration which refers to the human assisted movement of populations within the natural range of the species 2) Assisted range expansion which refers to the human assisted movement of a species just outside of the established natural range, mimicking natural range expansion 3) Assisted long distance migration which refers to the human assisted movement of species outside of their natural range into areas which would not be colonized in the absence of human assistance (Ste-Marie et al. 2011, Winder et al. 2011). Proponents of assisted migration have recommended the movement of seed from south to north, and higher in elevation in order to match populations to areas they are predicted to be adapted

or most productive based on climate projections (Rehfeldt et al. 2001, St Clair and Howe 2007, Aitken et al. 2008, Rehfeldt et al. 2014, Coops et al. 2016). Assisted migration will likely expose these populations to changes in climate and therefore pathogens and disease pressure to which they are not accustomed. Due to the close association of severe impacts of *Rhabdocline* and SNC with maladapted populations, it is likely that these foliage diseases will affect reforestation with or without assisted migration under current climate change predictions (Boyce 1961, Stone 1997, Manter et al. 2005, Mueller and Hellmann 2008, Stone et al. 2008b, Lee et al. 2013).

Climate influences the distribution and impacts associated with SNC and *Rhabdocline*. Climate variables influential to the development of *Rhabdocline* spp and *P. gaeumannii* include spring/summer precipitation, mean winter temperature and continentality. *Rhabdocline* spp and *P. gaeumannii* require high spring/summer precipitation for the successful dispersal, germination and infection of host tissue (Capitano 1999, Stone et al. 2008a). These pathogens reproduce annually, fruiting once a year and therefore the conditions during sporulation (May – August) will largely dictate the level of disease severity. Severe out breaks can be tied to rapid increases in moisture (Brandt 1960, Boyce 1961, Michaels and Chastagner 1984, Capitano 1999). Mild mean winter temperatures, such as those experienced in coastal Oregon and Washington, have consistently been associated with areas experiencing high disease pressure (Hansen et al. 2000, Manter et al. 2005, Rosso and Hansen 2003, Stone et al. 2007, Shaw 2011). Low winter temperatures negatively affect development of fungal pathogens by inhibiting the colonization of host tissue and are therefore highly influential in the spatial distribution

and level of disease severity (Agrios 2005). Continentality (the difference between the mean temperature of the warmest and coldest months of the year) was identified by Zhou et al. (2012) as one of the most influential among a large selection of climate variables on needle retention in Swiss Needle Cast affected areas. Extreme heat and cold temperatures 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)

Winter temperatures and spring/summer precipitation have steadily increased in the Pacific Northwest throughout the last century (Mote 2003, Abatzoglou et al. 2013, Mildrexler et al. 2016). It is estimated that spring precipitation (March through May) has increased at a rate of 2%-5% a decade, with average spring precipitation from 2009-2012, 30% above the twentieth century normals (30 year averages). Temperatures in the Pacific Northwest have increased at an estimated rate of 0.2 °C per decade (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 2008b, Black et al. 2008). The observed changes in these conditions coincide with the increase in the geographic range and severity of the current SNC epidemic which aerial survey has shown increasingly visible symptoms in plantations, with 2015 estimated at 237,145 hectares in Oregon (Figure 2.3) (Norlander and Kanaskie 2015).

The genetic diversity of Douglas-fir has proven to be a valuable tool in the management of both *Rhabdocline* and SNC. This genetic diversity has enabled the identification of populations which exhibit superior adaptation to different growing

conditions through expression of traits such as drought tolerance, increased cold hardiness, and tolerance to SNC (Johnson 2002, Jayawickrama et al. 2012, Bansal et al. 2015a, Bansal et al. 2015b). Using knowledge of this variation to identify populations that are adapted to future climates is among the most promising of adaptive management strategies aimed at mitigating the negative impacts of climate change (St Clair and Howe 2007, Aitken et al. 2008, Bansal et al. 2015a, Bansal et al. 2015b). The relative susceptibility of different populations of Douglas-fir to Rhabdocline and Swiss needle cast has played an integral role in the selection of productive and adapted seed sources for natural and plantation forests across the world and it is likely that this will continue into the future (Randall and Berrang 2002, Lavender and Hermann 2014).

Variation in resistance and or tolerance to foliar pathogens has been observed among Douglas-fir populations (Hood 1982, Hoff 1987, McDermott and Robinson 1989, Chastagner 2001, Johnson 2002, Jayawickrama et al. 2012). This variation has been attributed to climatic conditions at the seed source, with tolerant/resistant populations originating under climatic conditions conducive to foliar pathogens (Hood 1982, Hoff 1987, McDermott and Robinson 1989). Tolerance according to is the ability of an organism to sustain the effects of a pathogen without dying or suffering serious loss (Agrios 2005). Resistance is the ability of an organism to completely exclude or overcome the effects of a pathogen (Agrios 2005). Studies have identified resistant populations of inland Douglas-fir to Rhabdocline needle cast (Catal et al. 2010). Variation has been observed in the resistance of the coastal variety of Douglas-fir to Rhabdocline but little is known as to the variation across its broad geographic range (

Boyce 1961). Significant progress has been made through tree improvement programs in the selection of SNC tolerant populations of the coastal variety resulting in significant gains in growth over unimproved stock (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 to offset losses from impacts due to SNC. The limited scope of past studies on the tolerance/resistance of Westside Douglas fir to both Rhabdocline and SNC leaves a large knowledge gap as to how tolerance/resistance varies across the wide range of Westside Douglas-fir.

Reciprocal transplant, provenance studies provide insight into the relative impacts changes in climate will have on different populations of trees. These studies provide a platform from which to examine the variation in adaptation in adaptive traits such as frost tolerance, drought resistance as well as resistance to pathogens (Kawecki and Ebert 2004). Reciprocal transplant studies have been influential in identifying resistant/tolerant populations or genotypes of many different forests tree species to many different diseases and insects (McDermott and Robinson 1989, Hood and Kimberley 2005, Enderle et al. 2013).

Reciprocal transplant studies enable the use of climatic transfer distances (Booth 1990, Rehfeldt 1995, Rehfeldt et al. 2003, Gould et al. 2012, Bansal et al 2015a, Bansal et al. 2015b, Ford et al. 2016). Climatic transfer distance is the difference in climate between where a seed comes from and where it is grown (Rehfeldt 1999, Rehfeldt et al. 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 incidence and impacts of pathogens (Gould et al. 2011, Gould et al. 2012, Bansal et al 2015a, Bansal et al. 2015b, Ford et al. 2016).

This current study is part of the Douglas-fir Seed Source Movement Trials (SSMT), a large common garden, reciprocal transplant study of coastal Douglas-fir (Gould et al. 2012, Bansal et al 2015a, Bansal et al. 2015b, Ford et al. 2016). The SSMT is comprised of 9 test sites and 120 populations that were chosen to represent the range of growing conditions experienced by coastal Douglas-fir from Northern California through Western Oregon, to Western Washington State, USA (Figure 2.3). The SSMT provides an ideal platform from which to study the response of these populations to “Assisted population migration” and will help to elucidate the impact SNC and Rhabdocline will have on these populations (Kaweki and Ebert 2004, Ste-Marie et al. 2011, Winder et al. 2011).

I assessed the relationship between the resistance/tolerance to Rhabdocline and Swiss needle cast using the climatic transfer distance between the population source and the test site. I modeled this relationship with the transfer distances of climate variables that have been shown to be influential on the distribution and severity of these foliage diseases. I hypothesized that:

1. There are differences in the levels of resistance/tolerance among populations planted at these test sites.
2. These differences are a function of a difference in climate between the population source climate and the climate of the test site.

3. Populations from source climates most similar to that of the test site are the least susceptible to *Rhabdocline* and SNC.

Testing these hypotheses serves to further integrate forest pathology knowledge into the autecology of Douglas-fir, establishes a base of knowledge from which to better understand the range in susceptibility of Douglas-fir populations to *Rhabdocline* spp. and *P. gaumannii*, and identifies the climatic transfer distances related to severe impacts by important forest pathogens. Furthermore, my results can inform predictions regarding assisted migration.

Methods:

This study is part of a large reciprocal transplant provenance study known as the Douglas-fir Seed Source Movement Trials (SSMT) (Gould et al. 2011, Gould et al. 2012, Bansal et al 2015a, Bansal et al. 2015b, Ford et al. 2016). The SSMT consists of nine planting sites, with 120 open pollinated Douglas-fir seed sources (families) representing 12 different geographic regions ranging from Northern California to Southern Washington, from high elevation to coastal (Figure 3). Each of these twelve regions consists of five separate populations. Each of the 60 populations consists of 2 half-sib families sourced from dominant or codominant woods run trees (not genetically improved stock). Both parents (families) within each population were located at least 100 m from each other but represent a similar climate, elevation and aspect. These seed sources were chosen to represent the range of conditions experienced by Douglas-fir west of the Cascade Crest, in the Pacific Northwest. They were planted at nine different test sites located on three bands of latitude, one in southern Oregon, one in northern Oregon

and one in southern Washington (Figure 2.3). There were four replications (blocks) at each test site. Within each site, each block was divided into 12 sections and one region was randomly assigned to each section. Within each section, 20 seedlings, representing 2 families from each of 5 populations were planted. A total of 960 seedlings were planted at each site. Seedlings were planted at a 3.6 m by 3.6 m spacing, vegetation was controlled to reduce competition, and the sites were fenced to exclude browse.

Regional climate and ecological setting

The seed sources and test sites were chosen to capture the variation experienced by coastal Douglas-fir (Table 2.1). The populations and test sites of this study range from Northern California to Southern Washington west of the Cascade crest and Sierra Nevada Mountains. The northern portion of this region, as described by the northern Oregon and Southern Washington Regions and test sites, is largely characterized by a maritime climate of mild, wet winters with long frost free periods and relatively mild, dry summers. There are large 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 (Franklin and Dyrness 1973).

Individual tree assessments

All test trees present in the SSMT were assessed for disease severity and disease symptoms associated with SNC and Rhabdochline (8,960 trees in total). Surveys were conducted from March 23 – May 29 of 2015. The timing of the survey at each site was determined by data previously collected pertaining to the date at which 50% of test trees

on that site had undergone bud burst. This is the period when the signs and symptoms associated with both of these diseases are most visible.

Infection severity ratings were estimated based on the presence of fruiting bodies of each fungal pathogen. *P. gaeumannii* severity was rated on both the north and south side of each tree on a secondary lateral branch on the fourth whorl from the top of the tree. Ratings ranged from 0-3; 0 corresponding to no pseudothecia present on the underside of the needle, 1 corresponding to 1-33% stomata occluded, 2 corresponding to 33-66% stomata occluded, and 3 corresponding to greater than 66% of stomata occluded by pseudothecia. Ratings were made utilizing 15-25x hand lenses, at least 15 needles were assessed on both the north and south sides of the tree. *Rhabdocline* spp infection level was also rated on the north and south sides of the tree but was estimated over the entire crown on each respective side. Ratings for *Rhabdocline* spp. also ranged from 0-3 and were based on the same percentages as SNC. 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.

Three attributes were used to assess symptoms of disease: crown density, crown color, and needle retention. Crown density was rated on a scale ranging from 1-4; a 1 corresponding to a sickly sparse crown lacking in needle retention, and a 4 corresponding to a full healthy crown. Crown color was rated on a scale from 1-3; a 1 corresponding to a green healthy crown color and a 3 corresponding to highly chlorotic, sickly crown color. Needle retention was rated on a secondary lateral branch located on the fourth whorl and on the south side of the tree. Needle retention was estimated as the proportion

of needles retained in each year of growth e.g. 1.5 refers to a tree holding 100% of its current year needles, 50% of its second year needles and no third year needles.

Climate values for locations of population sources and test sites were obtained using ClimateWNA (Wang 2015). I selected variables which have been identified in past literature that are influential on Swiss needle cast and Rhabdocline needle cast disease occurrence and severity; mean winter temperature, spring/summer precipitation, and continentality (Parker 1970, Michaels and Chastagner 1984, Chastagner et al. 1990, Rosso and Hansen 2003, Manter et al. 2005, Stone et al. 2007, Stone et al. 2008b, Zhao et al. 2011, Lee 2015). Climate data for source locations represent the average from 1961-1991, while climate data for the test sites represents the average from 2008-2013. Climate data for sites were averaged over this time period (2008-2013) in order to represent the conditions in which the test trees have grown. I calculated transfer distance by subtracting the climate value at the population source from the climate value at the test site. Due to differences in the scale of each of the climate transfer distances, each climate transfer distance was standardized by subtracting its mean and dividing by its standard deviation.

Analysis:

The response variables for our analyses were calculated as follows: *Rhabdocline* spp. and *P. gaumannii* 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 where ratings of 1 and 2 were coded as 1 reflecting sparse unhealthy crown density and 3 and 4 were coded as 0 indicating healthy full crown density.

In addition to the full data set, we created 2 subsets of data for our analysis. The full dataset was comprised of all the data collected and was analyzed to assess the crown density in the presence of both diseases, SNC and *Rhabdocline*. The full dataset was also to analyze *Rhabdocline* spp. infection severity.

The analysis in the presence of all diseases, hereafter referred to as the all disease analysis, was not used to assess the level of infection by *P. gaeumannii* or disease symptoms in relation to SNC. Severe impacts associated with trees susceptible to *Rhabdocline* spp. prevented accurate assessments of *P. gaeumannii* infection and damage associated with SNC. Therefore, two subsets of the full dataset were created in order to assess the variation in crown density related to SNC and the level of infection by *P. gaeumannii*. Trees with *Rhabdocline* spp. ratings of 2 or 3 were removed from one subset of the data for analysis of crown density related to SNC in the absence of trees with moderate to severe *Rhabdocline* spp. infection. Analysis using this subset is referred to as the SNC symptom analysis. A second subset was created to analyze the variation in the infection levels of *P. gaeumannii* based on estimates of pseudothecia density. Trees with less than one year of needles and/or high levels of *Rhabdocline* spp. infection prevented accurate assessment of *P. gaeumannii* pseudothecia density because stand counts are done with 2nd year needles, and were therefore removed from the full data set to create the *P. gaeumannii* analysis dataset. Analysis using this dataset is hereafter referred to as the *P. gaeumannii* infection analysis. The removal of trees susceptible to *Rhabdocline* spp. from these datasets most heavily impacted the presence of California and inland Oregon regions. Therefore the sample size of these regions is reduced in these datasets.

Interpreting these results and using the transfer distances associated with the SNC impacts analysis and *P. gaumannii* infection analysis should take this into account.

The effects of the transfer distance of the climate variables on the probabilities of low crown density and high infection severity was analyzed using generalized linear mixed models with the probit link function for our Bernoulli distributed responses (crown density, *Rhabdocline* spp. infection severity and *P. gaumannii* infection severity (Stroup 2013). The analysis was conducted using R version 3.2.3 (2015). We used multiple random effects in our linear model. 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 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 that would converge with this combination in the model. Some models failed to converge if this combination was included in the random effects of the model and in these cases it was omitted. The combination of population and site was omitted from the random effects for the analysis of *Rhabdocline* spp. infection using the all disease analyses as well as the models corresponding to crown density and crown color using the SNC impacts analyses.

The statistical models (Appendix Table 4.1 and 4.2) tested include fixed effects for the climate transfer distance variables representing continentality index, mean winter temperature and May through September precipitation. Past analysis of provenance studies have 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 (Akaike 1973). The model with the lowest score was selected as the best supported model (Akaike 1973, Burnham et al. 2010). Models that differed by less than 2 AIC units were considered the same and in this case the simplest model of those in question was selected based on the principle of parsimony.

After selecting the preferred model, I summarized the impacts of the climate transfer distances individually. For each climate variable in question I set the value of the climate transfer distances not in question to their means, while the value of the climate variable in question varied across its range within the dataset. This process was applied to each climate variable in the selected model and the relative effect of each climate transfer distance on the populations was interpreted. To obtain the distribution of predicted probabilities of moderate to severe disease symptoms or infection over all the transfer distances in question, the model was also run without holding any of the other variables constant. We created boxplots of the predicted probabilities from the model for each region.

Transfer distance

Results obtained from this analysis were also used to estimate low risk transfer distances beyond which unacceptably high probabilities of disease symptoms or infection ($\geq 25\%$) are estimated to occur. This acceptable probability of moderate to severe *Rhabdocline* spp. infection and low crown density (25%) is an arbitrary threshold that I considered acceptable or low risk. Referring to climatic transfers that are low risk in this manner is meant to demonstrate how these models and estimated probabilities can be used

by land managers to determine a transfer distance related to these climate transfer variables. Individual land managers likely have different opinions as to what is considered low risk and therefore can utilize these models to estimate the transfer related to that specific probability of low crown density and *Rhabdocline* spp. infection.

May through September precipitation and mean winter temperatures were the most influential transfer distances in the susceptibility to these foliar diseases. These transfer distances displayed the largest variation in responses, and therefore these climate transfers were used to assess low risk transfer distances. No patterns were observed in relation to the probabilities of moderate to severe *P. gaeumannii* infection and therefore low risk transfer distances were not identified for this response variable. Crown density, in the absence of trees susceptible to *Rhabdocline* spp., was chosen to represent susceptibility to SNC disease symptoms in the identification of low risk transfer distances. Low risk transfer distances were also calculated for the probability of moderate to severe *Rhabdocline* spp. infection. 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 disease. Therefore low risk transfers in relation to crown density in the presence of all disease is not included but can be inferred based on the estimated probabilities of *Rhabdocline* spp..

Geographic Distribution of Probabilities

Two sets of maps were created in relation to Washington and California regions represented in this study. One set of maps estimates the average probabilities of low crown density in the absence of trees highly susceptible to *Rhabdocline* spp. and the other

set of maps estimates the probability of moderate to severe *Rhabdocline* spp. infection. The probabilities in relation to each set of maps were calculated for current time period, and projected out to 2080 under moderate 4.5 and high 8.5 emissions scenarios using HadGEM2 climate projections (Jones et al. 2011).

These maps were created using climate data from Climate WNA (Wang et al. 2011). Future climate projections were obtained from ClimateNA v5.10 software package (available at <http://tinyurl.com/ClimateNA>) as described by Wang et al. (2016). Transfer distances were calculated between the average of the region climate variable and the value for that climate variable in each grid cell of the raster of each climate variable provided by ClimateWNA /Climate NA. the values for the current probabilities are the averages for the climatic normal of 1961-1990. Projected climate values were obtained using HadGEM2 climate projections for 4.5 (low) and 8.4 (high) emissions scenarios projected to year 2080. Grid cells of each climate raster are 1000 by 1000 m resolution. These transfer distances were then scaled by subtracting the global mean and dividing by the global standard deviation as was done with the original model. These scaled transfer distance variables were input into the models selected for crown density and *Rhabdocline* spp. infection along with the model coefficients to estimate the probabilities. Probabilities were obtained for each grid cell, each cell was colored according to this probability.

Results:

I have excluded needle retention and crown color from the results presented below due to a lack of strong trends from which to establish informative conclusions. The results for crown color were not well distributed amongst binomial rating system which

the data was condensed into. The original multinomial three level system that was used in the field resulted in the vast majority of trees being rated as 2 referring to moderately chlorotic crown color. I have decided this data is not an accurate depiction of crown health and have therefore withdrawn this response from the results presented. Figures and tables for this response can be seen in the Appendix (Figures 4.1- 4.6, Tables 4.3-4.8). Needle retention exhibited very weak or insignificant relationships with climate transfer distances. We observed little variation in needle retention on the fourth whorl of eight year old trees and therefore this response was also omitted from the results presented. Results from the needle retention analysis can be observed in the Appendix (Figures 4.7- 4.12, Tables 4.9-4.14). The probabilities related to the susceptibility to moderate to severe *Rhabdocline* spp. infection mirrored the probabilities of low crown density in the presence of all disease. Therefore, results for crown density in the presence of all disease has also been omitted from the results presented below. Probabilities of low crown density in relation to all disease can be inferred from the probabilities of moderate to severe *Rhabdocline* spp. infection. The results of crown density in the presence of all disease are presented in the Appendix (Figures 4.13- 4.15, Tables 4.15-4.17).

The trends exhibited by needle retention and crown color, although rather weak, did follow similar trends as crown density. Crown density can be assumed to be an accurate indicator of crown health. Johnson et al. (2002) determined that crown density was the single best disease symptom with which to estimate tolerance/resistance to SNC. Crown density was also shown to be the most heritable of the disease symptoms associated with SNC.

***P. gaeumannii* Infection**

High levels of moderate to severe *P. gaeumannii* infection was observed at every site except Stone nursery and Evans creek where no infection was observed based on pseudothecia counts (Table 2.2). The lower percentage of trees infected related to the regions of southern Oregon and California is hypothesized to be due to the impacts of *Rhabdocline* and other influences on crown health. Although the trees rated as having moderate to severe *Rhabdocline* spp. infection have been removed, it is likely there is still an influence from this pathogen. Some trees exhibiting severely chlorotic crown color were observed to have lower infection levels by *P. gaeumannii*. Regions with the healthiest crown density and crown color were rated as having the highest percentage of trees exhibiting moderate to severe *P. gaeumannii* infection based on pseudothecia density of 2nd year needles. It is possible the coastal regions which are associated with healthiest crown characteristics are able to tolerate a higher level of infection while the southern regions cast their needles prior to high infection levels due to an intolerance. Other pathogens, such as *Rhabdocline* spp., are also hypothesized to influence these trends. Percentages displayed in Table 2.2 should not be interpreted as indicating a higher level of tolerance associated with the Regions of southern Oregon and northern California.

No pseudothecia were observed at Evans Creek or Stone Nursery indicating inhospitable conditions at these sites. Evans Creek and Stone Nursery have the lowest levels of MSP and mean annual precipitation. These sites are also characterized by cool winters and hot summer conditions (high continentality). The lack of fruiting bodies at

Evans Creek and Stone Nursery illustrate the sensitivity of *P. gaeumannii* to climate conditions.

Selected model:

The linear term for mean winter temperature transfer distance was selected as the fixed effect in this model (Appendix Table 4.2). The selected model included random effects for Site, Population and Family and a random error term which accounts for the f^{th} family in the g^{th} population of the h^{th} region of the i^{th} block in the j^{th} site. It is assumed all random effects and error terms are independent

Variance components:

A model was fit with only variance components (no fixed effects) and a model was fit including the same variance components plus the covariates described in the selected model section above. The climatic transfer distance of mean winter temperature was not influential on the probability of moderate to severe infection by *P. gaeumannii*. The model variance due to random effects does not change with the addition of MWT transfer distance as a fixed effect. Site accounts for the majority of model variance due to random effects in both models (Table 2.3) indicating that the site conditions were highly influential on the level of infection by *P. gaeumannii*. Little variation was observed in populations or families within populations.

Influence of Transfer Distance on *P. gaeumannii*

There were no patterns observed in the severity of infection by *P. gaeumannii*. Climatic transfer distance did not influence the probabilities of infection (Figure 2.4). The furthest transfers in either direction, increasing or decreasing in MWT, displayed very similar probabilities of moderate to severe *P. gaeumannii* infection (Table 2.4). Populations transferred from source climates of warm MWT to test sites of cool MWT were estimated to have lower probabilities of moderate to severe infection. These differences are very minor and can be considered to be insignificant.

There is little variation between the regions in relation to MWT (Figure 2.5). The differences in estimated distribution of probabilities among the regions are less than 3%. There is a pattern of increasing probabilities with inland regions exhibiting a slightly higher probability than the coastal regions and the high elevation regions exhibiting the highest estimated probabilities (Figure 2.5). These differences are very small, less than a 3% difference in probabilities.

Crown Density Analysis:

Crown density results are presented in the absence of trees susceptible to *Rhabdocline* spp. in order to illustrate the variation in susceptibility to SNC. The removal of trees that exhibited moderate to severe *Rhabdocline* spp. infection increases the percentage of trees associated with healthy crown density (Table 2.5). High elevation regions displayed the lowest percentage of trees with healthy crown density. Coastal regions and low elevation regions of northern Oregon and southern Washington are largely associated with the highest percentage of trees with healthy crown density. Coastal regions from areas most conducive to high pathogen pressure exhibited the

highest percentage of trees with healthy crown density (Table 2.5). The removal of trees susceptible to Rhabdocline improved the standing of the local regions at the high elevation sites of northern Oregon (Soda320) and Washington (Doorstop) indicating that Rhabdocline is highly influential on the crown density of these regions

Selected model:

A model with a linear and quadratic term for May through September precipitation, a linear and quadratic term for mean winter temperature, and a linear term for continentality as fixed effects was selected (Appendix Table 4.2). This model included random effects for site, population, family and a random error term which accounts for the f^{th} family in the g^{th} population of the h^{th} region of the i^{th} block in the j^{th} site. It is assumed all random effects and error terms are independent

Variance components

A model was fit with only variance components (no fixed effects) and a model was fit including the same variance components plus the covariates described in the selected model section above. Inclusion of the selected covariates in the model reduced the total variance due to random effects from .667 to .34 (Table 2.6). The inclusion of the selected covariates is influential on the random effects of population and site with little to no effect on the random effect for family. Variation among sites accounts for the majority of variance due to the random effects. The small proportion of model variance due to random effects explained by family indicates that there is little additional variation from within populations (Table 2.6). The large change in the site random effects indicates that

variation among sites is highly influential on disease pressure and the susceptibility to low crown density (Table 2.6).

Influence of Climate Transfer Distance on Crown Density

The severe impacts of *Rhabdocline* spp. on trees that were susceptible to this pathogen prevented the accurate assessment of impacts due to SNC. This analysis was run with the trees highly susceptible to *Rhabdocline* spp. removed as described in the methods section. Therefore, these results assume there are no trees susceptible to *Rhabdocline* spp. and therefore is associated with increased risk.

The highest probabilities of low crown density are associated with the furthest transfer of populations from low to high MSP, with the lowest probabilities associated with the furthest transfers from high to low (Table 2.7 and Figure 2.6). The highest probabilities in relation to MWT are associated with the transfer from cool to warm and the lowest probabilities are associated with the transfer from warm to cool (Table 2.7 and Figure 2.6).

Local populations exhibited low probabilities of low crown density, well below the 25% upper limit and can therefore be assumed to be adapted to the disease severity of their source climate (Table 2.7 and Figure 2.6). The threshold of low risk transfer in relation to MSP is estimated to be an increase in MSP of 337 mm (Figure 2.6).

Probability of low crown density is highest for the southern regions which is largely driven by MSP transfer (Figure 2.7). The north to south gradient in the estimated probabilities are similar to those displayed in the analysis of the probabilities of moderate to severe *Rhabdocline* spp. infection in relation to MSP (Figure 2.7 compared to 2.14).

The effects of MWT are greatest on the high elevation regions. Probabilities increase with distance from the coast, being higher for the low elevation regions than for coastal regions and highest for the high elevation regions (Figure 2.7). These patterns can also be observed in the percentage of trees within each region that exhibited healthy crown density (Table 2.6).

The influences of these two transfer distances can be observed in the distribution of the estimated probabilities of low crown density allowing all variables to vary across their range (Figure 2.8). Southern regions of California and inland southern Oregon are associated with high probabilities of low crown density. This is influenced by MSP (Figure 2.7). These regions are associated with low levels of MSP (Table 2.1). Inland regions exhibit higher probabilities than did the coastal regions and high elevation regions are associated with the highest probabilities (Figure 2.8). This is strongly influenced by MWT as these regions are associated with low MWT (Table 2.1).

Geographic Distributions of Low Crown Density

The geographic areas associated with the highest estimated probabilities of low crown density based on the model selected in this analysis are estimated to be areas west of the coastal mountain ranges of Washington and Oregon as well as the western slopes of the northern Washington Cascades. These figures (Figure 2.9 and 2.10) display the differences in probabilities between northern regions and southern regions. Southern regions from California are associated with high probabilities of low crown density in association with transfers north and west while northern regions from Washington are associated with very low probabilities of low crown density in association with transfers

across the Pacific Northwest. These patterns remain constant with projections to 2080 under both high and low emissions scenarios.

Movement of California regions north and west into areas of high precipitation such as the areas west of the coast Range Mountains of Oregon and Washington and the western slopes of the Cascade Mountains is associated with high probabilities of low crown density. The transfers of the highest current probabilities displayed in Figure 2.9 are characterized by the movement from low MSP to high MSP as well as from low to high MWT. California coast region displays an increased susceptibility with movement to high elevations. This is may be influenced by cold damage rather than foliar diseases.

High elevation Washington Cascades displayed the highest current probabilities of low crown density within the Washington regions (Figure 2.10). Movement of Washington Cascades high elevation region is associated with the transfer of trees from low to high winter temperatures which was related to high probabilities of infection in this study (Figure 2.7). The highest probabilities are associated with movement into areas west of the coast Range Mountains of Oregon and Washington. (Figure 2.10). The coastal and low elevation regions of Washington exhibit low probabilities of low crown density in relation to transfers across most of the Pacific Northwest.

The probability of low crown density based on climatic conditions predicted by the HadGEM2 climate projections for 4.5 (low) and 8.4 (high) emissions scenarios projected to year 2080 did not result in large changes to the estimated probabilities of low crown density in relation to the model used in this analysis (Figures 2. 9 and 2.10). Slight increases in probabilities can be seen. However, these areas are small and very difficult to

discern. According to the HadGEM2 climate projections for 4.5 (low) and 8.4 (high) emissions scenarios, the changes in these climate variables are not conducive to an increase in foliage diseases and therefore disease symptoms. These changes include increased continentality, 3°C (4.5 scenario) and 4°C (8.5 scenario), and decreases in MSP, 61mm (4.5) and 46 mm (8.5). Winter temperature, shown to be most influential to infection by *P. gaeumannii*, is predicted to increase, 2°C (4.5) and 4°C (8.5), creating increasingly conducive conditions in areas where precipitation is not a limiting factor. The influence of this increase may be reduced due to increased continentality and decreased MSP. Based on the results of this study, it is estimated that there will be small changes in the estimated probabilities of low crown density associated with the transfer of populations from northern or southern regions. Therefore, the probabilities associated with the transfer of these populations within the Pacific Northwest is predicted to remain similar to those currently estimated (Figure 2.9 and 2.10).

***Rhabdocline* spp. Infection**

Rhabdocline spp. infection was observed at each test site. Percentages associated with each region at each site varied (Table 2.8). The Washington test sites were estimated to have the highest percentage of tree displaying moderate to severe *Rhabdocline* spp. infection of all three bands of latitude presented in this study. The high elevation Washington site, Doorstop, displayed the highest percentages of all the test sites. Doorstop, Buckhorn2 and Soda320 had the highest percentage of infection, Soda320 and Doorstop are both high elevation sites, indicating a high level of disease presence at high elevation as observed in this study.

The two inland southern Oregon sites, Evans Creek and Stone Nursery which represent the hot and dry climates inhabited by Douglas-fir had very low percentages of *Rhabdocline* spp. infection. The majority of trees which had symptoms that were attributed to *Rhabdocline* spp. were from the California coast region. Due to the lack of fruiting bodies of *Rhabdocline* spp. on either of these sites diagnoses of infections were based only on crown symptoms. Therefore, it is possible the disease symptoms attributed to *Rhabdocline* spp. on these two sites are due to other factors such as insects or nutrient deficiencies. Furthermore, California coast did not exhibit a high susceptibility to *Rhabdocline* spp. on other test sites where *Rhabdocline* spp. was accurately identified based on the presence of fruiting bodies (Table 2.8). Therefore, it is likely the damage observed at Evans creek and Stone nursery was not due to *Rhabdocline* spp..

California Sierra and California Klamath regions had the highest percentages of trees exhibiting moderate to severe disease symptoms across the study. Within each band of latitude the high elevation regions exhibited the highest percentage of trees with moderate to severe infection. Washington coast is associated with the lowest percentage of trees displaying moderate to severe disease symptoms, followed by Oregon coast north, Oregon coast south and California coast. The region local to each site is associated with the among the lowest of the percentages of trees displaying moderate to severe infection. The only exceptions to this were associated with the high elevation sites and regions of northern Oregon (Sodas) and southern Washington (Doorstop). Regions local to these test sites exhibited higher infection levels than many of the other regions.

Selected model

A model with linear terms for the climatic transfer distances of mean winter temperature (MWT), May through September precipitation and continentality as fixed effects was selected (Appendix 4.1). This model included random effects for Site, Population and Family and a random error term for the f^{th} family in the g^{th} population of the h^{th} region of the i^{th} block in the j^{th} site. It is assumed all random effects and error terms are independent.

Variance components

A model was fit with only variance components (no fixed effects) and a model was fit including the same variance components plus the covariates described in the selected model section above. Inclusion of the selected covariates in the model reduced the total variance due to random effects from 1 to .47 (Table 2.9). The inclusion of the selected covariates is influential on the random effects of population and site with little to no effect on the random effect for family. Variation among populations accounts for the majority of variance due to the random effects.. The small proportion of model variance due to random effects explained by family indicates that there is little additional variation from within populations (Table 2.9).

Influence of Climate Transfer distances on *Rhabdocline* spp. Infection

May through September precipitation (MSP) is the most influential transfer distance influencing the probabilities of moderate to severe *Rhabdocline* spp. infection (Figure 2.13). Transferring populations from source climates of low MSP to planting

environments of high MSP is estimated to result in high probabilities of moderate to severe *Rhabdocline* spp. infection. The most extreme transfers of populations in either direction, low to high or high to low MSP, are associated with the highest and lowest probabilities of *Rhabdocline* spp. infection respectively (Table 2.10 and Figure 2.11). Transferring populations from high to low MSP is associated with very low probabilities of moderate to severe *Rhabdocline* spp. infection.

Mean winter temperature (MWT) and continentality transfer distances displayed weak relationships with the probabilities of moderate to severe *Rhabdocline* spp. infection (Figure 2.11). Probabilities are estimated to increase with transfers of populations from cool to warm MWT and high to low continentality (Figure 2.11). These results indicate that MSP is the most accurate predictor of the probability of moderate to severe *Rhabdocline* spp. infection (Table 2.10 and Figure 2.11).

Local populations are associated with low probabilities of moderate to severe *Rhabdocline* spp. infection, well below the low risk transfer threshold of 25% probability (Table 2.10). Transfers of populations beyond 251 mm increase in MSP are estimated to result in greater than 25% probability of moderate to severe *Rhabdocline* spp. infection. Decreasing MSP transfers did not increase probabilities of *Rhabdocline* spp. infection in this study (Figure 2.11). Low risk transfer distances of MWT and continentality are of less importance than MSP. The low risk transfer thresholds associated with each of these climate transfers is illustrated by the vertical lines in Figure 2.11.

There is a strong pattern displayed in Figure 2.12, as the southern regions exhibit the highest probabilities when estimated on the effects of MSP. These regions are associated with the low MSP values (Table 2.1). The northern regions display very low

probabilities based on the effects of MSP, and are associated with higher MSP values (Table 2.1).

The highest estimated probabilities of moderate to severe *Rhabdocline* infection are associated with MWT are in relation to the high elevation regions (Figure 2.12). Probabilities increase from coastal regions to low elevations and are greatest for the high elevation regions (Figure 2.12). The estimated effect of Continentality is similar to that of MWT. Little difference in the effects is observed between low elevation inland regions and high elevation regions in relation to continentality (Figure 2.12).

The influences of these transfer distances can be observed in the distribution of the estimated probabilities of moderate to severe *Rhabdocline* spp. infection allowing all variables to vary across their range (Figure 2.13). The distributions of the estimated probabilities of moderate to severe *Rhabdocline* spp. infection follow strong geographic patterns as southern regions exhibit higher probabilities than northern regions and high elevation regions exhibit higher probabilities than low elevation regions. The high probabilities of *Rhabdocline* spp. infection of the high elevation regions is most strongly influenced by MWT while the high probabilities of the southern regions is most strongly influenced by MSP (Figure 2.13).

Geographic Distribution- *Rhabdocline* spp. infection

The geographic areas associated with the highest estimated probabilities of moderate to severe *Rhabdocline* spp. infection for susceptible source regions, based on the model selected in this analysis, are estimated to be areas west of the coastal mountain

ranges of Washington and Oregon as well as the western slopes of the northern Washington Cascades. Differences in susceptibility can be observed in the comparison of the figures related to the Washington coast regions (Figure 2.15) and California regions (Figure 2.14). Southern regions are associated with high probabilities of infection in association with transfers north and west while northern regions are associated with very low probabilities of infection in association with transfers across the Pacific Northwest. These transfers are characterized by the movement of trees from regions of low MSP to sites of high MSP.

Movement of California regions north and west into areas of high precipitation such as the areas west of the coast Range Mountains of Oregon and Washington and the western slopes of the Cascade Mountains is associated with high probabilities of moderate to severe *Rhabdocline* spp. infection. The transfers of the highest current probabilities displayed in Figure 2.14 are characterized by the movement from low MSP to high MSP as well as from low to high MWT. California coast region displays the lowest probabilities of the California regions and is associated with the highest MSP and MWT (Table 2.1).

Movement of Washington high elevation Cascades region displayed the highest probabilities of infection within the Washington regions. This is influenced by MWT transfer distance (Figure 2.15). Washington coast and Washington Cascades low elevation are associated with low probabilities of *Rhabdocline* spp. infection in this study. The highest probabilities in relation to the Washington regions are associated with the

transfers west of the coastal mountain range of Washington and Oregon and are most severe in the coastal areas of the Olympic peninsula (Figure 2.15).

The probability of moderate to severe *Rhabdocline* spp. for source populations based on climatic conditions predicted by HadGEM2 climate projections for 4.5 (low) and 8.4 (high) emissions scenarios projected to year 2080 did not result in large changes to the estimated probabilities of severe *Rhabdocline* spp. infection in relation to the model used in this analysis (Figures 2.14 and 2.15). Slight increases in the probabilities can be seen. However, these changes are small and very difficult to discern. According to the HadGEM2 climate projections for 4.5 (low) and 8.4 (high) emissions scenarios the changes projected in these climate variables are not conducive to an increase in foliage diseases. These changes include increased continentality, 3°C (4.5) and 4°C (8.5), and decreases in MSP, 61mm (4.5) and 46 mm (8.5). MSP was shown to be most influential to the probabilities of infection and therefore a decrease in MSP will likely reduce the prevalence of *Rhabdocline* needle cast. Winter temperature is predicted to increase, 2°C (4.5 scenario) and 4°C (8.5 scenario), creating increasingly conducive conditions in areas where precipitation is not a limiting factor. Based on the results of this study, it is estimated that there will be small changes in the estimated probabilities associated with the transfer of populations. Therefore, the probabilities associated with the transfer of these populations within the Pacific Northwest is predicted to remain similar to those currently estimated (Figure 2.14 and 2.15).

Discussion:

Utilizing the common garden reciprocal transplant provenance study design (Gould et al. 2012, Bansal et al. 2015a, Bansal et al. 2015) of the Douglas-fir seed source movement trials, I confirmed my hypothesis that strong patterns in the susceptibility and symptom development of foliage diseases would be related to source climate characteristics. Symptoms of *P. gaeumannii* and infection by *Rhabdocline* spp. were related to the transfers from low to high May through September precipitation and cool to warm mean winter temperature. I also confirmed that local source populations consistently showed low disease expression. However other populations from source climates most conducive to high disease pressure were also resistant/tolerant to these foliage diseases.

Swiss Needle Cast

No variation in susceptibility to infection by *P. gaeumannii* was observed in the Douglas-fir test trees in this study. Wherever *P. gaeumannii* occurred, all the Douglas-fir had a similar level of infection. However, there was variation in disease expression, especially crown density. This further validates findings by Temel et al. (2004) who attributed variation in susceptibility to SNC disease symptoms to a tolerance rather than resistance to the pathogen. Studies in New Zealand by Stone et al. (2007) also noted no significant differences in infection levels among seed sources. However, common garden studies by Hood (1982) and McDermott and Robinson (1989) noted variation in infection

levels and attributed this to resistance rather than tolerance. Many test trees, specifically from Washington coast, displayed severe infections but did not display disease symptoms. Trees from this region had healthy crown color and high crown density despite having among the heaviest infection levels, further supporting the hypothesis of a tolerance rather than a resistance of Douglas-fir to *P. gaumannii*.

Swiss needle cast has long been associated with Douglas fir that is grown as an exotic or in vegetation zones not associated with the dominance of Douglas fir (Boyce 1940, Hansen et al. 2000, Shaw et al. 2011). This disease was first noted in Switzerland in 1925 by Richard Gaumann. The disease quickly spread throughout the plantations in Europe causing significant losses (Boyce 1940). Swiss needle cast was not a problem in the native range of Douglas-fir, where *P. gaumannii* is thought to be native, until the 1980s when it began to emerge as a significant disease in the coastal forests of Oregon. Since then hectares affected have steadily increased causing serious reductions in growth which are estimated to be as high as 52% (Hansen et al. 2000, Maguire et al. 2002, Black et al. 2010, Shaw et al. 2011, Norlander and Kanaskie 2015).

Climate has been identified as an important factor in the distribution of SNC and the expanding range of the current SNC epidemic (Manter 2005, Stone 2008, Black et al. 2010, Lee 2013). The rise of the current SNC epidemic in Oregon and Washington has coincided with the conversion of coastal forests to monocultures of Douglas-fir and changes in the climate of the Pacific Northwest that include warmer winters and increases in spring and summer precipitation (Hansen et al. 2000, Stone et al. 2008a, Shaw et al. 2011, Abatzoglou et al. 2014). Both of these changes entail exposing Douglas-fir

populations to changes in climate conditions that are conducive or increasingly conducive to *P. gaeumannii* development, possibly resulting in the exposure of populations to pathogen pressure to which they are not adapted. These changes have been implicated in the expanding range of the current epidemic of SNC.

Disease severity experienced by populations of Douglas-fir is dictated by climate (Manter et al. 2005, Stone et al. 2008a, Black et al. 2011, Lee 2013). Manter et al. (2005) demonstrated that winter temperature and spring leaf wetness were the variables most highly correlated with fruiting body abundance. Lee et al. (2013) noted that summer precipitation and winter temperature were important factors to disease development and distribution. Black et al (2011) noted that severe impacts and the rise of the current SNC epidemic are associated with long term warming trends, specifically since 1984.

The coastal forests of Oregon and Washington, characterized by high spring and summer precipitation and mild winter temperatures, are associated with the highest disease severity related to SNC (Hansen et al. 2000, Shaw et al. 2011). Decreasing disease severity has been observed with movement inland from the coast (Hood 1982, Hansen 2000). This decrease has been attributed to climate factors which limit the development *P. gaeumannii* mainly low winter temperatures and dry spring and summer conditions (Rosso and Hansen 2003, Manter et al. 2005, Stone 2008a, Lee et al. 2013). Thus, the source climate of Douglas-fir populations determines the disease pressure to which they are exposed. This is influential on the level of disease pressure populations of Douglas-fir are exposed, and influences the level of susceptibility of populations (Hood 1982, McDermott and Robinson 1989).

Populations from source climates limiting to the development of *P. gaeumannii*, low May through September precipitation and/or low winter temperatures, were associated with the highest probabilities of exhibiting low crown density. Transferring these populations into sites of high MSP and high MWT resulted in increased probability of SNC symptoms. McDermott and Robinson (1989), referring to a common garden study, stated that the relative susceptibility of each population was highly correlated with mean precipitation at the weather station nearest to the population source. Although the authors did not indicate the importance of the time of year in which precipitation was observed, past studies have shown that spring and summer precipitation is the most important for the development of severe SNC (Capitano 1999, Rosso and Hansen 2003, Manter et al. 2005, Lee et al. 2013). Hood (1982) demonstrated that populations from coastal regions of high spring and summer precipitation were lightly infected while regions from the dry interior California, Washington and British Columbia displayed high infection levels. Populations identified as susceptible in both of these studies were also from inland areas characterized by lower winter temperatures than coastal seed sources. Low winter temperatures inland from the coast and at high elevations restricts the development of *P. gaeumannii*. Hansen et al. (2000) attributed the delayed development of pseudothecia at higher elevations, further inland in the coast range, to lower winter temperatures.

Sensitivity of *P. gaeumannii* to climatic conditions has resulted in geographic patterns in the susceptibility of Douglas-fir populations to SNC. Populations from high elevation regions in this study displayed a high susceptibility to low crown density and

were associated with the highest levels of susceptibility within each band of latitude (each band of latitude consisted of a coastal, low and high elevation region). The populations from the southern regions in this study were associated with the highest levels of susceptibility to low crown density. Increasing susceptibility of populations from further inland from the coast has been noted in past studies (Hood and Wilcox 1971, Hood 1982). Susceptibility has been shown increase in populations from further south, higher in elevation and further from the coast (Hood and Wilcox 1971, Hood 1982). Early European provenance studies revealed the relatively high levels of susceptibility of the inland variety of Douglas-fir and led to the selection of Westside, mainly coastal Douglas-fir (var. *menziesii*) seed sources for planting in European plantations (Lavender and Herman 2014)

***Rhabdocline* spp.**

Rhabdocline needle cast of Douglas-fir is widely regarded as an issue of off-site planting of non-local seed sources (Stone 1997). Serious losses due to Rhabdocline have been significantly reduced since the inception of seed zones which restrict the movement of seeds and ensure the use properly adapted seed sources (Stone 1997). Rhabdocline remains a problem for Christmas trees growers due to the preference of some growers to grow the inland variety of Douglas-fir (var *glauca*) which is associated with high susceptibility to this pathogen (Brandt 1960, Boyce 1961). Therefore much research has focused on this variety of Douglas-fir identifying variation in the susceptibility to *Rhabdocline* spp.. Although variation has been anecdotally noted in the Westside variety

(var.*menziesii*) (Boyce 1961), our study is the first to assess the susceptibility to *Rhabdocline* spp. among populations of Westside Douglas-fir (var. *menziesii*).

Variation in susceptibility to infection by *Rhabdocline* spp. is influenced by the seed source. Infection by *Rhabdocline* spp. has been observed to vary widely in plantations and test sites with trees completely uninfected located next to heavily infected trees (Brandt 1960, Boyce 1961). Thus, indicating resistance as opposed to tolerance. Early accounts noted the high susceptibility of inland Douglas-fir and the relative resistance of Westside Douglas-fir (Brandt 1960, Boyce 1961). The inland variety of Douglas-fir (var. *glauca*) has been identified as highly susceptible but research has identified patterns in resistance and some populations of the inland variety of Douglas-fir have been identified as being completely resistant (Catal et al. 2010). *Rhabdocline* played a large part in the selection of seed sources both where Douglas-fir is grown as an exotic and in the natural range of Douglas-fir (Stone 1997, Lavender and Herman 2014).

Geographic patterns have been observed in relation to the susceptibility of Douglas-fir populations to *Rhabdocline* spp. Studies of the inland variety of Douglas-fir (var.*glauca*) have indicated that elevation of the seed source is influential on the level of susceptibility of populations to *Rhabdocline* needle cast. High elevation seed sources have been consistently shown to exhibit higher levels of susceptibility than populations from low elevations (Hoff 1987). Latitude has also been shown to influence the level of susceptibility of populations to *Rhabdocline* as populations from lower latitudes have been shown to be more susceptible than populations from higher latitudes (Stephan 1973). This study further validates these trends but in relation to Westside Douglas-fir.

Susceptibility in this study was directly influenced by both elevation and latitude.

Increased susceptibility was observed in relation to high elevation seed sources, with the high elevation regions being the most susceptible on each band of latitude represented in the SSMT. These results agree with the findings of Hoff (1987). Populations from the furthest south, lowest latitude, in this study were the most susceptible populations in the study, susceptibility decreased in regions from further north solidifying trends observed by Stephan (1973).

Geographic trends in susceptibility to *Rhabdocline* are likely driven by climatic conditions. High elevation sites are likely more inhospitable to *Rhabdocline* spp. due to low winter temperatures and short growing seasons. Thus resulting in reduced selection pressure in these areas (Hoff 1987). Populations from further south (lower latitudes) are likely accustomed to lower levels of precipitation. North to south movement west of the Cascades is associated with a steep gradient in precipitation, decreasing with movement south (Franklin and Dyrness 1973). *Rhabdocline* spp. is highly dependent on precipitation in the early spring and summer (Chastagner et al. 1990, Brandt 1960) and therefore populations from drier climates associated with lower latitudes may experience lower disease and lower selection pressure for *Rhabdocline* spp. resistance.

May through September precipitation was shown to be the most important climatic transfer distance influencing the susceptibility to *Rhabdocline* spp. in this study. The movement of populations from regions of low May through September to regions of high May through September was associated with high levels of infection and disease symptoms related to *Rhabdocline* spp. The differences in susceptibility between the

interior variety of Douglas-fir and the Westside variety (var. *menziesii*) has long been known and is likely driven by differences in precipitation, specifically MSP, and lower winter temperatures (Brant 1960, Boyce 1961). Populations in this study of source climates most similar to interior Douglas-fir (var. *glauca*), populations from northern California and the Oregon Siskiyou, displayed the highest probabilities of *Rhabdocline* spp. infection. These populations are associated with the lowest May through September precipitation.

Populations display a level of resistance to *Rhabdocline* spp. that is dependent on the level of disease pressure experienced in their source climate (Brandt 1960, Stephan 1973, Hoff 1987). Although *Rhabdocline* is believed to be an indicator of offsite plantings (Stone 1997), the results of this study indicate it is more accurate refer to *Rhabdocline* as an indicator of populations that are or are not adapted to *Rhabdocline* disease pressure. Populations from areas conducive to high disease pressure such as coastal regions, displayed little response in terms of *Rhabdocline* spp. infection, when moved far from their current seed zone or region. This study provides clear evidence that the movement of populations from areas of low disease pressure such as high elevations and southern latitudes results in high disease severity.

Influences on Susceptibility

Results presented in this study indicate a large degree of adaptation to presence of *Rhabdocline* spp. and *P. gaumannii*. Natural selection for resistance/tolerance, or coevolution in relation to the pathogen, is commonly observed in trees under severe disease pressure over long periods of time (Kawecki and Ebert 2004, Ennos 2015).

Resistance and/or tolerance which confers benefits that out-weigh the costs of such traits exert strong selection pressure in favor of these traits (resistance/tolerance) (Telford et al. 2014, Ennos 2015). Species, such as Douglas-fir, which dominate large portions of the forested landscape, are associated with the selection of individuals for the resistance/tolerance to pathogens that are highly prevalent and influential to the success of the species, especially where a large degree of genetic variation is present (Ennos 2015). Our findings support these hypotheses.

In the current study populations from coastal regions, the regions most conducive to high disease pressure displayed the highest levels of resistance/ tolerance to these foliar diseases (Hansen et al. 2000, Manter et al. 2005, Stone et al. 2007, Stone et al. 2008a). This trend has been observed in past studies of *Rhabdocline*, SNC and Cedar leaf blight, as populations from regions most conducive to disease display the highest levels of resistance/ tolerance. (Hood 1982, Hoff 1987, McDermott and Robinson 1989, Russell et al. 2007)

Highly susceptible populations in this study are from source climates that are not conducive to pathogen development. Evans Creek and Stone nursery, the two sites chosen to represent the climates of the inland California and southern Oregon Siskiyou regions were observed to have no signs and few symptoms associated with either of the pathogens, indicating an inhospitable environment for these organisms and the development of disease (Tables 2 and 3). Populations from climates most similar to these test sites were estimated to have the highest probabilities of moderate to severe disease symptoms and *Rhabdocline* spp. infection. This implies that populations from source

climates most similar to these test sites (Evans Creek and Stone Nursery) have undergone very little disease pressure and, therefore, little to no selection pressure for resistance/tolerance to *Rhabdocline* or SNC (Hoff 1987, Rehfeldt 1995, Manter et al. 2005, Russell et al. 2007, Stone et al. 2007, Ennos 2015). This further supports the hypotheses that populations are suited to the disease pressure experienced at their source climate, thus indicating a high level of adaptation to disease pressure (Hood 1982, Hoff 1987, McDermott and Robinson 1989, Rehfeldt 1995).

Results of the current study displayed strong trends in relation to budburst timing and the level of susceptibility of populations. Although the mechanisms behind the levels of susceptibility of each population can only be speculated, the similarities between timing of bud burst and level of susceptibility to *Rhabdocline* and SNC are very strong. Populations from the dry regions of northern California and southern Oregon as well as the high elevation populations exhibit the earliest bud burst (Gould et al. 2011). These populations were associated with the highest probabilities of low crown density as well as *Rhabdocline* spp. infection. Early bud burst may expose these populations to a higher level of inoculum over a longer period of time when conditions are most conducive to infection. Early bud burst has been shown to lead to increased damage due to herbivorous insects in common garden studies (Sampaio et al. 2016). However, early bud burst has also been shown to reduce infection levels of infection of oak powdery mildew in English oak (*Quercus robur*) (Desprez-Loustau et al. 2010).

Coastal populations are associated with the latest budburst in this study and were associated with the lowest probabilities of low crown density and *Rhabdocline* spp.

infection (Gould et al. 2011). Later budburst may expose these populations to a lower level of inoculum as the amount of spores released by *Rhabdocline* spp. and *P.gaeumannii* have been shown to decrease as the summer progresses (Michaels and Chastagner 1984, Chastagner et al. 1990, Capitano 1999). *Phaeocryptopus.gaeumannii* and *Rhabdocline* spp. require specific conditions for successful germination and infection of host tissue and have been shown to be very sensitive to hot and dry conditions which may be more prevalent as the summer progresses. Thus, late bud burst may function as an avoidance strategy, exposing new growth later in the summer when hot dry days may be more common. Late bud burst has been implicated in both mitigating and promoting damage due to insect and fungal pathogens similar to early bud burst (Desprez-Loustau et al. 2010, Sampaio et al. 2016).

Although the phenology of Douglas-fir is well studied and models can provide relatively accurate estimates of growth initiation and cessation based variables such as forcing and chilling hours (Campbell and Sorensen 1973, St Clair and Howe 2007, Gould et al. 2011), the phenology of *P. gaeumannii* and *Rhabdocline* spp. is not as well understood and cannot be modeled as such as this point. Changes in climate may alter the phenology of Douglas-fir which may in turn alter the levels of susceptibility to *Rhabdocline* and SNC (Ford et al. 2016). Therefore, it is unclear as to whether changes in climate and subsequent changes in host phenology will influence the level of disease. Further research is needed to identify the mechanisms which dictate the respective levels of susceptibility.

Management Implications:

Douglas-fir populations transferred from low to high May through September precipitation and from low to high mean winter temperature were associated with high probabilities of low crown density and *Rhabdocline* spp. infection. These transfers were generally related to the movement of populations from arid regions of southern Oregon and northern California northward. Moving populations from south to north, exposing populations to increases in May through September precipitation, is associated with high probabilities of SNC and Rhabdocline needle cast. Projected climate conditions to 2080 are not predicted to significantly alter disease pressure. Therefore, high probabilities of SNC and Rhabdocline needle cast in relation to the movement of populations from arid southern regions to northern areas is predicted to remain high. Increasing winter temperatures will likely expose high elevation populations of Douglas-fir to increasing disease pressure which may result in significant losses due to the high levels of susceptibility associated with these regions. Local populations displayed low probabilities of *Rhabdocline* spp infection and SNC disease symptoms. Therefore, after taking other adaptive traits into account, it is likely local seed sources are currently well adapted to their source climate.

Rapid rates of climate change will influence the health and productivity of coastal Douglas-fir forests (St Clair and Howe 2007, Littell et al. 2010, Rehfeldt et al. 2014, Coops et al. 2016). These changes in climate will affect the influence of *Rhabdocline* spp. and *P. gaumannii* on the productivity of Westside Douglas-fir. Both of these pathogens are highly sensitive to climatic conditions which largely dictate the level of disease populations of Douglas-fir are exposed to (Rosso and Hansen 2003, Manter et al. 2005,

Stone et al. 2008a, Lee et al. 2013). Douglas-fir populations will likely be exposed to new climatic conditions and the changes in disease pressure that may accompany these changes regardless of management strategies imposed (Manter et al. 2005, Stone et al. 2008a, Mueller and Hellmann 2008, Woods et al. 2010). Changes in climate have already been implicated in the expanding range of the current SNC epidemic (Black et al. 2010, Stone et al. 2008a) which is responsible for considerable losses in coastal Oregon (Maguire et al. 2002).

The 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 identified populations from source climates of cool winters and dry summers to be a viable option in future reforestation efforts due to the high drought tolerance of these populations (Bansal et al. 2015a). Results from the current study indicate that these populations are the most susceptible to SNC and *Rhabdocline* needle cast. These results urge caution in the transfer of drought tolerant populations of cool winters and dry summers to locations predicted to but not currently experiencing drought conditions, resulting in the transfer from low to high precipitation.

The movement of populations from south to north is related to high probabilities of moderate to severe disease symptoms and *Rhabdocline* spp. infection. Due to predictions of warmer climatic conditions and increasing drought, movement in this direction is recommended by many proponents of assisted migration (Rehfeldt et al.

2001, St Clair and Howe 2007, Rehfeldt et al. 2014, Coops et al. 2016). This transfer is associated with high probabilities of low crown density and moderate to severe *Rhabdocline* spp. infection. Susceptibility to these pathogens will likely influence the productivity of the populations being transferred from south to north

Winter temperatures are predicted to increase likely leading to the increased presence of foliar pathogens such as *Rhabdocline* spp. and *P. gaeumannii* in areas where low winter temperatures had restricted the development of pathogens (Ferguson 1997, Manter et al. 2005, Stone et al. 2007, Mote and Salathé 2010, Abatzoglou et al. 2013, Lee et al. 2015). High elevation populations were shown to be highly susceptible to *Rhabdocline* spp. infection and disease symptoms associated with both Rhabdocline needle cast and SNC. Past studies of foliage diseases have noted the same trends (Hood 1982, Hoff 1987, Zhang et al. 1997, Russell et al. 2007). Warmer winter temperatures at high elevations may lead to increased losses due to Rhabdocline and SNC in high elevation Douglas-fir stands due to the high levels of susceptibility associated with these populations. A study by Lee et al. (2015) predicts that SNC disease pressure will increase in areas where pathogen development is limited only by low winter temperatures, such as in high elevation inland stands. The movement of low elevation populations, which are not associated with high susceptibility to foliage diseases, up in elevation may mitigate these losses. Other adaptive traits such as cold hardiness and frost tolerance should always be considered in the transfer of populations of Douglas-fir to new locations (Campbell and Sorensen 1973, St Clair and Howe 2007, Gould et al. 2011, Bansal et al. 2015a, Bansal et al. 2015b)

Populations of source climates most similar to the test sites (local) exhibited low probabilities of moderate to severe disease symptoms and infection due to *P. gaeumannii* and *Rhabdocline* spp.. Local populations were not associated with the lowest probabilities for every trait in relation to every climate transfer distance in this analysis. Therefore, susceptibility of coastal Douglas-fir to Rhabdocline and SNC disease symptoms does not strictly conform to the “Local vs Foreign” criterion put forth by Kraweki and Ebert (2004). However, this does not imply that the local populations are not adapted. The probabilities of moderate to severe disease symptoms and Rhabdocline infection related to the local populations of transfer distance of zero were always low and only slightly greater than the populations that exhibited the lowest probabilities. When considered in conjunction with other adaptive traits such as cold hardiness and drought tolerance local populations may be the best adapted.

Variance components identified large variation in relation to the populations in this study. Little variation was attributed to families within populations indicating little variation from within populations. Although genetic parameters were not calculated as part of this analysis, variance components show little variation within populations in the resistance/ tolerance to SNC and Rhabdocline needle cast. Johnson (2002) noted the fairly strong heritabilities associated with crown density, the low variation within populations support to these findings. This indicates that the resistance/tolerance of a population to these foliar diseases can be estimated fairly accurately based on the climate of the population source.

Changes in climate may expose Douglas-fir populations to changes in pathogen pressure within their native ranges or seed zones. Observed and predicted changes in climate have and may continue to expose populations to conditions increasingly conducive to high pathogen pressure resulting in increased disease severity (Manter et al. 2005, Shaw et al. 2011, Abatzoglou et al. 2014, Mildrexler et al. 2016). Lee et al (2013) predicted increases SNC disease pressure in areas where precipitation does not limit the growth of *P. gaeumannii*, areas such as the coastal regions of Oregon and Washington as well as high elevation inland stands which receive a minimum of 110 mm of summer precipitation.

Projecting probabilities calculated in the current study to 2080 under both moderate (4.5) and high (8.5) carbon emission scenarios did not reveal large changes in the probabilities of low crown density and *Rhabdocline* spp. infection (Figures 2.9, 2.10, 2.16 and 2.17). Decreases in May through September and increases in continentality likely influenced the lack of significant change in disease probabilities. Increases in mean winter temperature in the climate projections may increase disease severity in areas where precipitation is not limiting. However, major shifts in disease pressure were not observed using these climate projections and the models from the current study. Zhou et al. (2011) predicted that regional conditions will become less conducive to foliage diseases such as SNC due to an increase in continentality based on predictive climate models. An increase in needle retention was predicted in areas currently affected by SNC. Regardless of how changes in climate manifest, knowledge of the relationships between host, pathogen and climate is vital to proper management of diseases such as *Rhabdocline*

and SNC (Agrios 2005, Shaw et al. 2011). Therefore, based on these results populations of Douglas-fir will not be exposed to a significant increase in disease pressure within their current seed zones before 2080.

Knowledge of transfer distances which are associated with moderate to severe disease impacts and infection by *Rhabdocline* spp. will aid in the establishment of proper recommendations for seed transfer. Through this analysis I have created a tool with which land managers can use to obtain estimated probabilities of disease symptoms associated with *Rhabdocline* needle cast and SNC as well as *Rhabdocline* spp. infection. It is recommended that the climate transfer distances in this study, most importantly mean winter temperature and May through September precipitation, be taken into account when making reforestation and adaptive management decisions especially in the movement of populations from south to north. Changes in climate and management strategies will have a large impact on reforestation of Douglas-fir. Through this study we have filled a knowledge gap as to the variation among west side Douglas-fir populations in the resistance/tolerance to the infection and disease caused by *Rhabdocline* spp and *P. gaeumannii*.

Literature Cited

- Akaike, H. 1974. "A New Look at the Statistical Model Identification." IEEE Transactions on Automatic Control 19 (6): 716–23.
doi:10.1109/TAC.1974.1100705.
- Abatzoglou, J. T., D. Rupp, and P. Mote. 2014. "Seasonal Climate Variability and Change in the Pacific Northwest of the United States." Journal of Climate 27 (5): 2125–2142. doi:10.1175/JCLI-D-13-00218.1.
- Agrios, G. N. 2005. Plant Pathology. Academic Press.
- Aitken, S. N., S. Yeaman, J. A. Holliday, T. Wang, and S. Curtis-McLane. 2008. "Adaptation, Migration or Extirpation: Climate Change Outcomes for Tree Populations." Evolutionary Applications 1 (1): 95–111. doi:10.1111/j.1752-4571.2007.00013.x.
- Aubin, I., C. M. Garbe, S. Colombo, C. R. Drever, D. W. McKenney, C. Messier, J. Pedlar, et al. 2011. "Why We Disagree about Assisted Migration: Ethical Implications of a Key Debate Regarding the Future of Canada's Forests." The Forestry Chronicle 87 (6): 755–65. doi:10.5558/tfc2011-092.
- Bansal, S., C. A. Harrington, P. J. Gould, and J. B. St. Clair. 2015a. "Climate-Related Genetic Variation in Drought-Resistance of Douglas-Fir (*Pseudotsuga menziesii*). (Report)" 21 (2): 947.

- Bansal, S., J. B. St. Clair, C. A. Harrington, and P. J. Gould. 2015b. "Impact of Climate Change on Cold Hardiness of Douglas-Fir (*Pseudotsuga Menziesii*): Environmental and Genetic Considerations." *Global Change Biology* 21 (10): 3814–26. doi:10.1111/gcb.12958.
- Black B.A., D.C. Shaw, J.K. Stone. 2010. Impacts of Swiss needle cast on overstory Douglas-fir forests of the western Oregon Coast Range. *For. Ecol. Manag.* 259: 1673-1680
- Booth, T. H. 1990. "Mapping Regions Climatically Suitable for Particular Tree Species at the Global Scale." *Forest Ecology and Management* 36 (1): 47–60. doi:10.1016/0378-1127(90)90063-H.
- Boyce, J. S. 1940. "A needle-cast of Douglas Fir associated with *Adelopus gaumanni*." *Phytopathology*. 30 (8): 649–655 .
- Boyce, J. S. 1961. *Forest Pathology*. 1961 Third Edition edition. N.Y.; Toronto: McGraw.
- Brandt, R. W. 1960. *The Rhabdocone Needle Cast of Douglas Fir* /. Syracuse : State University College of Forestry,. <http://www.biodiversitylibrary.org/item/126103>.
- Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2010. "AIC Model Selection and Multimodel Inference in Behavioral Ecology: Some Background, Observations, and Comparisons." *Behavioral Ecology and Sociobiology* 65 (1): 23–35. doi:10.1007/s00265-010-1029-6.

- Campbell, R. K., and F. C. Sorensen. 1973. "Cold-Acclimation in Seedling Douglas-Fir Related to Phenology and Provenance." *Ecology* 54 (5): 1148–51.
doi:10.2307/1935582.
- Cannell, M. G. R., and R. I. Smith. 1986. "Climatic Warming, Spring Budburst and Forest Damage on Trees." *Journal of Applied Ecology* 23 (1): 177–91.
doi:10.2307/2403090.
- Capitano. 1999. "The Infection and Colonization of Douglas-Fir by *Phaeocryptopus Gaeumannii*" Corvallis, Oregon: Oregon State University.
- Catal, M., G. C. Adams, and D. W. Fulbright. 2010. "Evaluation of Resistance to Rhabdocline Needlecast in Douglas Fir Variety Shuswap, with Quantitative Polymerase Chain Reaction." *Phytopathology* 100 (4): 337–344.
doi:10.1094/PHYTO-100-4-0337.
- Chastagner, G. A., R.S. Byther, and K.L. Riley. 1990a. Recent Research on Foliage Diseases :conference Proceedings : Carlisle, Pennsylvania, May 29-June 2, 1989 /. Washington, D.C. : <http://hdl.handle.net/2027/umn.31951d02988383q>.
- Chastagner, G. A. 2001. "Susceptibility of Intermountain Douglas-Fir to Rhabdocline Needle Cast When Grown in the Pacific Northwest." *Plant Health Progress*.
doi:10.1094/PHP-2001-1029-01-RS.
- Coops, N C., R.H. Waring, A. Plowright, J. Lee, and T. E. Dilts. 2016. "Using Remotely-Sensed Land Cover and Distribution Modeling to Estimate Tree Species

Migration in the Pacific Northwest Region of North America.” *Remote Sensing* 8 (1): 65. doi:10.3390/rs8010065.

Desprez-Loustau, M. L., J. Aguayo, C. Dutech, K. J. Hayden, C. Husson, B. Jakushkin, B. Marçais, D. Piou, C. Robin, and C. Vacher. 2015. “An Evolutionary Ecology Perspective to Address Forest Pathology Challenges of Today and Tomorrow.” *Annals of Forest Science* 73 (1): 45–67. doi:10.1007/s13595-015-0487-4.

Enderle, R., F. Peters, A. Nakou, and B. Metzler. 2013. “Temporal Development of Ash Dieback Symptoms and Spatial Distribution of Collar Rots in a Provenance Trial of *Fraxinus Excelsior*.” *European Journal of Forest Research* 132 (5–6): 865–76. doi:10.1007/s10342-013-0717-y.

Ennos, R. A. 2015. “Resilience of Forests to Pathogens: An Evolutionary Ecology Perspective.” *Forestry* 88 (1): 41–52. doi:10.1093/forestry/cpu048.

Ferguson, S. A. ; 1997. A Climate-Change Scenario for the Columbia River Basin. <http://www.treesearch.fs.fed.us/pubs/26876>.

Ford, K. R., C. A. Harrington, S. Bansal, P. J. Gould, and J. B. St Clair. 2016. “Will Changes in Phenology Track Climate Change? A Study of Growth Initiation Timing in Coast Douglas-Fir.” *Global Change Biology*, April. doi:10.1111/gcb.13328.

Franklin, J. F., and C. T. ; Dyness. 1973. Natural Vegetation of Oregon and Washington. <http://www.treesearch.fs.fed.us/pubs/26203>.

- Gould, P.J., C. A. Harrington, and B. J. St Clair. 2011. "Incorporating Genetic Variation into a Model of Budburst Phenology of Coast Douglas-Fir (*Pseudotsuga Menziesii* var. *menziesii*)" Canadian Journal of Forest Research 41: 139–50.
- Gould, P. J., C. A. Harrington, J. B. St Clair, and S. Thomas. 2012. "Growth Phenology of Coast Douglas-Fir Seed Sources Planted in Diverse Environments." Tree Physiology 32 (12): 1482–1496. doi:10.1093/treephys/tps106.
- Hansen, E. M., J. K. Stone, B. R. Capitano, P. Rosso, W. Sutton, L. Winton, A. Kanaskie, and M. G. McWilliams. 2000a. "Incidence and Impact of Swiss Needle Cast in Forest Plantations of Douglas-Fir in Coastal Oregon." Plant Disease 84 (7): 773–778. doi:10.1094/PDIS.2000.84.7.773.
- Hoff, R J. 1987. Susceptibility of Inland Douglas-Fir to Rhabdocone Needle Cast. U.S. Dept. of Agriculture, Forest Service, Intermountain Research Station.
- Hood, I. A. and Wilcox, M. D.: Variation in susceptibility to chlorosis and needle cast associated with *Phaeocryptopus gaeumannii* in an 11-year-old Douglas-fir provenance trial. N.Z. For.Res. Inst. For. Path. Rep. No. 72 (1971).
- Hood, I. A. 1982. "*Phaeocryptopus Gaeumannii* on *Pseudotsuga Menziesii* in Southern British Columbia." New Zealand Journal of Forestry Science 12 (3): 415–424.
- Hood, I. A., and M. O. Kimberley. 2005. "Douglas Fir Provenance Susceptibility to Swiss Needle Cast in New Zealand." Australasian Plant Pathology 34 (1): 57–62. doi:10.1071/AP04080.

IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp

Jayawickrama K., D. C. Shaw, and T. Z. YE. 2012. “Genetic Selection in Coastal Douglas-Fir for Tolerance to Swiss Needle Cast Disease”. Proceedings of the fourth international workshop on the genetics of host-parasite interactions in forestry: Disease and insect resistance in forest trees. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. 372 pp.

Johnson. 2002. “Genetic Variation of Douglas-Fir to Swiss Needle Cast as Assessed by Symptom Expression.” *Silvae Genetica* 51: 80–86.

Johnson, G. R., F. C. Sorensen, J. B. St Clair, and R. C. Cronn. 2004. “Pacific Northwest Forest Tree Seed Zones A Template for Native Plants?” *Native Plants Journal* 5 (2): 131–40. doi:10.2979/NPJ.2004.5.2.131.

Johnson, R., F. Temel, K. Jayawickrama, and others. 2002. “Genetic Studies Involving Swiss Needle Cast.” *Swiss Needle Cast Cooperative Annual Report*, 38–43.

Jones, C. D., J. K. Hughes, N. Bellouin, S. C. Hardiman, G. S. Jones, J. Knight, S. Liddicoat, et al. 2011. “The HadGEM2-ES Implementation of CMIP5 Centennial Simulations.” *Geosci. Model Dev.* 4 (3): 543–70. doi:10.5194/gmd-4-543-2011.

Kastner, W. W., S.M. Dutton, D.M. Roche. 2001. “Effects of Swiss Needle Cast on Three Douglas-Fir Seed Sources on a Low-Elevation Site in the Northern Oregon

- Coast Range: Results after Five Growing Seasons.” *Western Journal of Applied Forestry* 16: 31–34.
- Kawecki, T. J., and D. Ebert. 2004. “Conceptual Issues in Local Adaptation.” *Ecology Letters* 7 (12): 1225–41. doi:10.1111/j.1461-0248.2004.00684.x.
- Kurkela, T. 1981. *Growth Reduction in Douglas Fir Caused by Rhabdochline Needle Cast. Communicationes Instituti Forestalis Fenniae*. Helsinki: Finnish Forest Research Institute.
- Lavender, D. P., and R. K. Hermann. 2014. *Douglas-Fir: The Genus Pseudotsuga*. Corvallis, OR : Forest Research Publications Office, Oregon State University. <http://ir.library.oregonstate.edu/xmlui/handle/1957/47168>.
- Lee, E. H., P. A. Beedlow, R. S. Waschmann, C. A. Burdick, and D. C. Shaw. 2013. “Tree-Ring Analysis of the Fungal Disease Swiss Needle Cast in Western Oregon Coastal Forests.” *Canadian Journal of Forest Research* 43 (8): 677–90. doi:10.1139/cjfr-2013-0062.
- Littell, J. S., E. E. Oneil, D. McKenzie, J. A. Hicke, J. A. Lutz, R. A. Norheim, and M. M. Elsner. 2010. “Forest Ecosystems, Disturbance, and Climatic Change in Washington State, USA.” *Climatic Change* 102 (1–2): 129–58. doi:10.1007/s10584-010-9858-x.
- Maguire, D. A., A. Kanaskie, W. Voelker, R. Johnson, and G. Johnson. 2002. “Growth of Young Douglas-Fir Plantations across a Gradient in Swiss Needle Cast Severity.” *Western Journal of Applied Forestry* 17 (2): 86–95.

- Manter, D. K., P. W. Reeser, and J. K. Stone. 2005. "A Climate-Based Model for Predicting Geographic Variation in Swiss Needle Cast Severity in the Oregon Coast Range." *Phytopathology* 95 (11): 1256–1265.
doi:<http://dx.doi.org.ezproxy.proxy.library.oregonstate.edu/10.1094/PHYTO-95-1256>.
- McDermott, J. M., and R. A. Robinson. 1989. "Provenance Variation for Disease Resistance in *Pseudotsuga menziesii* to the Swiss Needle-Cast Pathogen, *Phaeocryptopus gaeumannii*" *Canadian Journal of Forest Research* 19 (2): 244–246. doi:10.1139/x89-034.
- Michaels, E., and G. A. Chastagner. 1984. "Seasonal Availability of *Phaeocryptopus Gaeumannii* Ascospores and Conditions That Influence Their Release." *Plant Disease* 68 (11): 942–944.
- Mildrexler, D., Z. Yang, W. B. Cohen, and D. M. Bell. 2016. "A Forest Vulnerability Index Based on Drought and High Temperatures," February.
doi:10.1016/j.rse.2015.11.024.
- Mote, P. W. 2003. "Trends in Temperature and Precipitation in the Pacific Northwest during the Twentieth Century."
<https://research.libraries.wsu.edu:8443/xmlui/handle/2376/1032>.
- Mote, P. W., and E.P. Salathé Jr. 2010. "Future Climate in the Pacific Northwest." *Climatic Change* 102 (1–2): 29–50. doi:10.1007/s10584-010-9848-z.

- Mueller, J. M., and J. J. Hellmann. 2008. "An Assessment of Invasion Risk from Assisted Migration." *Conservation Biology: The Journal of the Society for Conservation Biology* 22 (3): 562–67. doi:10.1111/j.1523-1739.2008.00952.x.
- Norlander D., A. Kanaski. (2014). 2014 Swiss Needle Cast Aerial Survey. Oregon Department of Forestry.
- Parker, A. K. 1970. "Effect of Relative Humidity and Temperature on Needle Cast Disease of Douglas-Fir." *Phytopathology* 60 (August): 1270.
- Randall, W. K., and Berrang, P. (2002). "Washington Tree Seed Transfer Zones." Washington State Department of Natural Resources.
- Rehfeldt, G. E. 1995. "Genetic Variation, Climate Models and the Ecological Genetics of *Larix Occidentalis*." *Forest Ecology and Management* 78 (1–3): 21–37. doi:10.1016/0378-1127(95)03602-4.
- Rehfeldt, G. E, N. M. Tchebakova, and L. K. Barnhardt. 1999. "Efficacy of Climate Transfer Functions: Introduction of Eurasian Populations of *Larix* into Alberta." *Canadian Journal of Forest Research* 29 (11): 1660–68. doi:10.1139/x99-143.
- Rehfeldt, G., W. Wykoff, and C. Ying. 2001. "Physiologic Plasticity, Evolution, and Impacts of a Changing Climate on *Pinus Contorta*." *Climatic Change* 50 (3): 355–376. doi:10.1023/A:1010614216256.
- Rehfeldt, G. E., N. M. Tchebakova, L. I. Milyutin, E. I. Parfenova, W. R. Wykoff, and N. A. Kouzmina. 2003. "Assessing Population Responses to Climate in *Pinus*

- Sylvestris* and *Larix* Spp. of Eurasia with Climate-Transfer Models.” Eurasian Journal of Forest Research - Hokkaido University (Japan).
<http://agris.fao.org/agris-search/search.do?recordID=JP2004006358>.
- Rehfeldt, G. E., B. C. Jaquish, C. Sáenz-Romero, D. G. Joyce, L. P. Leites, J. B. St Clair, and J. López-Upton. 2014. “Comparative Genetic Responses to Climate in the Varieties of *Pinus Ponderosa* and *Pseudotsuga Menziesii*: Reforestation.” *Forest Ecology and Management* 324 (July): 147–57. doi:10.1016/j.foreco.2014.02.040.
- Rosso, P. H., and E. M. Hansen. 2003. “Predicting Swiss Needle Cast Disease Distribution and Severity in Young Douglas-Fir Plantations in Coastal Oregon.” *Phytopathology* 93 (7): 790–798.
- RStudio Team (2015). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL <http://www.rstudio.com/>.
- Russell, J. H., H. H. Kope, and P. Ades. 2007. “Variation in Cedar Leaf Blight (*Didymascella Thujina*) Resistance of Western Redcedar (*Thuja Plicata*).” *Canadian Journal of Forest Research* 37 (10): 1978–86. doi:10.1139/X07-034.
- Sampaio, T., M. Branco, E. Guichoux, R. J. Petit, J. S. Pereira, M. C. Varela, and M. H. Almeida. 2016. “Does the Geography of Cork Oak Origin Influence Budburst and Leaf Pest Damage?” *Forest Ecology and Management* 373 (August): 33–43. doi:10.1016/j.foreco.2016.04.019.
- Shaw, D. C., G. M. Filip, A. Kanaskie, D. A. Maguire, and W. A. Littke. 2011. “Managing an Epidemic of Swiss Needle Cast in the Douglas-Fir Region of

- Oregon: The Role of the Swiss Needle Cast Cooperative.” *Journal of Forestry* 109 (2): 109–119.
- St.Clair, J. B., N. L. Mandel, and K. W. Vance-Borland. 2005. “Genecology of Douglas Fir in Western Oregon and Washington.” *Annals of Botany* 96 (7): 1199–1214.
doi:10.1093/aob/mci278.
- St Clair, J. B., and G. T. Howe. 2007. “Genetic Maladaptation of Coastal Douglas-fir Seedlings to Future Climates.” *Global Change Biology* 13 (7): 1441–1454.
doi:10.1111/j.1365-2486.2007.01385.x.
- Ste-Marie, C., E. A. Nelson, A. Dabros, and M. Bonneau. 2011. “Assisted Migration: Introduction to a Multifaceted Concept.” *The Forestry Chronicle* 87 (6): 724–30.
doi:10.5558/tfc2011-089.
- Stephan BR. 1973. Über Anfälligkeit und Resistenz von Douglasien-Herkünften gegenüber *Rhabdocline pseudotsugae*. *Silvae Genet.* 22: 149-153
- Stone, J. 1997. *Rhabdocline needle cast*. Pages 54-55 in: *Compendium of Conifer Diseases*. E. M. Hansen and K. J. Lewis, eds. The American Phytopathological Society, St. Paul, MN
- Stone, J. K., I. A. Hood, M. S. Watt, and J. L. Kerrigan. 2007. “Distribution of Swiss Needle Cast in New Zealand in Relation to Winter Temperature.” *Australasian Plant Pathology* 36 (5): 445–54. doi:10.1071/AP07049.

- Stone, J. K., B. R. Capitano, and J. L. Kerrigan. 2008a. "The Histopathology of on Douglas-Fir Needles." *Mycologia* 100 (3): 431–444.
- Stone, J. K., L. B. Coop, and D.K. Manter. 2008b. "Predicting Effects of Climate Change on Swiss Needle Cast Disease Severity in Pacific Northwest Forests." *Canadian Journal of Plant Pathology* 30 (2): 169–176.
doi:10.1080/07060661.2008.10540533.
- Stroup, W.W., 2012. *Generalized linear mixed models: modern concepts, methods and applications*. CRC press.pp 317
- Sturrock, R. 2012. "Climate Change and Forest Diseases: Using Today's Knowledge to Address Future Challenges." *Forest Systems* 21 (2): 329–36.
doi:10.5424/fs/2012212-02230.
- Telford, A., S. Cavers, R. A. Ennos, and J. E. Cottrell. 2014. "Can We Protect Forests by Harnessing Variation in Resistance to Pests and Pathogens?" *Forestry*, April, cpu012. doi:10.1093/forestry/cpu012.
- Temel, F., G. R. Johnson, and J. K. Stone. 2004. "The Relationship between Swiss Needle Cast Symptom Severity and Level of *Phaeocryptopus Gaeumannii* Colonization in Coastal Douglas-Fir (*Pseudotsuga Menziesii* Var. *Menziesii*)." *Forest Pathology* 34 (6): 383–394.
doi:http://dx.doi.org.ezproxy.proxy.library.oregonstate.edu/10.1111/j.1439-0329.2004.00379.x.

- Wang, Tongli, Andreas Hamann, David L. Spittlehouse, and Trevor Q. Murdock. 2011. "ClimateWNA—High-Resolution Spatial Climate Data for Western North America." *Journal of Applied Meteorology and Climatology* 51 (1): 16–29. doi:10.1175/JAMC-D-11-043.1.
- Wang, T., Hamann, A., Spittlehouse, D.L. and Carroll, C. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS One* 11: e0156720
- Winder, R., E. Nelson, and T. Beardmore. 2011. "Ecological Implications for Assisted Migration in Canadian Forests." *The Forestry Chronicle* 87 (6): 731–44. doi:10.5558/tfc2011-090.
- Woods, A. J., K. D. Coates, and A. Hamann. 2005. "Is an Unprecedented Dothistroma Needle Blight Epidemic Related to Climate Change?" *BioScience* 55 (9): 761–69. doi:10.1641/0006-3568(2005)055[0761:IAUDNB]2.0.CO;2.
- Woods, A. J., D. Heppner, H. H. Kope, J. Burleigh, and L. Maclauchlan. 2010. "Forest Health and Climate Change: A British Columbia Perspective." *The Forestry Chronicle* 86 (4): 412–22. doi:10.5558/tfc86412-4.
- Zhang, J. W., N. B. Klopfenstein, and G. W. Peterson. 1997. "Genetic Variation in Disease Resistance of *Juniperus Virginiana* and *J. Scopulorum* Grown in Eastern Nebraska." *Silvae Genetica* 46 (1): 11–
- Zhao, J., D. B. Mainwaring, D. A. Maguire, and A. Kanaskie. 2011. "Regional and Annual Trends in Douglas-Fir Foliage Retention: Correlations with Climatic

Variables.” *Forest Ecology and Management* 262 (9): 1872–86.

doi:10.1016/j.foreco.2011.08.008.

Figures

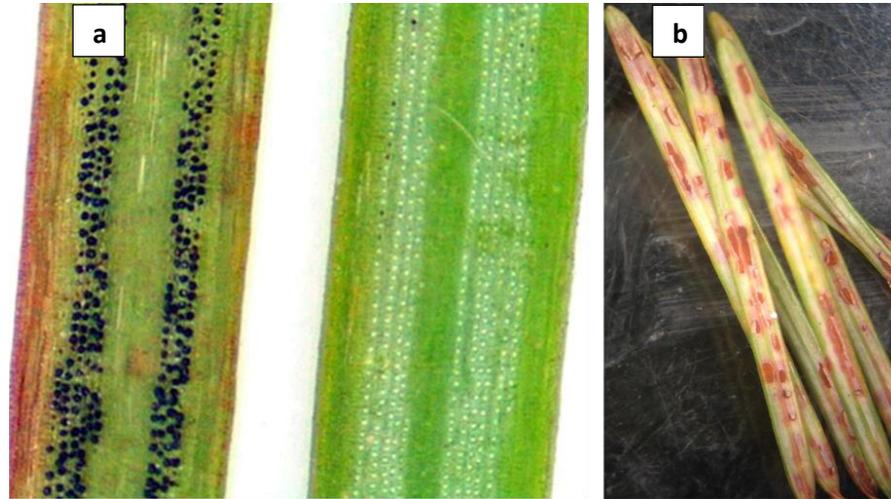


Figure 2.1 a- Fruiting bodies of *P. gaeumannii* left compared to uninfected needle right. b- Fruiting bodies of *R. pseudotsugae*.

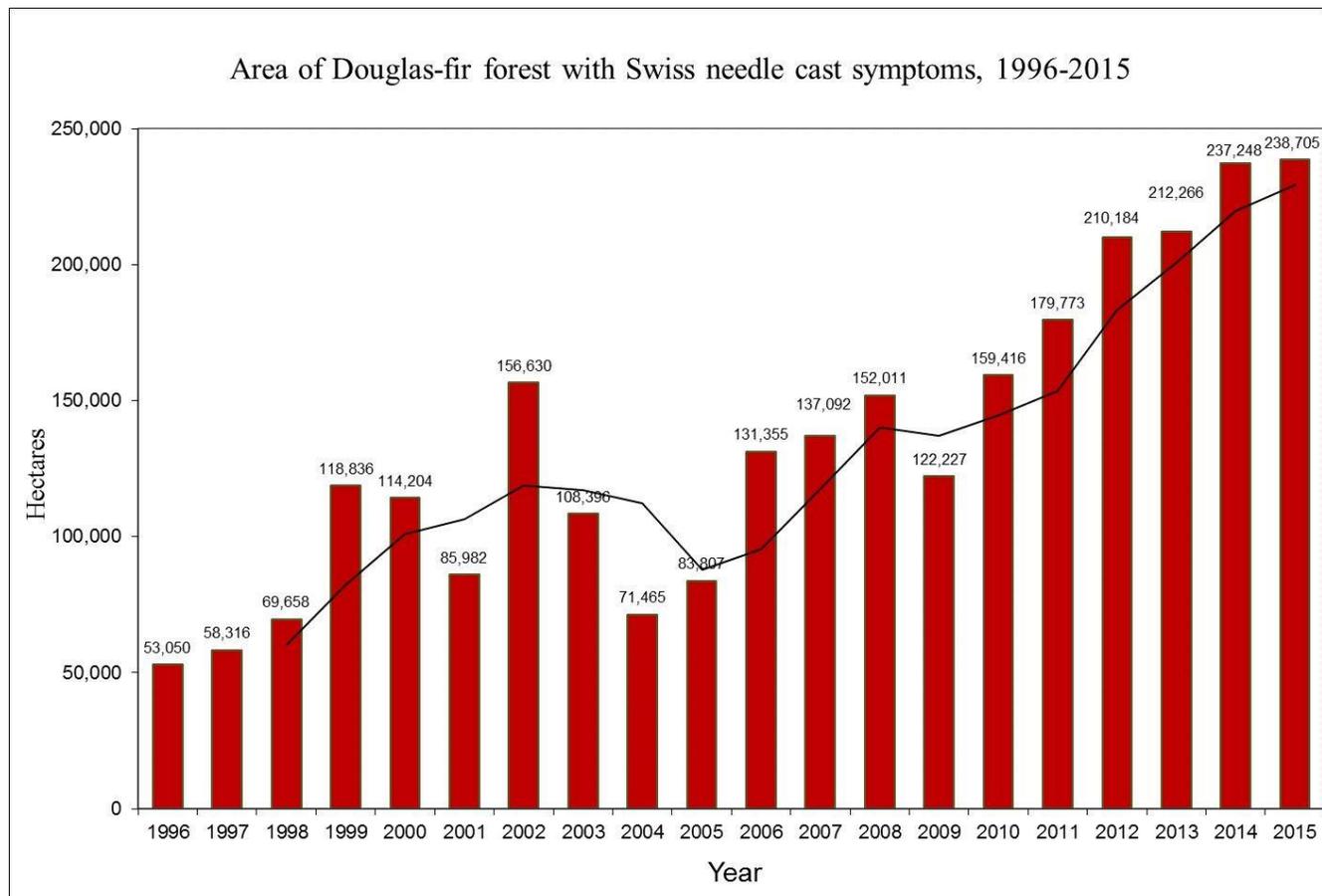


Figure 2.2 Area in Oregon affected by Swiss needle cast symptoms 1996-2015 (Oregon Department of Forestry 2015).

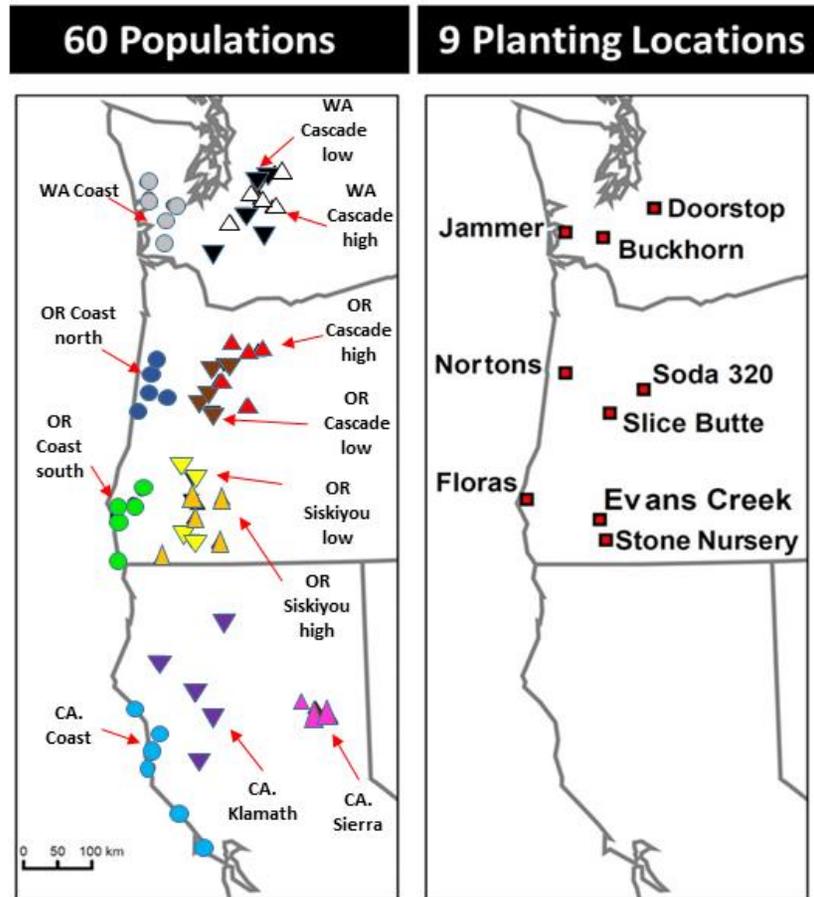


Figure 2.3 Locations of seed sources (left) and test sites (right) of the Douglas-fir seed source movement trials.

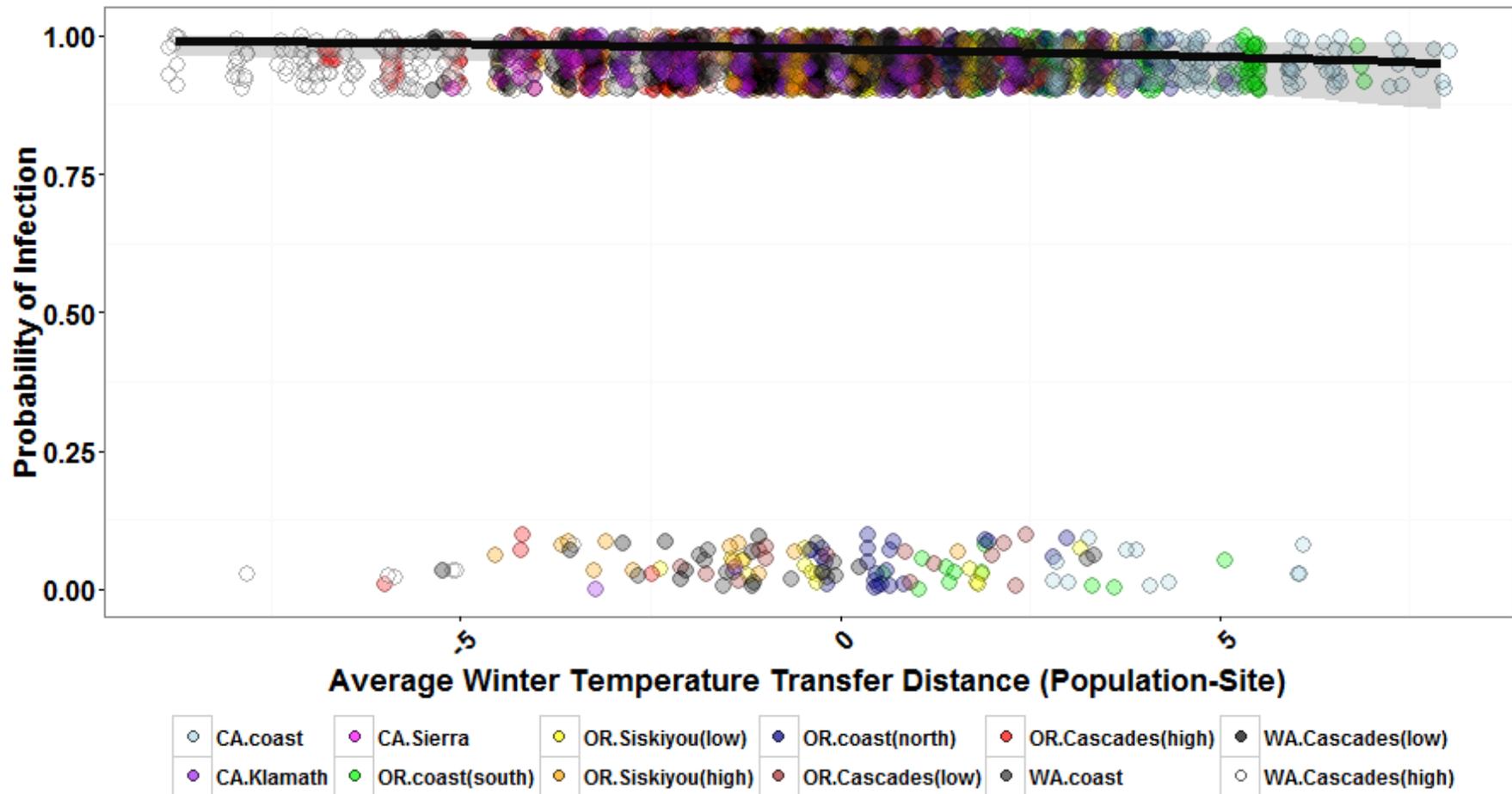


Figure 2.4 Estimated probabilities of moderate to severe *P. gaumannii* infection versus mean winter temperature transfer distance and 95% confidence intervals with raw data. Data are from all trees in the Douglas-fir Seed Source Movement trials at the seven sites where *Rhabdocline* spp. and *P. gaumannii* were identified as present.

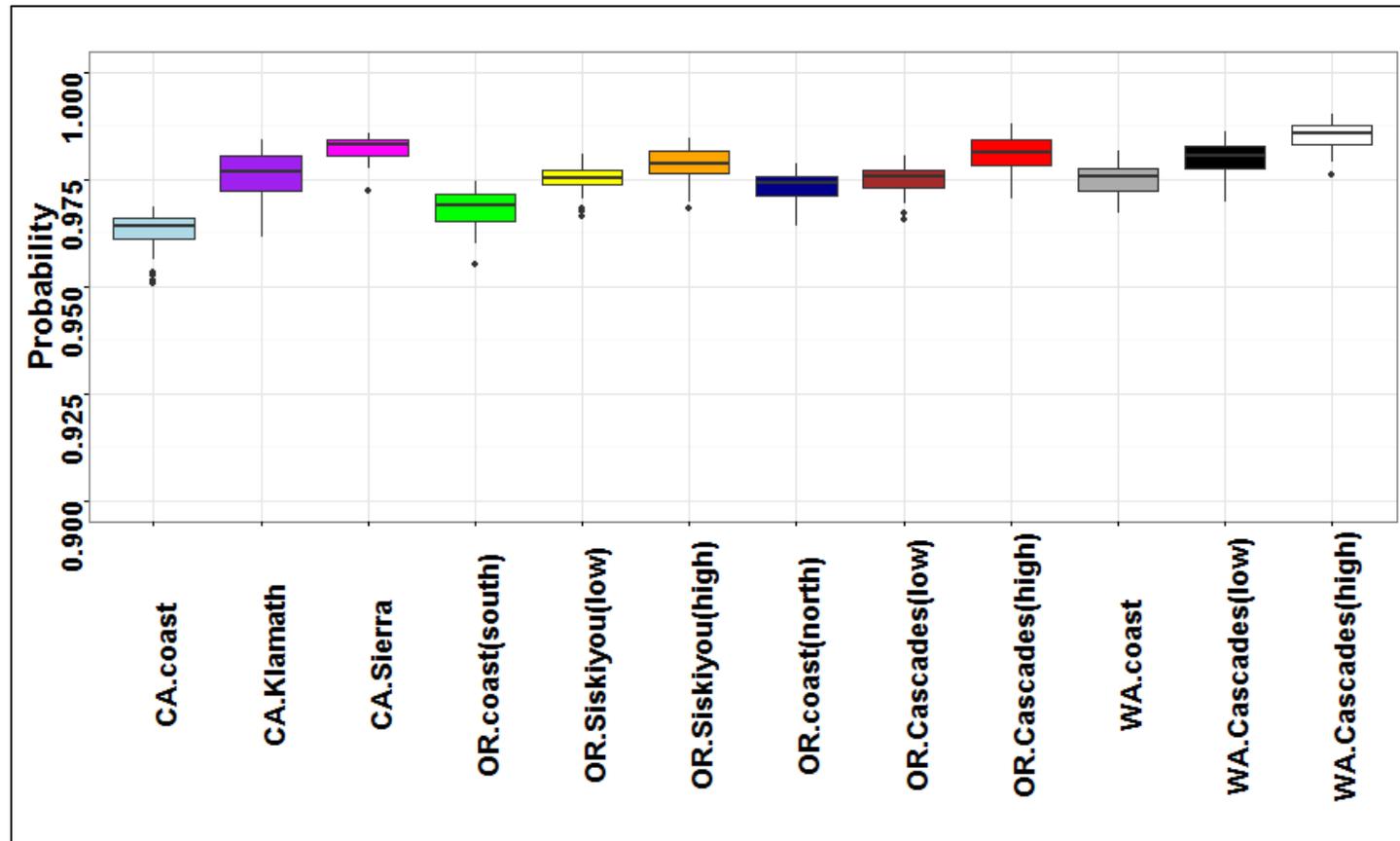


Figure 2.5 Distributions of the estimated probabilities of moderate to severe *P. gaeumannii* infection in relation to each region over the seven sites in the Douglas-fir Seed Source Movement Trials which displayed signs of *Rhabdocline* spp. and *P. gaeumannii*. Probability scale ranges from 0.9 to 1.0. The x axis displays the regions and is labeled by band of latitude (three regions per band) in order from north to south and from coast to high elevation within each band.

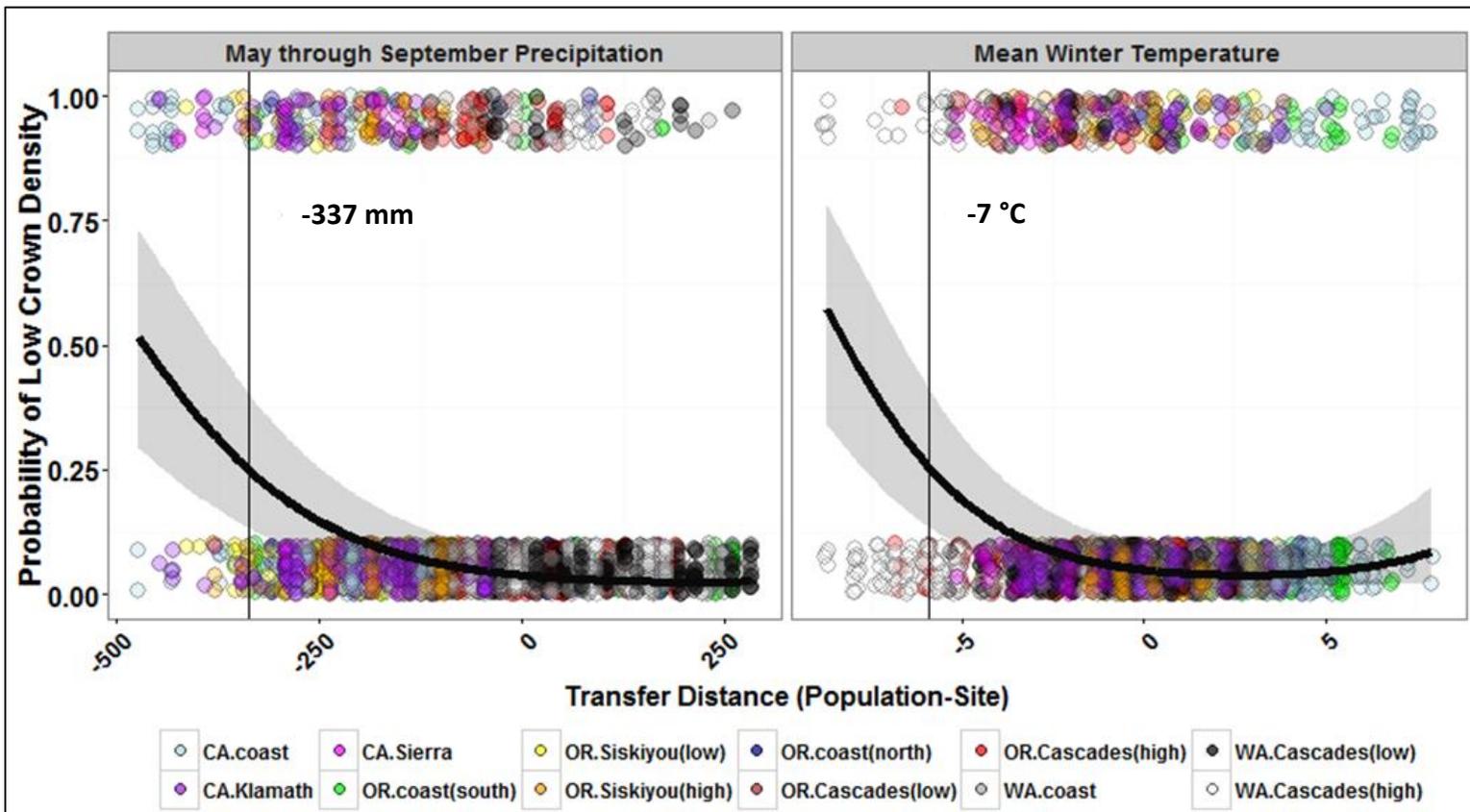


Figure 2.6 Estimated probabilities of low crown density versus climate transfer distances and 95% confidence intervals with the raw data. Each plot holds the other climate transfer distance to its mean. Probabilities are hypothesized to be due to Swiss needle cast (trees susceptible to *Rhabdocline* spp. removed). Data are from all trees in the Douglas-fir Seed Source Movement Trials at the seven sites where *Rhabdocline* spp. and *P. gaumannii* were identified as present. The vertical line indicates the threshold after which probabilities are estimated to be greater than 25%.

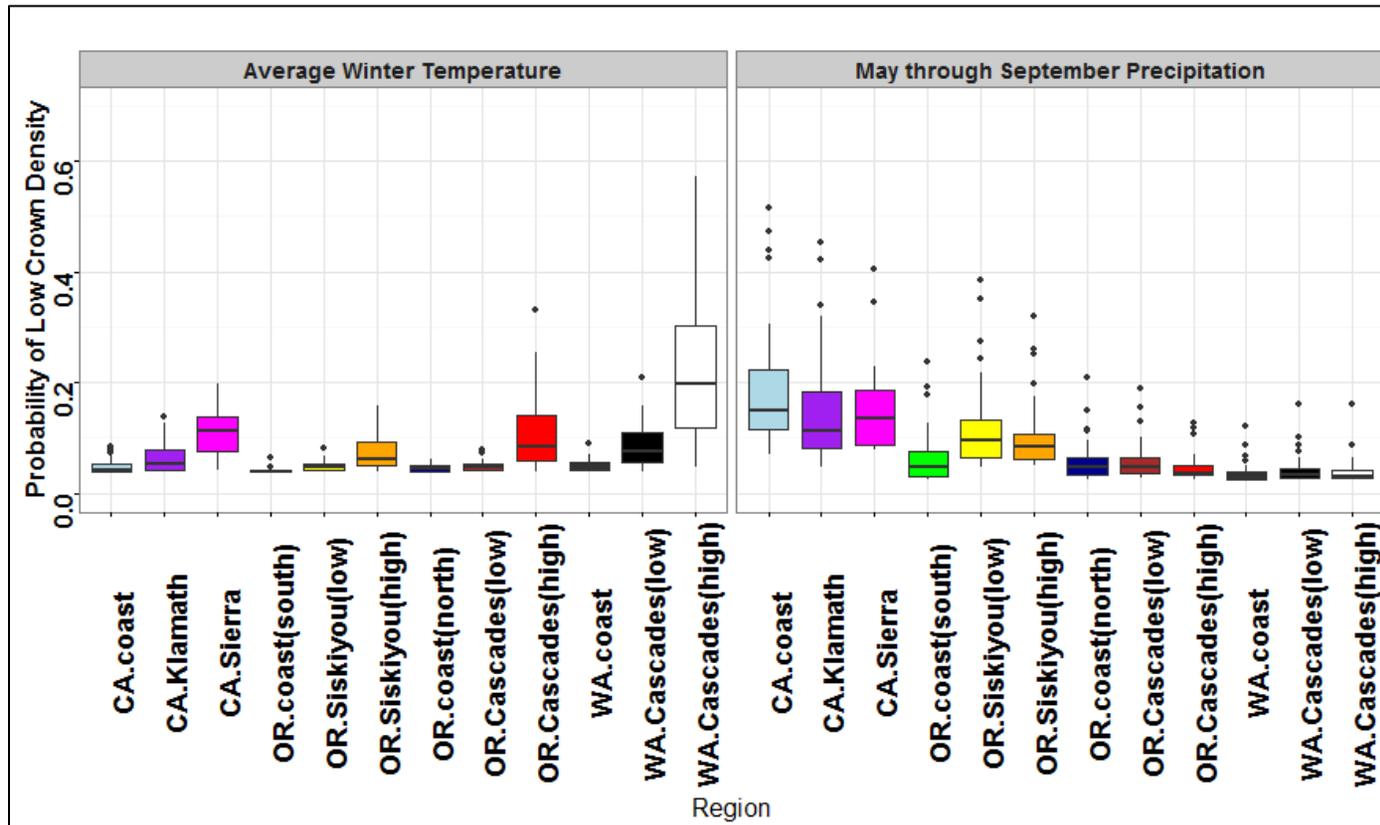


Figure 2.7 Estimated distribution of probabilities of low crown density in relation to each climate transfer distance holding the other climate transfer distance to its mean. Probabilities of low crown density are hypothesized to be due to Swiss needle cast (trees susceptible to *Rhabdocline* spp. removed). Data are in relation to all 12 regions at all seven sites of the Douglas-fir Seed Source Movement Trials which displayed signs of *Rhabdocline* spp. and *P. gaumannii*. The x axis displays the regions and is labeled by band of latitude (three regions per band) in order from north to south and from coast to high elevation within each band.

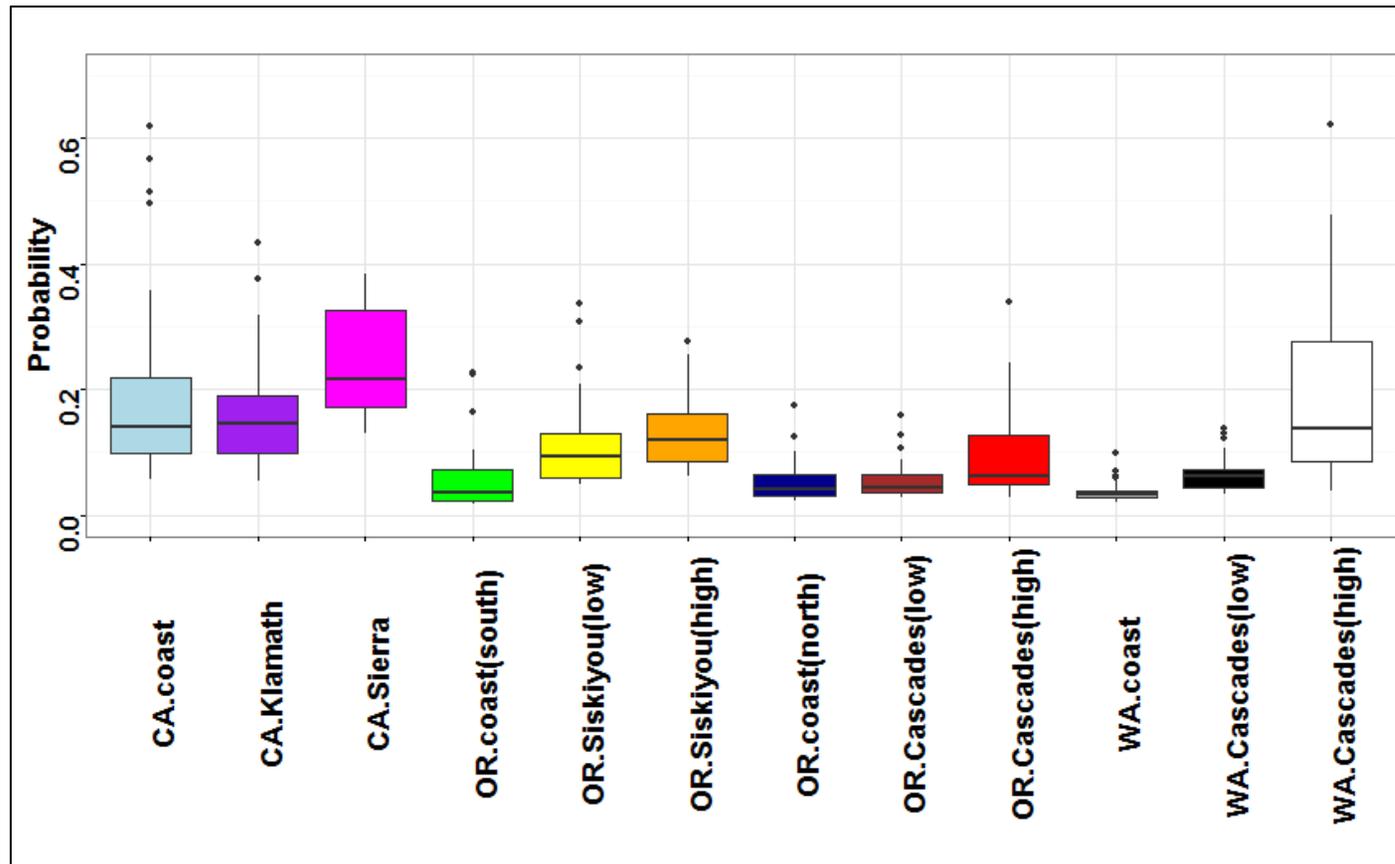


Figure 2.8 Distribution of the estimated probabilities of low crown density with all explanatory variables varying over their entire range in the dataset. Probabilities of low crown density are hypothesized to be due to Swiss needle cast (trees susceptible to *Rhabdocline* spp. removed). Data are in relation to all 12 regions at all seven sites of the Douglas-fir Seed Source Movement Trials which displayed signs of *Rhabdocline* spp. and *P. gaeumannii*. The x axis is labeled by band of latitude in order from north to south and from coast to high elevation within each band. The x axis displays the 12 regions and is labeled by band of latitude (three regions per band) in order from north to south and from coast to high elevation within each band.

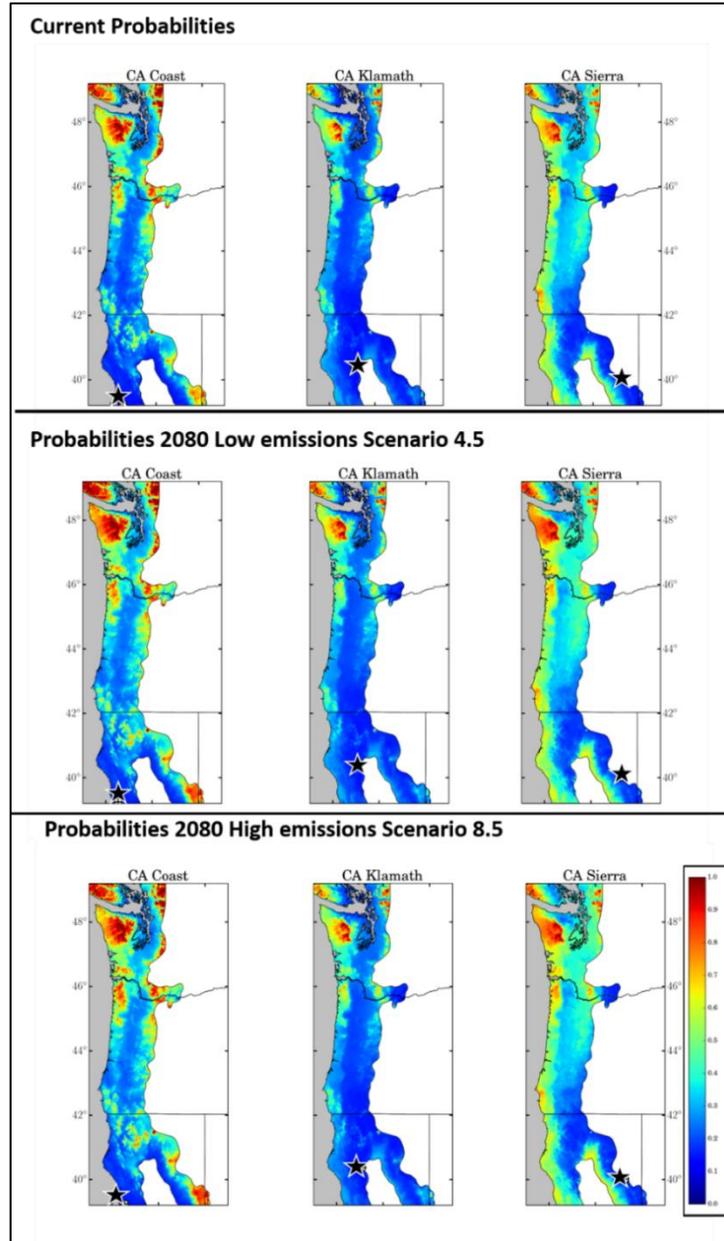


Figure 2.9 Geographic distribution of estimated probabilities of low crown density in relation to the California regions of the Douglas-fir Seed Source Movement Trials (SSMT). Probabilities were estimated using the model selected using data from these regions in relations to the seven site of the SSMT which displayed signs of *P. gaemannii* and *Rhabdocline* spp and are hypothesized to be due to Swiss needle cast (trees susceptible to *Rhabdocline* spp. removed). Climate predictions were made using the HadGEM2 climate projections obtained from ClimateNA (Wang et al. 2016)

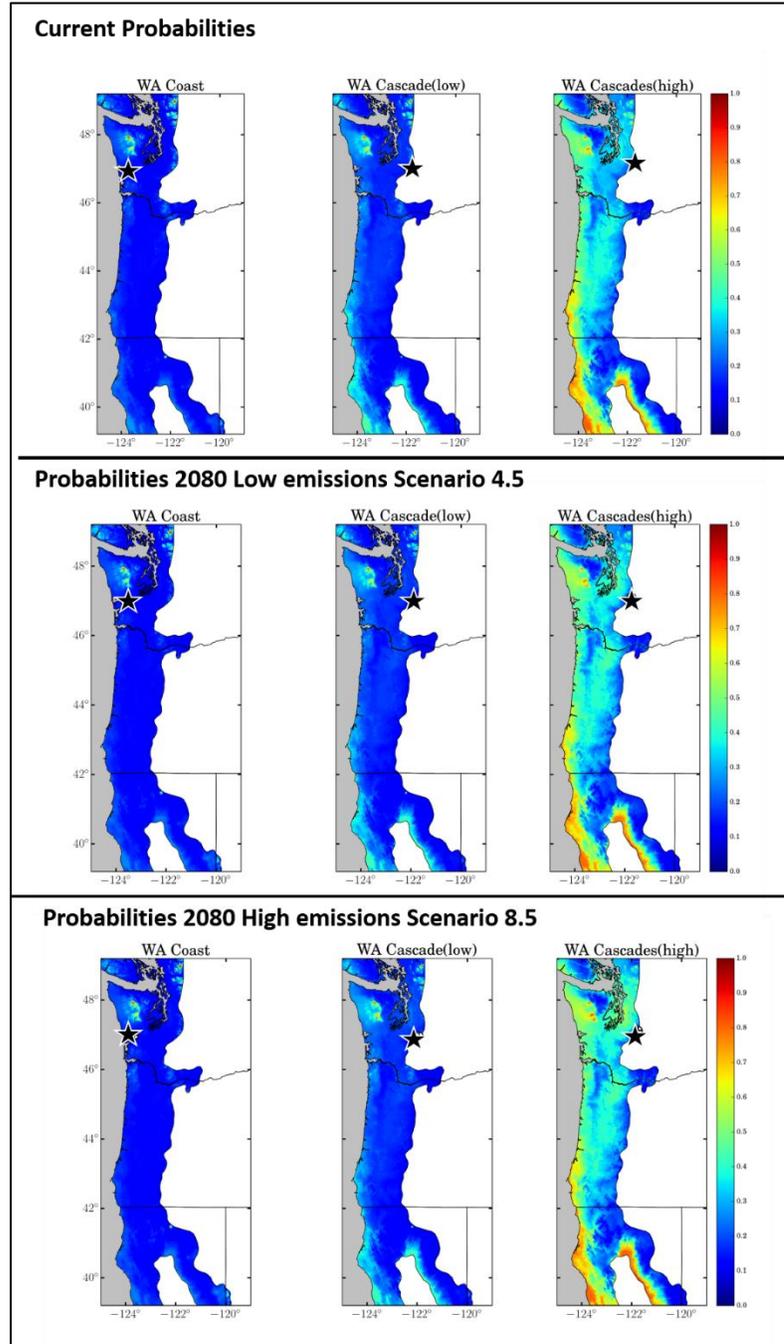


Figure 2.10 Geographic distribution of estimated probabilities of low crown density in relation to the Washington regions of the Douglas-fir Seed Source Movement Trials (SSMT). Probabilities were estimated using the model selected using data from these regions in relations to the seven site of the SSMT which displayed signs of *P. gaemannii* and *Rhabdocline* spp. and are hypothesized to be due to Swiss needle cast (trees susceptible to *Rhabdocline* spp. removed). Climate predictions were made using the HadGEM2 climate projections obtained from ClimateNA (Wang et al. 2013)

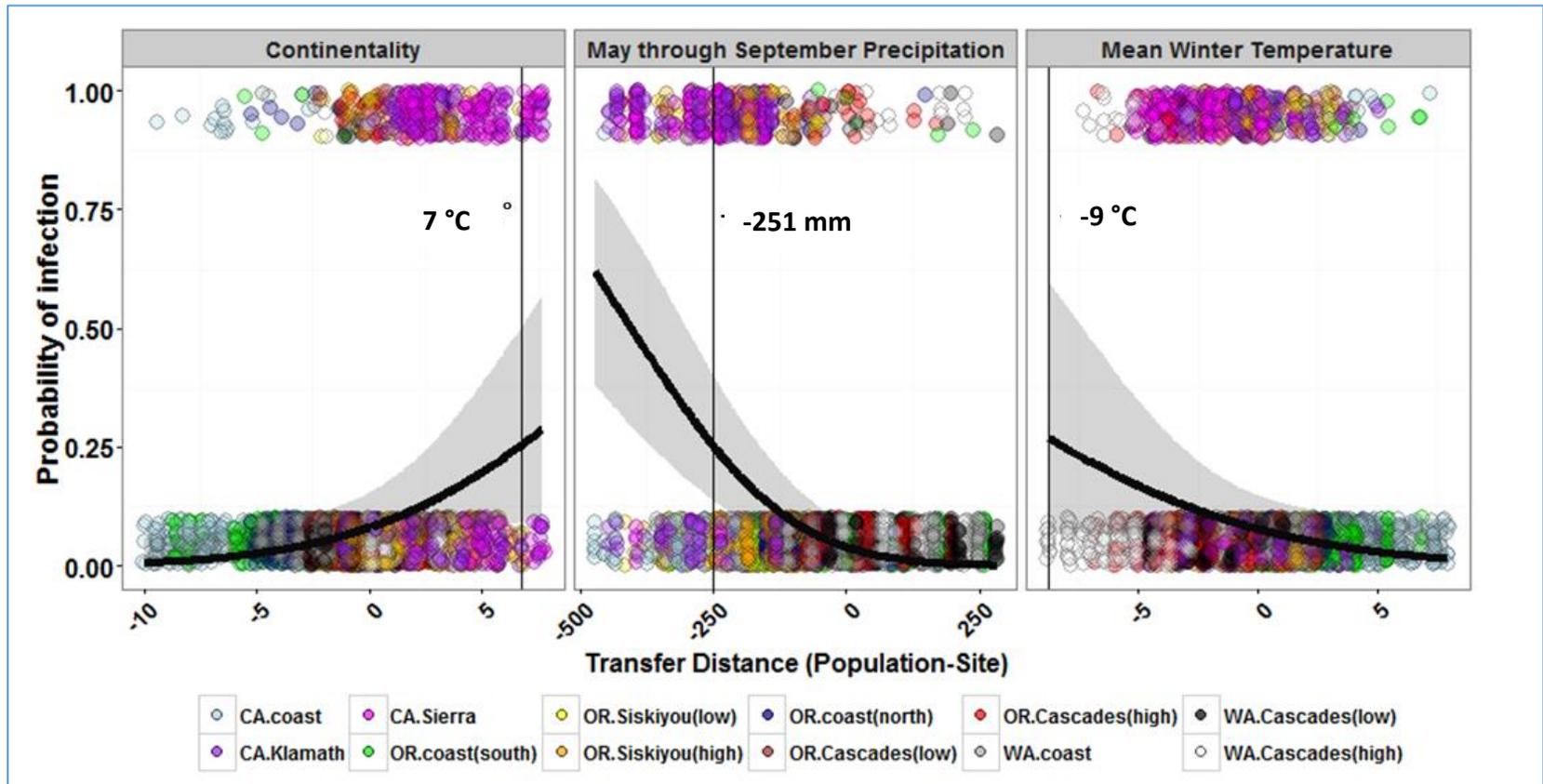


Figure 2.11 Estimated probabilities of moderate to severe *Rhabdocline* spp. infection versus climate transfer distance and 95% confidence intervals with raw data. Data are from all trees in the Douglas-fir Seed Source Movement trials at the seven sites where *Rhabdocline* spp. and *P. gaumannii* were identified as present. Each predicted line holds the other climate transfer distances to their mean. The vertical line the threshold after which probabilities are estimated to be greater than 25%.

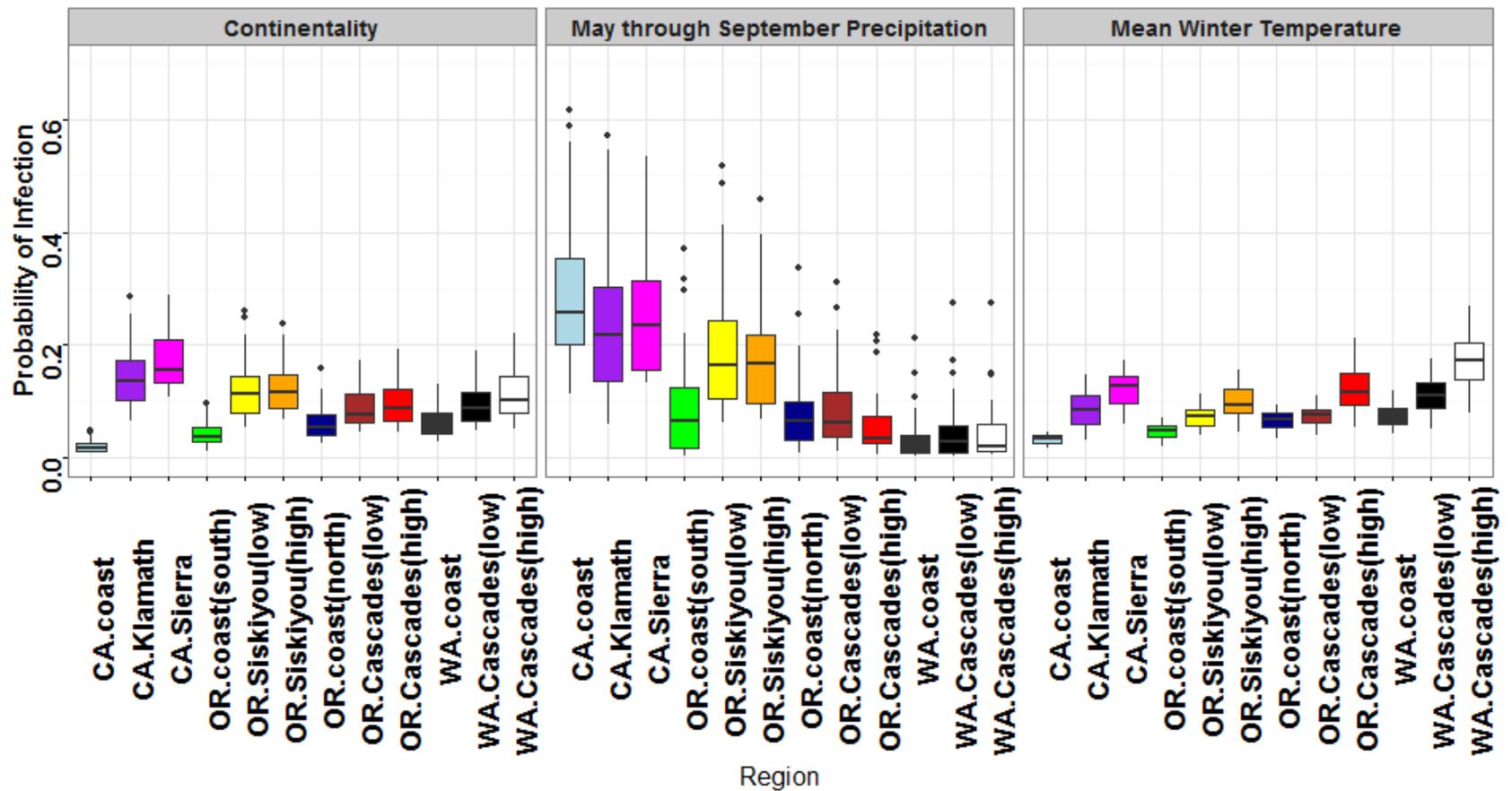


Figure 2.12 Estimated distribution of probabilities of moderate to severe *Rhabdocline* spp. infection in relation to each climate variable transfer distance, holding the other climate transfer distances to their mean. Probabilities are in relation to all regions of the Douglas-fir Seed Source Movement Trials and the seven sites which displayed signs of *P. gaemannii* and *Rhabdocline* spp.. The x axis displays the regions and is labeled by band of latitude (three regions per band) in order from north to south and from coast to high elevation within each band.

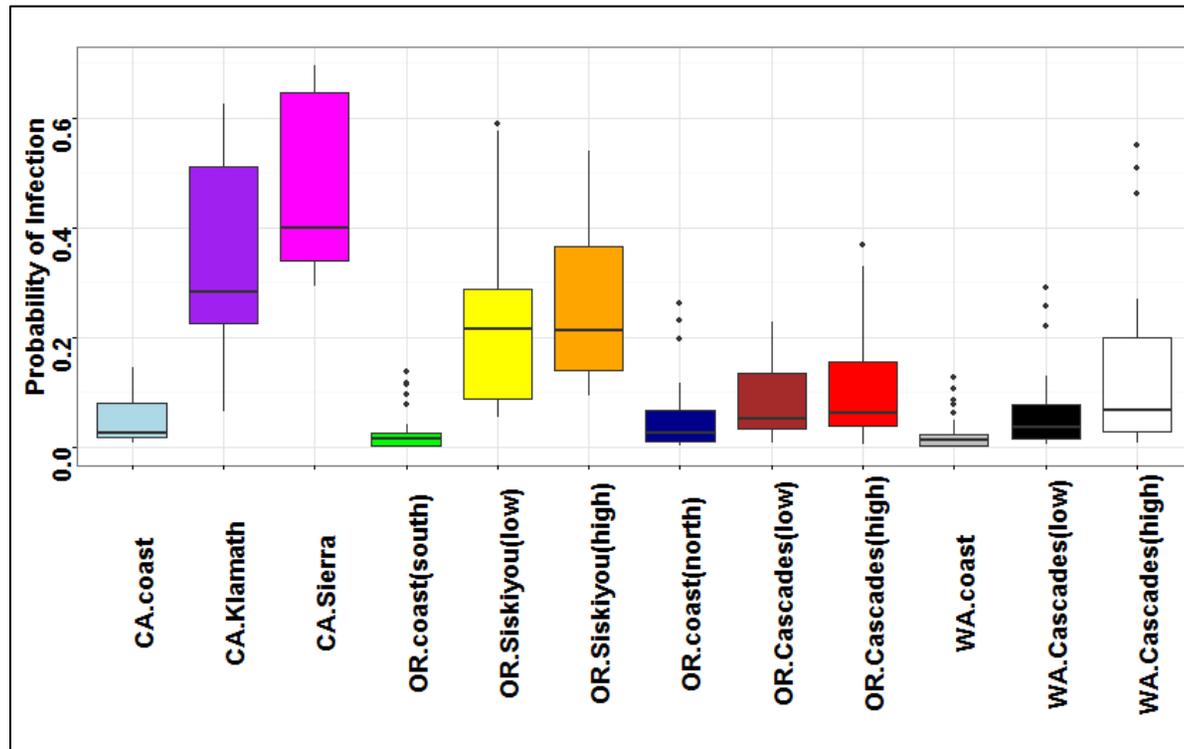


Figure 2.13 Distribution of the estimated probabilities of moderate to severe *Rhabdocline* spp. infection with all explanatory variables varying over their entire range in the dataset. Probabilities are in relation to all 12 regions at all seven sites of the Douglas-fir Seed Source Movement trials which displayed signs of *Rhabdocline* spp. and *P. gaeumannii*. The x axis is labeled by band of latitude in order from north to south and from coast to high elevation within each band. The x axis displays the 12 regions and is labeled by band of latitude (three regions per band) in order from north to south and from coast to high elevation within each band.

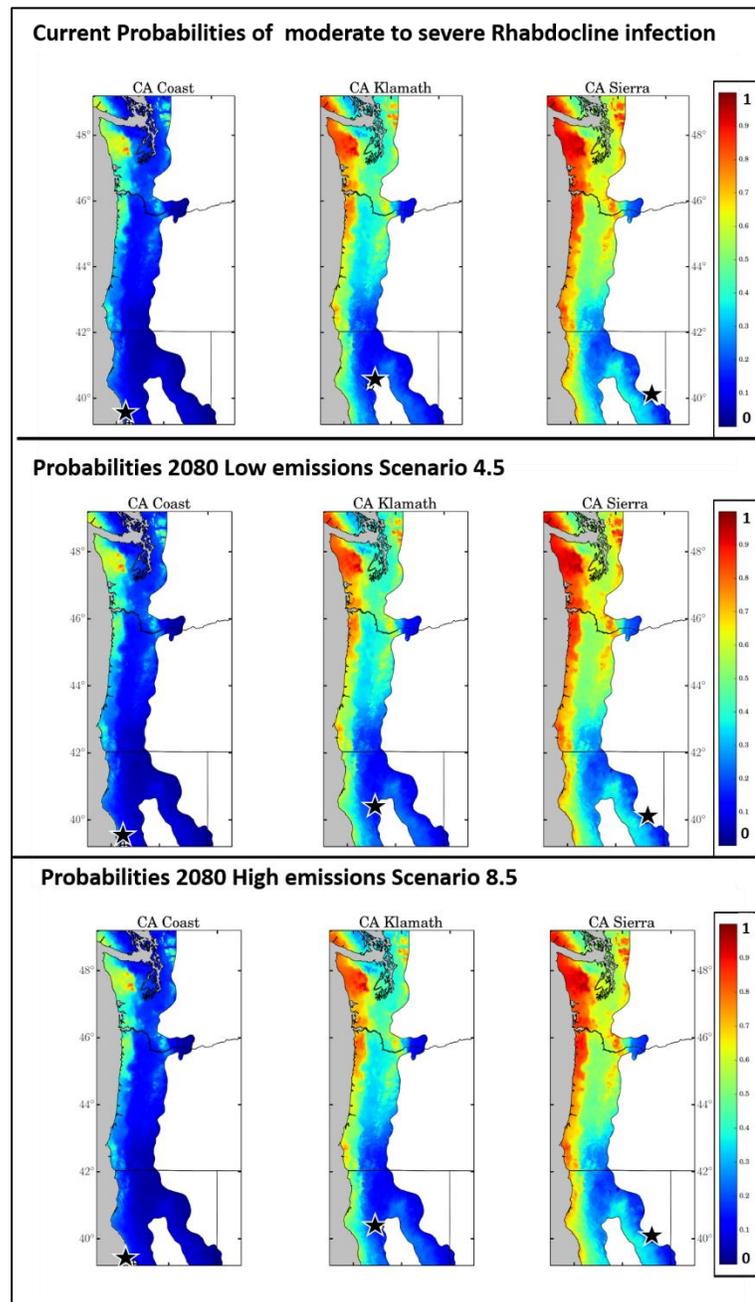


Figure 2.14 Geographic distribution of estimated probabilities of moderate to severe *Rhabdocline* spp. infection in relation to the California regions of the Douglas-fir Seed Source Movement Trials (SSMT). Probabilities were estimated using the model selected using data from these regions in relations to the seven site of the SSMT which displayed signs of *P. gaeumannii* and *Rhabdocline* spp. Climate predictions were made using the HadGEM2 climate projections obtained from ClimateNA (Wang et al. 2013).

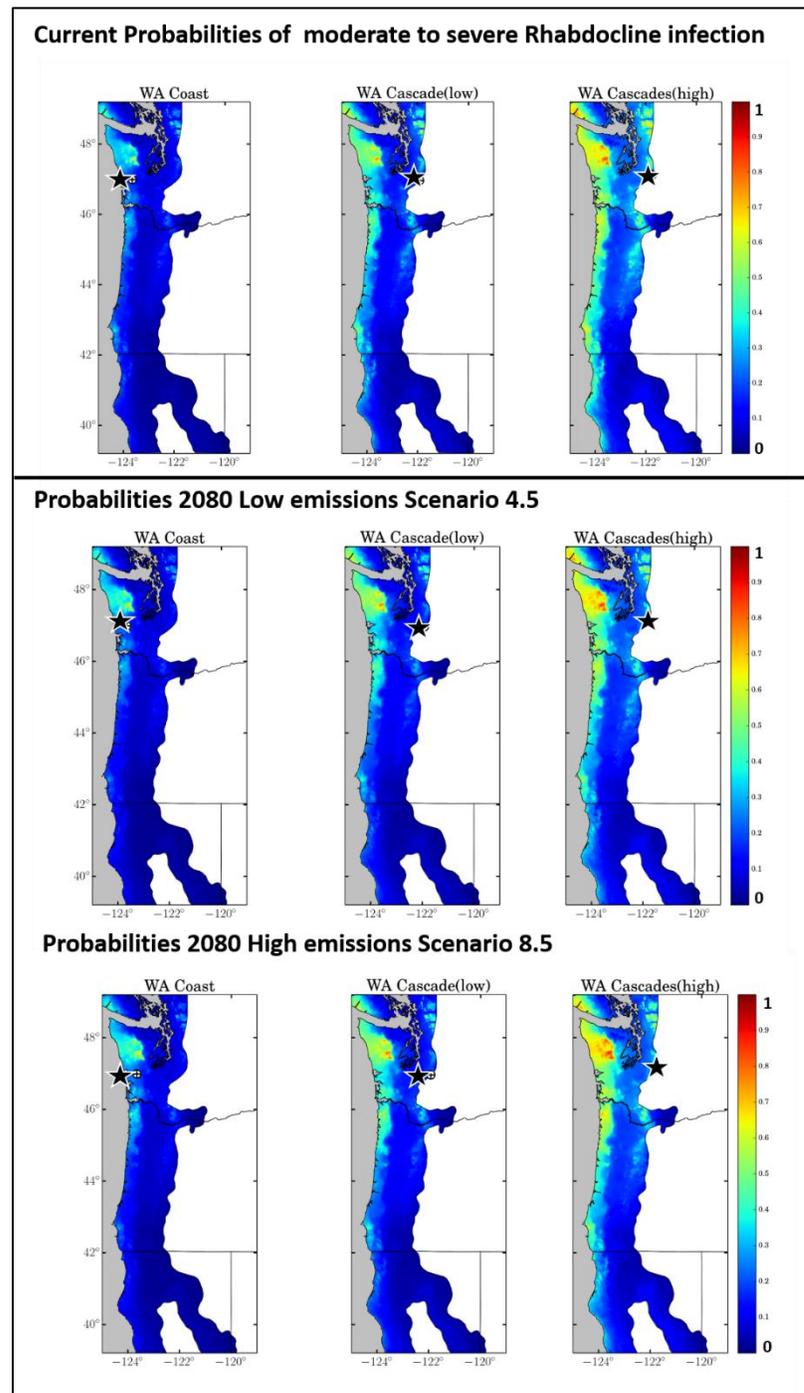


Figure 2.15 Geographic distribution of estimated probabilities of moderate to severe *Rhabdocline spp.* infection in relation to the Washington regions of the Douglas-fir Seed Source Movement Trials (SSMT). Probabilities were estimated using the model selected using data from these regions in relations to the seven site of the SSMT which displayed signs of *P. gaumannii* and *Rhabdocline spp.* Climate predictions were made using the HadGEM2 climate projections obtained from ClimateNA (Wang et al. 2013)

Tables

Table 2.1 Climate variables associated with the regions (top) and test sites (bottom) of the Douglas-fir Seed Source Movement Trials. Climate variables - TD- continentality, MSP- May through September precipitation, MAP- mean annual precipitation, MAT-mean annual temperature, MWT-mean winter temperature

Region	Latitude	Longitude	Elevation (m)	MSP (mm)	MAP (mm)	MAT (C°)	TD (C°)	MWT (C°)
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	42.9	-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

Table 2.2 Percentage of trees in each of the 12 regions in the Douglas-fir Seed Source Movement Trials (SSMT) rated as having moderate to severe *P. gaemannii* infection at each test site in the SSMT. Regions are ordered according to band of latitude from south to north, from coast to high elevation within each band. Sites are ordered in the same manner.

Region	FLORAS	STONE NURSERY	EVANS CREEK	NORTONS	SLICE BUTTE	SODA 320	JAMMER3	BUCKHORN2	DOOR STOP	Region Ave.
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 Ave.	85	0	0	83	91	89	93	91	86	

Table 2.3 Variance components associated with the random effects model (no fixed effects) and the selected *P. gaeumannii* infection model (trees susceptible to *Rhabdocline* spp and trees with less than one year of needles removed). Data are from all test trees at the 7 test sites which displayed signs of *Rhabdocline* spp. and *P.gaeumannii* in the Douglas-fir Seed Source Movement Trials

Random effects model				Selected model			
Source	Variance	SD	Model Variance Explained	Source	Variance	SD	Model Variance Explained
Family	0.03	0.12	7%	Family	0.01	0.12	2%
Population	0.06	0.24	15%	Population	0.05	0.23	12%
Site	0.32	0.56	78%	Site	0.35	0.59	85%
Total	0.41		100	Total	0.41		100

Table 2.4 Furthest climate transfer distances and the transfer distance of zero (local) with probability of moderate to severe *P. gaeumannii* infection and 95 % confidence intervals (trees susceptible to *Rhabdocline* spp. and trees with less than one year of needle retention removed). Data are from all test trees at the 7 test sites which displayed signs of *Rhabdocline* spp. and *P.gaeumannii* in the Douglas-fir Seed Source Movement Trials Variables - Climate variable: MWT.- mean winter temperature

Prediction Variable	Climate Variable (units)	Direction of Transfer	Distance	Probability of Low Crown Density (95% CI)
<i>P. gaeumannii</i> infection	MWT (°C)	Low to High	8.75	99% (96% - 99.8%)
		local	0	97% (93% - 99%)
		High to Low	7.93	95 (87% - 99%)

Table 2.5 Percentage of trees in each of the 12 regions of the Douglas-fir Seed Source Movement Trials (SSMT) rated as having healthy crown density at each test site of the SSMT (trees susceptible to *Rhabdocline* spp. removed). Regions are ordered according to band of latitude (three regions per band) from south to north, from coast to high elevation within each band. Sites are ordered in the same manner.

Region	FLORAS	STONE NURSERY	EVANS CREEK	NORTONS	SLICE BUTTE	SODA 320	JAMMER 3	BUCKHORN 2	DOOR STOP	Region Ave.
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 Ave.	68	97	98	97	96	85	83	93	78	

Table 2.6 Variance components associated with the random effects model (no fixed effects) and the selected crown density model (trees susceptible to *Rhabdocline* spp. removed). Data are from all test trees at the 7 test sites which displayed signs of *Rhabdocline* spp. and *P.gaeumannii* in the Douglas-fir Seed Source Movement Trials

Source	Random effects model			Source	Selected model		
	Variance	SD	Model Variance Explained		Variance	SD	Model Variance Explained
Family	0.05	0.22	7	Family	0.05	0.23	16%
Population	0.24	0.49	37	Population	0.08	0.28	23%
Site	0.37	0.61	56	Site	0.21	0.46	61%
Total	0.67		100	Total	0.34		100

Table 2.7 Furthest climate transfer distances and the transfer distance of zero (local) with probability of low crown density and 95 % confidence intervals (trees susceptible to *Rhabdocline* spp. removed). Data are from all test trees at the seven test sites which displayed signs of *Rhabdocline* spp. and *P.gaeumannii* in the Douglas-fir Seed Source Movement Trials Variables - Climate variables: MSP-May through September Precipitation, and MWT.- mean winter temperature

Prediction Variable	Climate Variable (units)	Direction of Transfer	Distance	Probability of Low Crown Density (95% CI)
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		8% (2% - 22%)

Table 2.8 Percentage of trees in each of the 12 regions of the Douglas-fir Seed Source Movement Trials (SSMT) with moderate to severe *Rhabdocline* spp. infection at each test site of the SSMT. Regions are ordered according to band of latitude from south to north, from coast to high elevation within each band. Sites are ordered in the same manner.

Region	Floras	STONE NURSERY	EVANS CREEK	NORTONS	SLICE BUTTE	SODA320	JAMMER3	BUCKHORN2	DOORSTOP	Region Average
CA.coast	3	33	25	9	1	6	5	13	5	11
CA.Klamath	28	0	1	23	34	36	29	48	51	28
CA.Sierra	75	0	1	52	92	90	67	77	83	60
OR.coast(south)	1	4	0	3	0	3	3	1	9	3
OR.Siskiyou(low)	14	1	0	7	11	15	9	12	32	11
OR.Siskiyou(high)	11	1	1	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	1	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	3	0	8	4	9	14	3	16	6
Site Average	12	4	2	11	13	17	13	18	23	

Table 2.9 Variance components associated with the random effects model (no fixed effects) and the selected model for *Rhabdocline* spp. infection in relation to all test trees at every test site in the Douglas-fir Seed Source Movement Trials.

Source	Random effects model			Source	Selected model		
	Variance	SD	Proportion Explained		Variance	SD	Proportion Explained
Family	0.02	0.14	2%	Family	0.019	0.14	4%
Population	0.91	0.96	92%	Population	0.24	0.49	51%
Site	0.07	0.26	6%	Site	0.21	0.46	45%
Total	1		100%	Total	0.469		100%

Table 2.10 Furthest climate transfer distances and the transfer distance closest to zero (local) with associated probabilities of moderate to severe *Rhabdocline* spp. infection and 95% confidence intervals. Data are from all test trees at the 7 test sites which displayed signs of *Rhabdocline* spp. and *P.gaeumannii* in the Douglas-fir Seed Source Movement Trials. Climate variables: MSP-May through September Precipitation, MWT.- mean winter temperature, and continentality.

Prediction Variable	Climate Variable (units)	Direction of Transfer	Distance	Probability (95% CI)
<i>Rhabdocline</i> spp.	MSP	Low to High	472.83	62% (38% - 82%)
		Local	-0.33	4% (2% -9%)
		High to Low	282.99	0.0014% (.0002%-0.9%)
	MWT.	Low to High	8.75	27% (7% -60%)
		Local	0	8% (4% -15%)
		High to Low	7.93	2% (.1% - 10%)
Continentality		Low to High	10	0.6% (.0003% - 6%)
		Local	0	8% (4% -15%)
		High to Low	7.68	29%(10% -57%)

Chapter 3: General Conclusions

There is a large degree of variation in the resistance/tolerance to disease symptoms associated with Rhabdocline and Swiss needle cast (SNC) among populations of west-side Douglas-fir. There is also a large degree of variation in the resistance to *Rhabdocline spp.* Strong geographic patterns are associated with the distribution of the resistance/tolerance observed in this study. Populations of source locations characterized by high precipitation, specifically May through September precipitation (MSP), mild winter temperatures (MWT) and low continentality index displayed low susceptibility to Rhabdocline and SNC. The climate conditions associated with these regions enable successful dispersal, germination, infection and colonization of host tissue by these pathogens indicating that these populations have been exposed to high levels of disease (Capitano 1999, Manter et al. 2005, Lee 2013). Transferring populations from source climates that are not conducive to Rhabdocline or SNC into climates characterized by conditions conducive to these pathogens is related to high probabilities of disease symptoms and *Rhabdocline spp.* infection. These transfers were related to movement from low to high MSP and cool to warm MWT and are generally related to the movement of populations from south to north and from high to low elevations.

The relationship between susceptibility and transfer distances of MSP, MWT and continentality indicates that these populations have undergone strong selection pressure from these pathogens, and have thus become adapted to disease pressure. Douglas-fir populations associated with the aforementioned conditions in this study are located in northern Oregon and southern Washington in coastal and low elevation regions. Coastal

populations displayed the highest resistance to Rhabdocline and highest tolerance to SNC. Populations most susceptible to these pathogens were from northern California and inland southern Oregon. High elevation populations displayed the highest levels of susceptibility within each band of latitude in this study. Climates of the most susceptible populations are characterized by low winter temperatures, low May through September precipitation and high continentality. These conditions are not conducive to high disease pressure and, thus, these populations have been exposed to a much lower level of disease than the populations from northern Oregon and southern Washington (Hood 1982, McDermott and Robinson 1989, Manter et al. 2005). The geographic patterns displayed in this study have been described in past studies and further solidify the relationship between elevation and latitude, which are highly correlated with temperature and precipitation, on the susceptibility of populations of various tree species, including Douglas-fir, to foliage diseases in western North America (Hoff 1987, McDermott and Robinson 1989, Russell et al. 2007).

The resistance/tolerance to these pathogens associated with population from areas conducive to high pathogen presence demonstrates the importance and influence of these foliar pathogens on the success of Douglas-fir populations. Resistance/tolerance would not be selected for if the pathogen was of little consequence to productivity and the competitive success of these populations (Ennos 2015). Douglas-fir is characterized by a large degree of variation in adaptive traits and the susceptibility to pathogens observed in this study follows this trend (Campbell 1973, St.Clair et al. 2005, Bansal et al. 2015a, Bansal et al. 2015b) . Populations exposed to the highest disease pressure, the coastal

populations, are associated with the highest resistance/tolerance to these foliar pathogens. These populations displayed the lowest, or nearly the lowest, probabilities of exhibiting disease symptoms and *Rhabdocline* spp. infection at every test site and were associated with transfers from high to low MSP and warm to cool MWT. Local populations were associated with very low probabilities of disease symptoms and *Rhabdocline* spp. infection, therefore, can be assumed to be adapted to the disease pressure of their source climate. Douglas-fir's high level of adaptation to *Rhabdocline* and SNC, as observed in this study, indicates that changes in climate will likely alter the relationship between populations and these foliage diseases which appears to be the result of long-term adaptation.

Changes in climate may expose Douglas-fir populations to these climatic transfers within their native ranges or seed zones. Observed patterns of climate change over the last 30 years in the Pacific Northwest have included increases in winter temperature and spring precipitation (Abatzoglou et al. 2014). These changes have coincided with the increasing range of the current SNC epidemic (Stone et al. 2007, Black et al. 2010), indicating that observed and predicted changes in climate have and may continue to expose populations to conditions increasingly conducive to disease conditions, indicating that current changes in climate may be exposing populations of Douglas-fir to higher pathogen presence (Abatzoglou et al. 2014, Norlander and Kanaskie 2015, Mildrexler et al. 2016). However, projecting probabilities based on these transfer distances to 2080 did not reveal large changes in the current study. Zhou et al. (2011) predicted that regional conditions will become less conducive to foliage diseases such as SNC due to an increase

in continentality; an increase in needle retention was predicted in areas currently affected by SNC. Regardless of how changes in climate manifest, knowledge of the relationships between host, pathogen and climate is vital to proper management of diseases such as Rhabdocline and SNC.

Assisted migration is among the most popular of adaptive management strategies aimed at mitigating the negative impacts of climate change (McLachlin 2007, St Clair and Howe 2007, Ste-Marie 2011, Winder, 2011). The movement of populations to new environments in which they are predicted to be adapted in the future as part of assisted migration strategies will likely lead to the exposure of these populations to new pathogens and disease pressure not experienced in their source locations. Changes in climate may also expose populations of Douglas-fir to disease pressure or pathogens to which they are not adapted in the absence of assisted migration or human intervention (Mueller and Hellmann 2008). The results from this study show that Douglas-fir populations are well-adapted to the disease pressure of their source locations. Therefore, movement into sites of higher disease pressure or exposure to higher disease pressure due to changes in climate at the source location will result in increased risk of impacts from these pathogens. Assisted migration proponents advocate for the movement of populations from south to north to maintain productivity. Movement in this direction is associated with increasing risk of impacts of these foliar diseases if appropriate transfer distances are not taken into account.

Results of this study provide a useful tool to estimate low risk transfer distances for Douglas-fir populations, in order to mitigate negative impacts of foliar pathogens.

May through September precipitation and average winter temperature transfer distances were identified as accurate indicators of the probability of exhibiting moderate to severe disease symptoms. In providing a picture of the geographic distribution of the tolerance/resistance of west-side Douglas-fir to these foliar pathogens and also providing estimated low risk transfer distances, I have provided valuable information to the forestry community. This knowledge will be valuable in the modification of seed and breeding zones and will assist in the proper implementation of adaptive management strategies such as assisted migration. This knowledge also offers further insight into the relationship between these pathogens, west-side Douglas-fir, and climate.

Literature Cited:

- Abatzoglou, J. T., D. Rupp, and P. Mote. 2014. "Seasonal Climate Variability and Change in the Pacific Northwest of the United States." *Journal of Climate* 27 (5): 2125–2142. doi:10.1175/JCLI-D-13-00218.1.
- Bansal, S., Harrington, C. A., Gould, P. J., and St. Clair, J. B. 2015a. Climate-related genetic variation in drought-resistance of Douglas-fir (*Pseudotsuga menziesii*). (Report), 21(2), 947.
- Bansal, S., J. B. St. Clair, C.A. Harrington, and P. J. Gould. 2015b. "Impact of Climate Change on Cold Hardiness of Douglas-Fir (*Pseudotsuga Menziesii*): Environmental and Genetic Considerations." *Global Change Biology* 21 (10): 3814–26. doi:10.1111/gcb.12958.
- Black BA, Shaw DC, Stone JK. 2010. Impacts of Swiss needle cast on overstory Douglas-fir forests of the western Oregon Coast Range. *For. Ecol. Manag.* 259: 1673-1680
- Campbell, R. K., and Sorensen, F. C. (1973). Cold-Acclimation in Seedling Douglas-Fir Related to Phenology and Provenance. *Ecology*, 54(5), 1148–1151.
<http://doi.org/10.2307/1935582>
- Capitano, B. 1999. "The Infection and Colonization of Douglas-Fir by *Phaeocryptopus Gaeumannii*" Corvallis, Oregon: Oregon State University.

- Ennos, R. A. (2015). Resilience of forests to pathogens: an evolutionary ecology perspective. *Forestry*, 88(1), 41–52. <http://doi.org/10.1093/forestry/cpu048>
- Hoff, R. J. (1987). Susceptibility of inland Douglas-fir to Rhabdocline needle cast. U.S. Dept. of Agriculture, Forest Service, Intermountain Research Station.
- Hood, I. A. 1982. “Phaeocryptopus Gaeumannii on Pseudotsuga Menziesii in Southern British Columbia.” *New Zealand Journal of Forestry Science* 12 (3): 415–424.
- Lee, E. H., P. A. Beedlow, R. S. Waschmann, C.A. Burdick, and D.C. Shaw. 2013. “Tree-Ring Analysis of the Fungal Disease Swiss Needle Cast in Western Oregon Coastal Forests.” *Canadian Journal of Forest Research* 43 (8): 677–90. doi:10.1139/cjfr-2013-0062.
- Manter, D. K., P. W. Reeser, and J. K. Stone. 2005. “A Climate-Based Model for Predicting Geographic Variation in Swiss Needle Cast Severity in the Oregon Coast Range.” *Phytopathology* 95 (11): 1256–1265. doi:<http://dx.doi.org.ezproxy.proxy.library.oregonstate.edu/10.1094/PHYTO-95-1256>.
- McDermott, J. M., and Robinson, R. A. (1989). Provenance variation for disease resistance in *Pseudotsugamenziesii* to the Swiss needle-cast pathogen, *Phaeocryptopusgaeumannii*. *Canadian Journal of Forest Research*, 19(2), 244–246. <http://doi.org/10.1139/x89-034>

- McLachlan, J. S., Hellmann, J. J., and Schwartz, M. W. (2007). A Framework for Debate of Assisted Migration in an Era of Climate Change. *Conservation Biology*, 21(2), 297–302. <http://doi.org/10.1111/j.1523-1739.2007.00676.x>
- Mildrexler, D., Yang, Z., Cohen, W. B., and Bell, D. M. (2016). A forest vulnerability index based on drought and high temperatures. <http://doi.org/10.1016/j.rse.2015.11.024>
- Mueller, J. M., and Hellmann, J. J. (2008). An assessment of invasion risk from assisted migration. *Conservation Biology: The Journal of the Society for Conservation Biology*, 22(3), 562–567. <http://doi.org/10.1111/j.1523-1739.2008.00952.x>
- Russell, J. H., Kope, H. H., and Ades, P. (2007). Variation in cedar leaf blight (*Didymascella thujina*) resistance of western redcedar (*Thuja plicata*). *Canadian Journal of Forest Research*, 37(10), 1978–1986. <http://doi.org/10.1139/X07-034>
- St Clair, B., and Howe, G. T. (2007). Genetic maladaptation of coastal Douglas-fir seedlings to future climates. *Global Change Biology*, 13(7), 1441–1454. <http://doi.org/10.1111/j.1365-2486.2007.01385.x>
- Ste-Marie, C., A. Nelson, E., Dabros, A., and Bonneau, M.-E. (2011). Assisted migration: Introduction to a multifaceted concept. *The Forestry Chronicle*, 87(6), 724–730. <http://doi.org/10.5558/tfc2011-089>
- Stone, J. K., L. B. Coop, and D. K. Manter. 2008. “Predicting Effects of Climate Change on Swiss Needle Cast Disease Severity in Pacific Northwest Forests.” *Canadian*

Journal of Plant Pathology 30 (2): 169–176.

doi:10.1080/07060661.2008.10540533.

Winder, R., Nelson, E., and Beardmore, T. (2011). Ecological implications for assisted migration in Canadian forests. *The Forestry Chronicle*, 87(6), 731–744.

<http://doi.org/10.5558/tfc2011-090>

Zhao, J., D. B. Mainwaring, D. A. Maguire, and A. Kanaskie. 2011. “Regional and Annual Trends in Douglas-Fir Foliage Retention: Correlations with Climatic Variables.” *Forest Ecology and Management* 262 (9): 1872–86.

doi:10.1016/j.foreco.2011.08.00

Bibliography

- Akaike, H. 1974. "A New Look at the Statistical Model Identification." IEEE Transactions on Automatic Control 19 (6): 716–23.
doi:10.1109/TAC.1974.1100705.
- Abatzoglou, J. T., D. Rupp, and P. Mote. 2014. "Seasonal Climate Variability and Change in the Pacific Northwest of the United States." Journal of Climate 27 (5): 2125–2142. doi:10.1175/JCLI-D-13-00218.1.
- Agrios, G. N. 2005. Plant Pathology. Academic Press.
- Aitken, S. N., S. Yeaman, J. A. Holliday, T. Wang, and S. Curtis-McLane. 2008. "Adaptation, Migration or Extirpation: Climate Change Outcomes for Tree Populations." Evolutionary Applications 1 (1): 95–111. doi:10.1111/j.1752-4571.2007.00013.x.
- Aubin, I., C. M. Garbe, S. Colombo, C. R. Drever, D. W. McKenney, C. Messier, J. Pedlar, et al. 2011. "Why We Disagree about Assisted Migration: Ethical Implications of a Key Debate Regarding the Future of Canada's Forests." The Forestry Chronicle 87 (6): 755–65. doi:10.5558/tfc2011-092.
- Bansal, S., C. A. Harrington, P. J. Gould, and J. B. St. Clair. 2015a. "Climate-Related Genetic Variation in Drought-Resistance of Douglas-Fir (*Pseudotsuga menziesii*). (Report)" 21 (2): 947.
- Bansal, S., J. B. St. Clair, C. A. Harrington, and P. J. Gould. 2015b. "Impact of Climate Change on Cold Hardiness of Douglas-Fir (*Pseudotsuga Menziesii*):

- Environmental and Genetic Considerations.” *Global Change Biology* 21 (10): 3814–26. doi:10.1111/gcb.12958.
- Black B.A., D.C. Shaw, J.K. Stone. 2010. Impacts of Swiss needle cast on overstory Douglas-fir forests of the western Oregon Coast Range. *For. Ecol. Manag.* 259: 1673-1680
- Booth, T. H. 1990. “Mapping Regions Climatically Suitable for Particular Tree Species at the Global Scale.” *Forest Ecology and Management* 36 (1): 47–60.
doi:10.1016/0378-1127(90)90063-H.
- Boyce, J. S. 1940. “A needle-cast of Douglas Fir associated with *Adelopus gaumanni*.” *Phytopathology*. 30 (8): 649–655 .
- Boyce, J. S. 1961. *Forest Pathology*. 1961 Third Edition edition. N.Y.; Toronto: McGraw.
- Brandt, R. W. 1960. *The Rhabdocline Needle Cast of Douglas Fir* /. Syracuse : State University College of Forestry,. <http://www.biodiversitylibrary.org/item/126103>.
- Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2010. “AIC Model Selection and Multimodel Inference in Behavioral Ecology: Some Background, Observations, and Comparisons.” *Behavioral Ecology and Sociobiology* 65 (1): 23–35.
doi:10.1007/s00265-010-1029-6.

- Campbell, R. K., and F. C. Sorensen. 1973. "Cold-Acclimation in Seedling Douglas-Fir Related to Phenology and Provenance." *Ecology* 54 (5): 1148–51.
doi:10.2307/1935582.
- Cannell, M. G. R., and R. I. Smith. 1986. "Climatic Warming, Spring Budburst and Forest Damage on Trees." *Journal of Applied Ecology* 23 (1): 177–91.
doi:10.2307/2403090.
- Capitano. 1999. "The Infection and Colonization of Douglas-Fir by *Phaeocryptopus Gaeumannii*" Corvallis, Oregon: Oregon State University.
- Catal, M., G. C. Adams, and D. W. Fulbright. 2010. "Evaluation of Resistance to Rhabdocline Needlecast in Douglas Fir Variety Shuswap, with Quantitative Polymerase Chain Reaction." *Phytopathology* 100 (4): 337–344.
doi:10.1094/PHYTO-100-4-0337.
- Chastagner, G. A., R.S. Byther, and K.L. Riley. 1990a. Recent Research on Foliage Diseases :conference Proceedings : Carlisle, Pennsylvania, May 29-June 2, 1989 /. Washington, D.C. : <http://hdl.handle.net/2027/umn.31951d02988383q>.
- Chastagner, G. A. 2001. "Susceptibility of Intermountain Douglas-Fir to Rhabdocline Needle Cast When Grown in the Pacific Northwest." *Plant Health Progress*.
doi:10.1094/PHP-2001-1029-01-RS.
- Coops, N C., R.H. Waring, A. Plowright, J. Lee, and T. E. Dilts. 2016. "Using Remotely-Sensed Land Cover and Distribution Modeling to Estimate Tree Species

Migration in the Pacific Northwest Region of North America.” *Remote Sensing* 8 (1): 65. doi:10.3390/rs8010065.

Desprez-Loustau, M. L., J. Aguayo, C. Dutech, K. J. Hayden, C. Husson, B. Jakushkin, B. Marçais, D. Piou, C. Robin, and C. Vacher. 2015. “An Evolutionary Ecology Perspective to Address Forest Pathology Challenges of Today and Tomorrow.” *Annals of Forest Science* 73 (1): 45–67. doi:10.1007/s13595-015-0487-4.

Enderle, R., F. Peters, A. Nakou, and B. Metzler. 2013. “Temporal Development of Ash Dieback Symptoms and Spatial Distribution of Collar Rots in a Provenance Trial of *Fraxinus Excelsior*.” *European Journal of Forest Research* 132 (5–6): 865–76. doi:10.1007/s10342-013-0717-y.

Ennos, R. A. 2015. “Resilience of Forests to Pathogens: An Evolutionary Ecology Perspective.” *Forestry* 88 (1): 41–52. doi:10.1093/forestry/cpu048.

Ferguson, S. A. ; 1997. A Climate-Change Scenario for the Columbia River Basin. <http://www.treesearch.fs.fed.us/pubs/26876>.

Ford, K. R., C. A. Harrington, S. Bansal, P. J. Gould, and J. B. St Clair. 2016. “Will Changes in Phenology Track Climate Change? A Study of Growth Initiation Timing in Coast Douglas-Fir.” *Global Change Biology*, April. doi:10.1111/gcb.13328.

Franklin, J. F., and C. T. ; Dyness. 1973. Natural Vegetation of Oregon and Washington. <http://www.treesearch.fs.fed.us/pubs/26203>.

- Goheen, E. M., and E. A. Willhite. 2006. Field Guide to the Common Diseases and Insect Pests of Oregon and Washington Conifers /. [Portland, Or.] : USDA Forest Service, Pacific Northwest Region ;
<http://www.biodiversitylibrary.org/bibliography/80321>.
- Gould, P.J., C. A. Harrington, and B. J. St Clair. 2011. “Incorporating Genetic Variation into a Model of Budburst Phenology of Coast Douglas-Fir (*Pseudotsuga Menziesii* var. *menziesii*)” Canadian Journal of Forest Research 41: 139–50.
- Gould, P. J., C. A. Harrington, J. B. St Clair, and S. Thomas. 2012. “Growth Phenology of Coast Douglas-Fir Seed Sources Planted in Diverse Environments.” Tree Physiology 32 (12): 1482–1496. doi:10.1093/treephys/tps106.
- Hagle, S. K., S. Tunnock, and K. E. Gibson. 2003. Field Guide to Diseases and Insect Pests of Northern and Central Rocky Mountain Conifers. Diseases and Insect Pests of Northern and Central Rocky Mountain Conifers. Missoula, Mont.: U.S. Dept. of Agriculture, Forest Service, State and Private Forestry, Northern Region.
<http://catalog.hathitrust.org/Record/007425449>.
- Hansen, E. M., J. K. Stone, B. R. Capitano, P. Rosso, W. Sutton, L. Winton, A. Kanaskie, and M. G. McWilliams. 2000a. “Incidence and Impact of Swiss Needle Cast in Forest Plantations of Douglas-Fir in Coastal Oregon.” Plant Disease 84 (7): 773–778. doi:10.1094/PDIS.2000.84.7.773.
- Hoff, R J. 1987. Susceptibility of Inland Douglas-Fir to Rhabdocline Needle Cast. U.S. Dept. of Agriculture, Forest Service, Intermountain Research Station.

- Hood, I. A. and Wilcox, M. D.: Variation in susceptibility to chlorosis and needle cast associated with *Phaeocryptopus gaeumannii* in an 11-year-old Douglas-fir provenance trial. N.Z. For.Res. Inst. For. Path. Rep. No. 72 (1971).
- Hood, I. A. 1982. “*Phaeocryptopus Gaeumannii* on *Pseudotsuga Menziesii* in Southern British Columbia.” New Zealand Journal of Forestry Science 12 (3): 415–424.
- Hood, I. A., and M. O. Kimberley. 2005. “Douglas Fir Provenance Susceptibility to Swiss Needle Cast in New Zealand.” Australasian Plant Pathology 34 (1): 57–62. doi:10.1071/AP04080.
- IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp
- Jayawickrama K., D. C. Shaw, and T. Z. YE. 2012. “Genetic Selection in Coastal Douglas-Fir for Tolerance to Swiss Needle Cast Disease”. Proceedings of the fourth international workshop on the genetics of host-parasite interactions in forestry: Disease and insect resistance in forest trees. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. 372 pp.
- Johnson, G. R., 2002. “Genetic Variation of Douglas-Fir to Swiss Needle Cast as Assessed by Symptom Expression.” *Silvae Genetica* 51: 80–86.
- Johnson, G. R., F. Temel, K. Jayawickrama, and others. 2002. “Genetic Studies Involving Swiss Needle Cast.” Swiss Needle Cast Cooperative Annual Report, 38–43.

- Johnson, G. R., F. C. Sorensen, J. B. St Clair, and R. C. Cronn. 2004. "Pacific Northwest Forest Tree Seed Zones A Template for Native Plants?" *Native Plants Journal* 5 (2): 131–40. doi:10.2979/NPJ.2004.5.2.131.
- Jones, C. D., J. K. Hughes, N. Bellouin, S. C. Hardiman, G. S. Jones, J. Knight, S. Liddicoat, et al. 2011. "The HadGEM2-ES Implementation of CMIP5 Centennial Simulations." *Geosci. Model Dev.* 4 (3): 543–70. doi:10.5194/gmd-4-543-2011.
- Kastner, W. W., S.M. Dutton, D.M. Roche. 2001. "Effects of Swiss Needle Cast on Three Douglas-Fir Seed Sources on a Low-Elevation Site in the Northern Oregon Coast Range: Results after Five Growing Seasons." *Western Journal of Applied Forestry* 16: 31–34.
- Kawecki, T. J., and D. Ebert. 2004. "Conceptual Issues in Local Adaptation." *Ecology Letters* 7 (12): 1225–41. doi:10.1111/j.1461-0248.2004.00684.x.
- Kurkela, T. 1981. *Growth Reduction in Douglas Fir Caused by Rhabdocline Needle Cast*. Communicationes Instituti Forestalis Fenniae. Helsinki: Finnish Forest Research Institute.
- Lavender, D. P., and R. K. Hermann. 2014. *Douglas-Fir: The Genus *Pseudotsuga**. Corvallis, OR : Forest Research Publications Office, Oregon State University. <http://ir.library.oregonstate.edu/xmlui/handle/1957/47168>.
- Lee, E. H., P. A. Beedlow, R. S. Waschmann, C. A. Burdick, and D. C. Shaw. 2013. "Tree-Ring Analysis of the Fungal Disease Swiss Needle Cast in Western Oregon

Coastal Forests.” *Canadian Journal of Forest Research* 43 (8): 677–90.

doi:10.1139/cjfr-2013-0062.

Littell, J. S., E. E. Oneil, D. McKenzie, J. A. Hicke, J. A. Lutz, R. A. Norheim, and M.

M. Elsner. 2010. “Forest Ecosystems, Disturbance, and Climatic Change in

Washington State, USA.” *Climatic Change* 102 (1–2): 129–58.

doi:10.1007/s10584-010-9858-x.

Maguire, D. A., A. Kanaskie, W. Voelker, R. Johnson, and G. Johnson. 2002. “Growth of

Young Douglas-Fir Plantations across a Gradient in Swiss Needle Cast Severity.”

Western Journal of Applied Forestry 17 (2): 86–95.

Manter, D. K., B. J. Bond, K. L. Kavanagh, P. H. Rosso, and G. M. Filip. 2000.

“Pseudothecia of Swiss Needle Cast Fungus, *Phaeocryptopus Gaeumannii*,

Physically Block Stomata of Douglas Fir, Reducing CO₂ Assimilation.” *New*

Phytologist 148 (3): 481–491. doi:10.1046/j.1469-8137.2000.00779.x.

Manter, D. K., P. W. Reeser, and J. K. Stone. 2005. “A Climate-Based Model for

Predicting Geographic Variation in Swiss Needle Cast Severity in the Oregon

Coast Range.” *Phytopathology* 95 (11): 1256–1265.

doi:http://dx.doi.org.ezproxy.proxy.library.oregonstate.edu/10.1094/PHYTO-95-

1256.

McDermott, J. M., and R. A. Robinson. 1989. “Provenance Variation for Disease

Resistance in *Pseudotsuga menziesii* to the Swiss Needle-Cast Pathogen,

Phaeocryptopus gaeumannii” Canadian Journal of Forest Research 19 (2): 244–246. doi:10.1139/x89-034.

Merrill, W. 1990. “Rhabdocline Needlecast Resistance in Douglas-Fir Seed Sources from the Southwestern United States.” Recent Research on Foliage Diseases : Conference Proceedings, Carlisle, Pennsylvania, May 29-June 2, 1989.

Michaels, E., and G. A. Chastagner. 1984. “Seasonal Availability of *Phaeocryptopus Gaeumannii* Ascospores and Conditions That Influence Their Release.” Plant Disease 68 (11): 942–944.

Mildrexler, D., Z. Yang, W. B. Cohen, and D. M. Bell. 2016. “A Forest Vulnerability Index Based on Drought and High Temperatures,” February. doi:10.1016/j.rse.2015.11.024.

Mote, P. W. 2003. “Trends in Temperature and Precipitation in the Pacific Northwest during the Twentieth Century.” <https://research.libraries.wsu.edu:8443/xmlui/handle/2376/1032>.

Mote, P. W., and E.P. Salathé Jr. 2010. “Future Climate in the Pacific Northwest.” Climatic Change 102 (1–2): 29–50. doi:10.1007/s10584-010-9848-z.

Mueller, J. M., and J. J. Hellmann. 2008. “An Assessment of Invasion Risk from Assisted Migration.” Conservation Biology: The Journal of the Society for Conservation Biology 22 (3): 562–67. doi:10.1111/j.1523-1739.2008.00952.x.

- Norlander D., A. Kanaski. (2014). 2014 Swiss Needle Cast Aerial Survey. Oregon Department of Forestry.
- Parker, A. K. 1970. "Effect of Relative Humidity and Temperature on Needle Cast Disease of Douglas-Fir." *Phytopathology* 60 (August): 1270.
- Randall, W. K., and Berrang, P. (2002). "Washington Tree Seed Transfer Zones." Washington State Department of Natural Resources.
- Rehfeldt, G. E. 1995. "Genetic Variation, Climate Models and the Ecological Genetics of *Larix Occidentalis*." *Forest Ecology and Management* 78 (1–3): 21–37.
doi:10.1016/0378-1127(95)03602-4.
- Rehfeldt, G. E, N. M. Tchebakova, and L. K. Barnhardt. 1999. "Efficacy of Climate Transfer Functions: Introduction of Eurasian Populations of *Larix* into Alberta." *Canadian Journal of Forest Research* 29 (11): 1660–68. doi:10.1139/x99-143.
- Rehfeldt, G., W. Wykoff, and C. Ying. 2001. "Physiologic Plasticity, Evolution, and Impacts of a Changing Climate on *Pinus Contorta*." *Climatic Change* 50 (3): 355–376. doi:10.1023/A:1010614216256.
- Rehfeldt, G. E., N. M. Tchebakova, L. I. Milyutin, E. I. Parfenova, W. R. Wykoff, and N. A. Kouzmina. 2003. "Assessing Population Responses to Climate in *Pinus Sylvestris* and *Larix* Spp. of Eurasia with Climate-Transfer Models." *Eurasian Journal of Forest Research - Hokkaido University (Japan)*.
<http://agris.fao.org/agris-search/search.do?recordID=JP2004006358>.

- Rehfeldt, G. E., B. C. Jaquish, C. Sáenz-Romero, D. G. Joyce, L. P. Leites, J. B. St Clair, and J. López-Upton. 2014. “Comparative Genetic Responses to Climate in the Varieties of *Pinus Ponderosa* and *Pseudotsuga Menziesii*: Reforestation.” *Forest Ecology and Management* 324 (July): 147–57. doi:10.1016/j.foreco.2014.02.040.
- Rosso, P. H., and E. M. Hansen. 2003. “Predicting Swiss Needle Cast Disease Distribution and Severity in Young Douglas-Fir Plantations in Coastal Oregon.” *Phytopathology* 93 (7): 790–798.
- RStudio Team (2015). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL <http://www.rstudio.com/>.
- Russell, J. H., H. H. Kope, and P. Ades. 2007. “Variation in Cedar Leaf Blight (*Didymascella Thujina*) Resistance of Western Redcedar (*Thuja Plicata*).” *Canadian Journal of Forest Research* 37 (10): 1978–86. doi:10.1139/X07-034.
- Sampaio, T., M. Branco, E. Guichoux, R. J. Petit, J. S. Pereira, M. C. Varela, and M. H. Almeida. 2016. “Does the Geography of Cork Oak Origin Influence Budburst and Leaf Pest Damage?” *Forest Ecology and Management* 373 (August): 33–43. doi:10.1016/j.foreco.2016.04.019.
- Shaw, D. C., G. M. Filip, A. Kanaskie, D. A. Maguire, and W. A. Littke. 2011. “Managing an Epidemic of Swiss Needle Cast in the Douglas-Fir Region of Oregon: The Role of the Swiss Needle Cast Cooperative.” *Journal of Forestry* 109 (2): 109–119.

- St.Clair, J. B., N. L. Mandel, and K. W. Vance-Borland. 2005. "Genecology of Douglas Fir in Western Oregon and Washington." *Annals of Botany* 96 (7): 1199–1214. doi:10.1093/aob/mci278.
- St Clair, J. B., and G. T. Howe. 2007. "Genetic Maladaptation of Coastal Douglas-fir Seedlings to Future Climates." *Global Change Biology* 13 (7): 1441–1454. doi:10.1111/j.1365-2486.2007.01385.x.
- Ste-Marie, C., E. A. Nelson, A. Dabros, and M. Bonneau. 2011. "Assisted Migration: Introduction to a Multifaceted Concept." *The Forestry Chronicle* 87 (6): 724–30. doi:10.5558/tfc2011-089.
- Stephan BR. 1973. Über Anfälligkeit und Resistenz von Douglasien-Herkünften gegenüber *Rhabdocline pseudotsugae*. *Silvae Genet.* 22: 149-153
- Stone, J. 1997. *Rhabdocline needle cast*. Pages 54-55 in: *Compendium of Conifer Diseases*. E. M. Hansen and K. J. Lewis, eds. The American Phytopathological Society, St. Paul, MN
- Stone, J. K., I. A. Hood, M. S. Watt, and J. L. Kerrigan. 2007. "Distribution of Swiss Needle Cast in New Zealand in Relation to Winter Temperature." *Australasian Plant Pathology* 36 (5): 445–54. doi:10.1071/AP07049.
- Stone, J. K., B. R. Capitano, and J. L. Kerrigan. 2008a. "The Histopathology of on Douglas-Fir Needles." *Mycologia* 100 (3): 431–444.

- Stone, J. K., L. B. Coop, and D.K. Manter. 2008b. "Predicting Effects of Climate Change on Swiss Needle Cast Disease Severity in Pacific Northwest Forests." *Canadian Journal of Plant Pathology* 30 (2): 169–176.
doi:10.1080/07060661.2008.10540533.
- Stroup, W.W., 2012. *Generalized linear mixed models: modern concepts, methods and applications*. CRC press. pp 317
- Sturrock, R. 2012. "Climate Change and Forest Diseases: Using Today's Knowledge to Address Future Challenges." *Forest Systems* 21 (2): 329–36.
doi:10.5424/fs/2012212-02230.
- Telford, A., S. Cavers, R. A. Ennos, and J. E. Cottrell. 2014. "Can We Protect Forests by Harnessing Variation in Resistance to Pests and Pathogens?" *Forestry*, April, cpu012. doi:10.1093/forestry/cpu012.
- Temel, F., G. R. Johnson, and J. K. Stone. 2004. "The Relationship between Swiss Needle Cast Symptom Severity and Level of *Phaeocryptopus Gaeumannii* Colonization in Coastal Douglas-Fir (*Pseudotsuga Menziesii* Var. *Menziesii*)." *Forest Pathology* 34 (6): 383–394.
doi:http://dx.doi.org.ezproxy.proxy.library.oregonstate.edu/10.1111/j.1439-0329.2004.00379.x.
- Wang, Tongli, Andreas Hamann, David L. Spittlehouse, and Trevor Q. Murdock. 2011. "ClimateWNA—High-Resolution Spatial Climate Data for Western North

- America.” *Journal of Applied Meteorology and Climatology* 51 (1): 16–29.
doi:10.1175/JAMC-D-11-043.1.
- Wang, T., Hamann, A., Spittlehouse, D.L. and Carroll, C. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS One* 11: e0156720
- Weir, J. R. 1917. “A Needle Blight of Douglas Fir.” *J. Agr. Res.* 10 (2), 99–103.
- Winder, R., E. Nelson, and T. Beardmore. 2011. “Ecological Implications for Assisted Migration in Canadian Forests.” *The Forestry Chronicle* 87 (6): 731–44.
doi:10.5558/tfc2011-090.
- Woods, A. J., K. D. Coates, and A. Hamann. 2005. “Is an Unprecedented *Dothistroma* Needle Blight Epidemic Related to Climate Change?” *BioScience* 55 (9): 761–69.
doi:10.1641/0006-3568(2005)055[0761:IAUDNB]2.0.CO;2.
- Woods, A. J., D. Heppner, H. H. Kope, J. Burleigh, and L. Maclauchlan. 2010. “Forest Health and Climate Change: A British Columbia Perspective.” *The Forestry Chronicle* 86 (4): 412–22. doi:10.5558/tfc86412-4.
- Zhang, J. W., N. B. Klopfenstein, and G. W. Peterson. 1997. “Genetic Variation in Disease Resistance of *Juniperus Virginiana* and *J. Scopulorum* Grown in Eastern Nebraska.” *Silvae Genetica* 46 (1): 11–
- Ying, C.C., and A. D. Yanchuk. 2006. “The Development of British Columbia’s Tree Seed Transfer Guidelines: Purpose, Concept, Methodology, and Implementation.”

Forest Ecology and Management, Perspectives on Site Productivity of Loblolly Pine Plantations in the Southern United States, 227 (1–2): 1–13.

doi:10.1016/j.foreco.2006.02.028.

Zhao, J., D. B. Mainwaring, D. A. Maguire, and A. Kanaskie. 2011. “Regional and Annual Trends in Douglas-Fir Foliage Retention: Correlations with Climatic Variables.” *Forest Ecology and Management* 262 (9): 1872–86.

doi:10.1016/j.foreco.2011.08

APPENDIX FIGURES

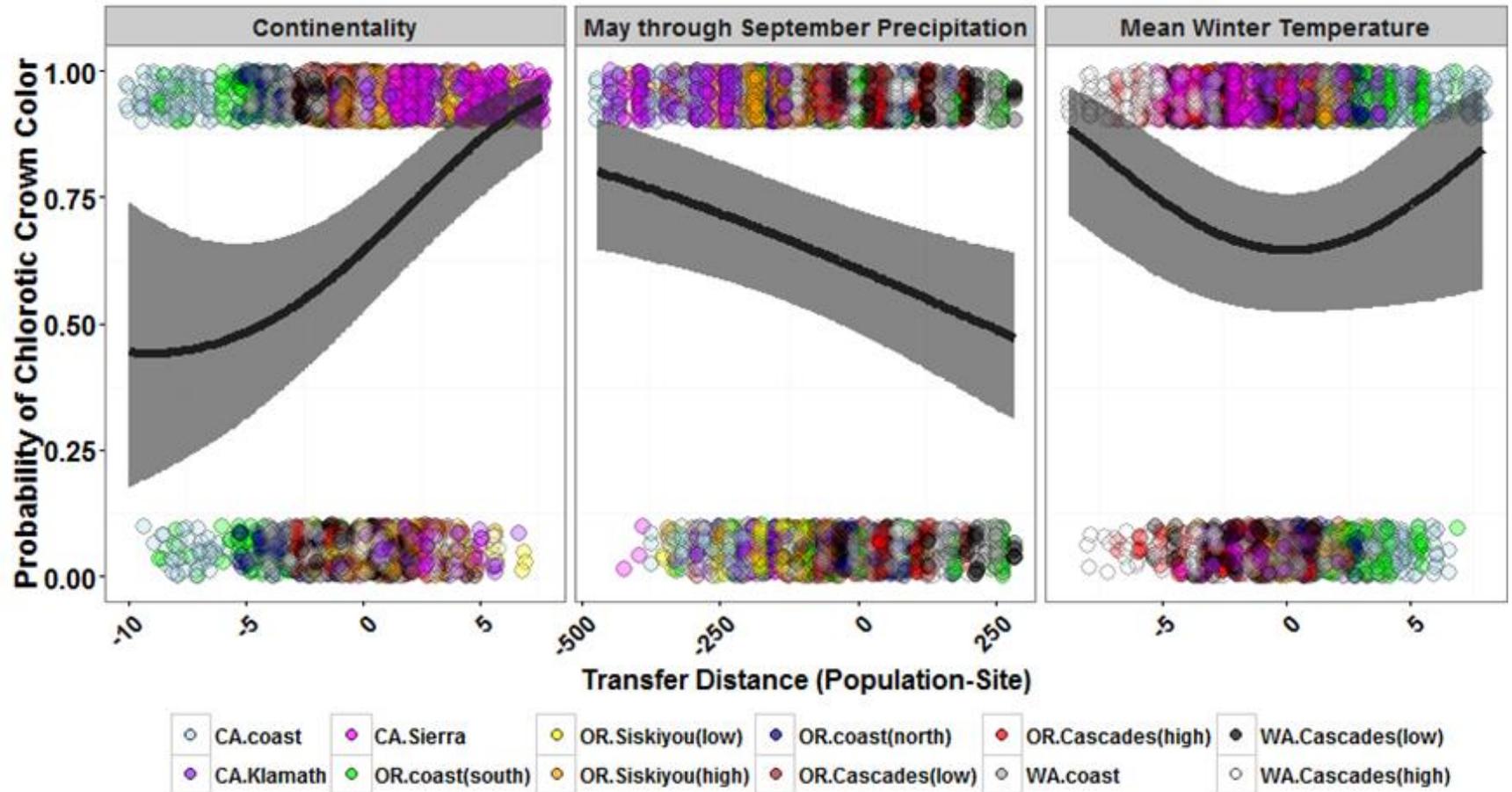


Figure 4.1 Estimated probabilities of chlorotic crown color (all disease present) versus climate transfer distance and 95% confidence intervals with raw data. Data are from all trees in the Douglas-fir Seed Source Movement trials at the seven sites where *Rhodocone* spp. and *P. gaumannii* were identified as present. Each predicted line holds the other climate transfer distances to their mean.

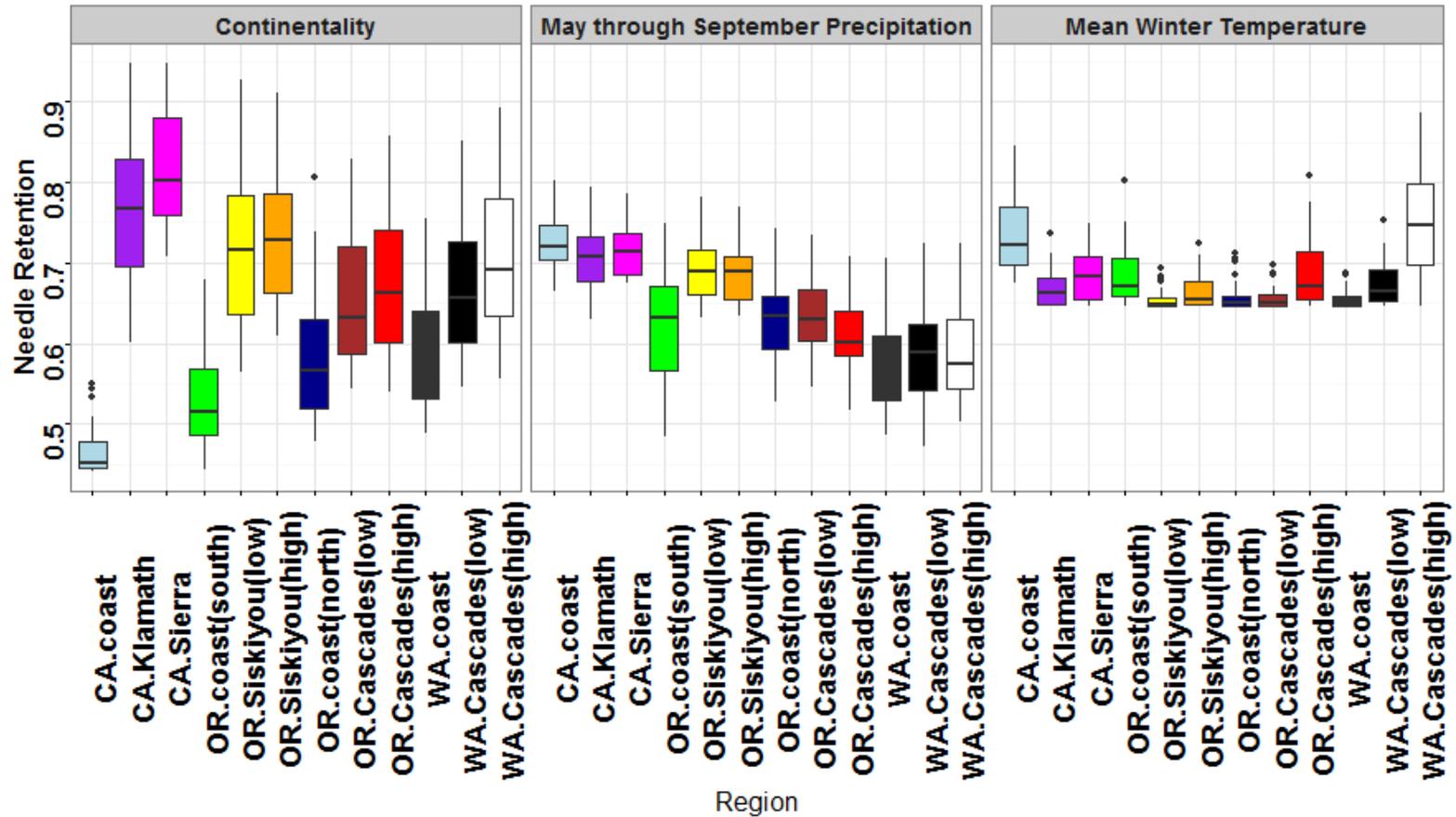


Figure 4.2 Estimated distribution of probabilities of chlorotic crown color (all disease present) in relation to each climate transfer distance holding the other climate transfer distance to its mean. Data are in relation to all 12 regions at all seven sites of the Douglas-fir Seed Source Movement Trials which displayed signs of *Rhabdocline* spp. and *P. gaeumannii*. The x axis displays the regions and is labeled by band of latitude (three regions per band) in order from north to south and from coast to high elevation within each band.

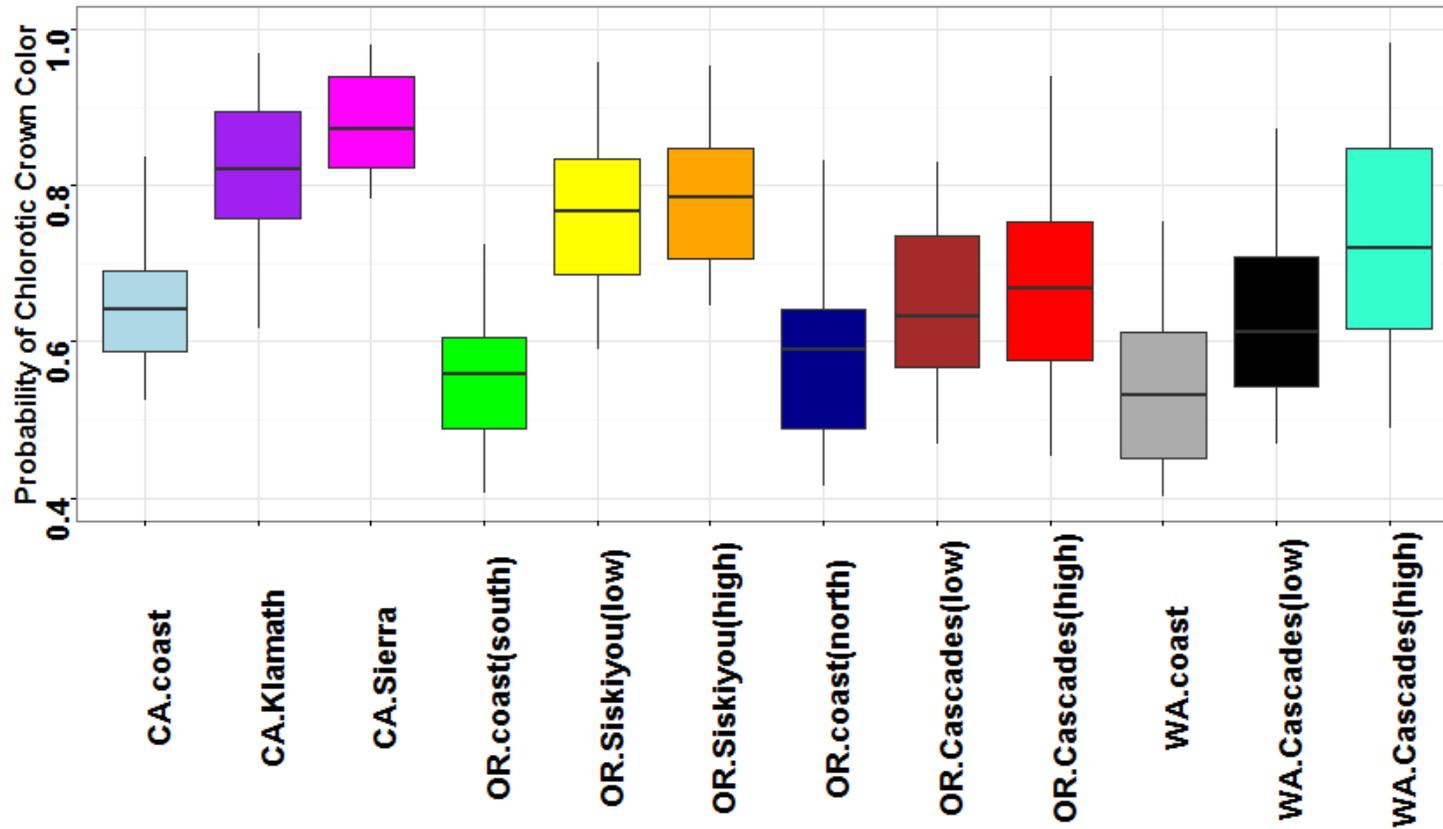


Figure 4.3 Distribution of the estimated probabilities of chlorotic crown color (all disease present) with all explanatory variables varying over their entire range in the dataset Data are in relation to all 12 regions at all seven sites of the Douglas-fir Seed Source Movement Trials which displayed signs of *Rhabdocline* spp. and *P. gaeumannii*. The x axis is labeled by band of latitude in order from north to south and from coast to high elevation within each band. The x axis displays the 12 regions and is labeled by band of latitude (three regions per band) in order from north to south and from coast to high elevation within each band

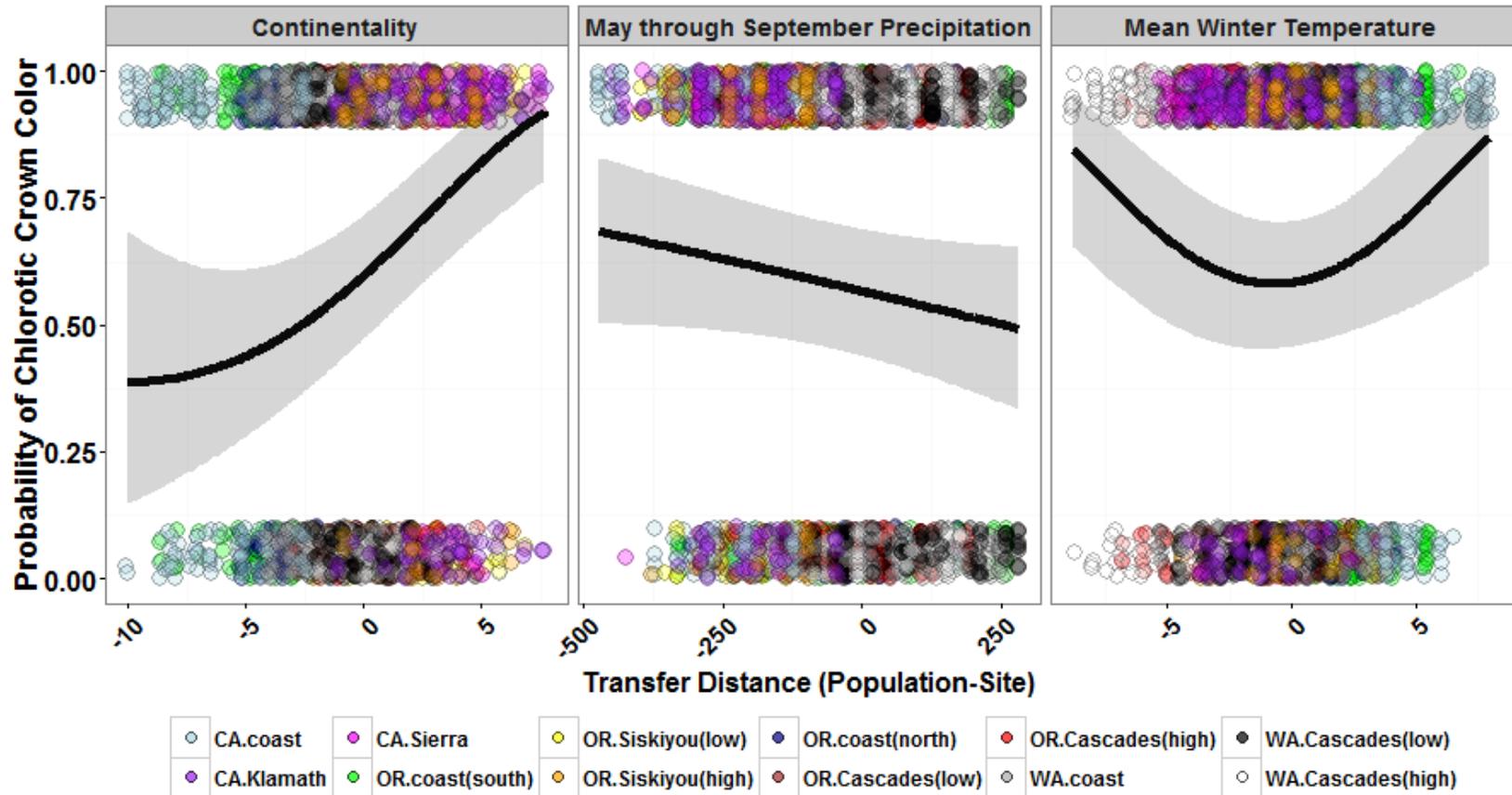


Figure 4.4 Estimated probabilities versus climate transfer distance of chlorotic crown color (trees susceptible to *Rhabdocline* spp. removed) and 95% confidence intervals with raw data. Data are from all trees in the Douglas-fir Seed Source Movement trials at the seven sites where *Rhabdocline* spp. and *P. gaumannii* were identified as present. Each predicted line holds the other climate transfer distances to their mean

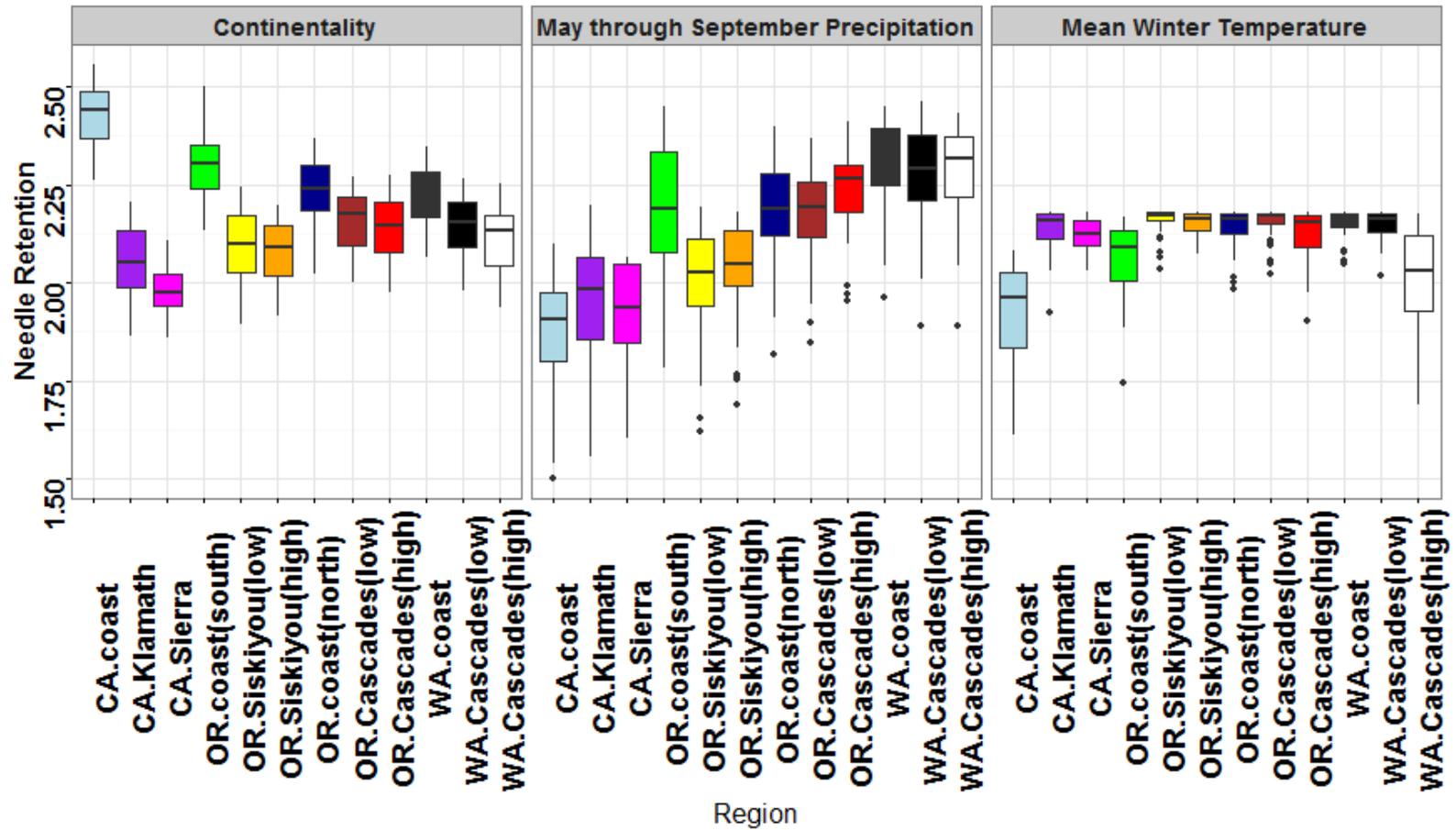


Figure 4.5 Estimated distribution of probabilities of chlorotic crown color, (trees susceptible to *Rhabdocline* spp. removed), in relation to each climate transfer distance, holding the other climate transfer distance to its mean. Data are in relation to all 12 regions at all seven sites of the Douglas-fir Seed Source Movement Trials which displayed signs of *Rhabdocline* spp. and *P. gaumannii*. The x axis displays the regions and is labeled by band of latitude (three regions per band) in order from north to south and from coast to high elevation within each band.

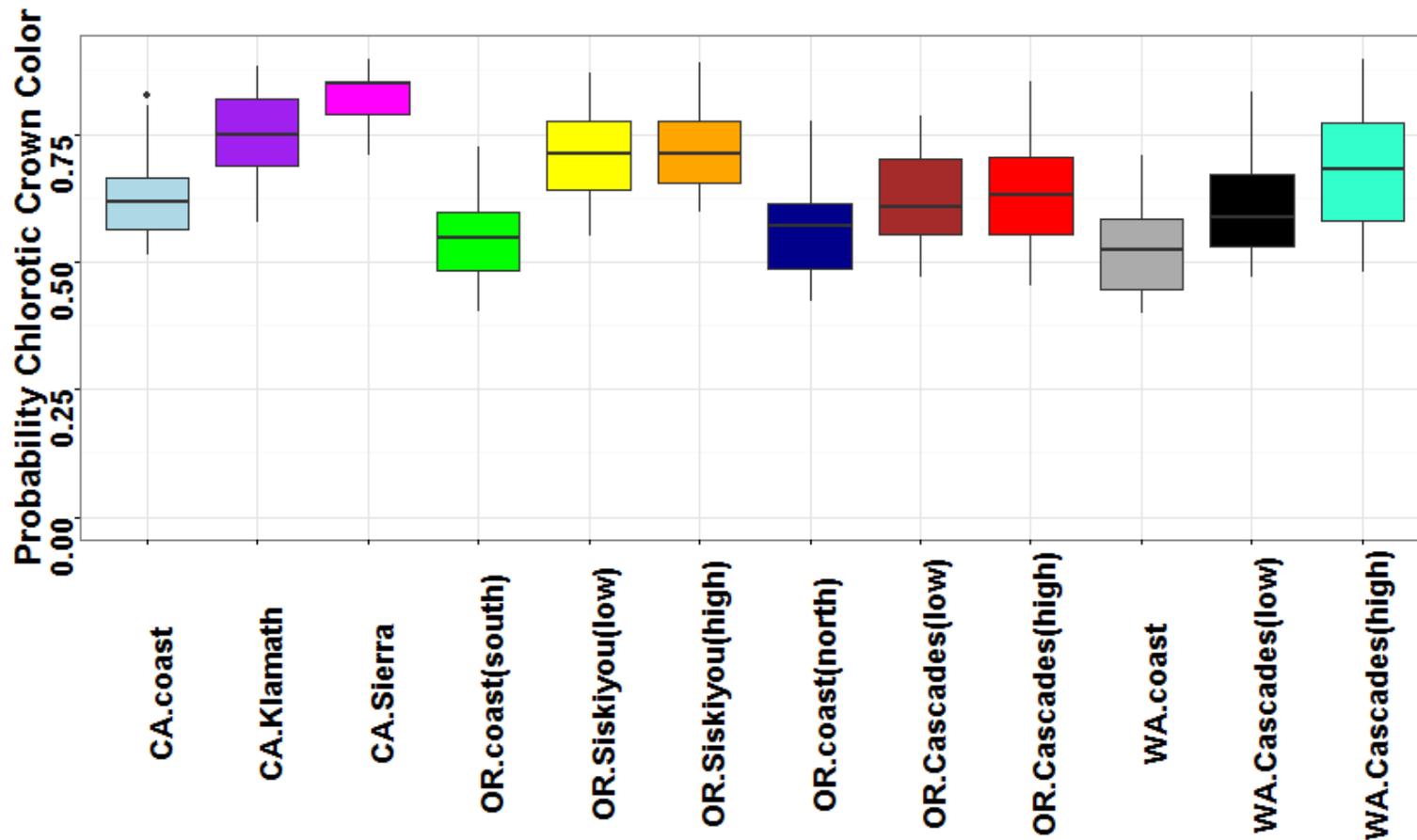


Figure 4.6 Distribution of the estimated probabilities of chlorotic crown color (trees susceptible to *Rhabdocline* spp. removed) with all explanatory variables varying over their entire range in the dataset. Data are in relation to all 12 regions at all seven sites of the Douglas-fir Seed Source Movement Trials which displayed signs of *Rhabdocline* spp. and *P. gaumannii*. The x axis is labeled by band of latitude in order from north to south and from coast to high elevation within each band. The x axis displays the 12 regions and is labeled by band of latitude (three regions per band) in order from north to south and from coast to high elevation within each band.

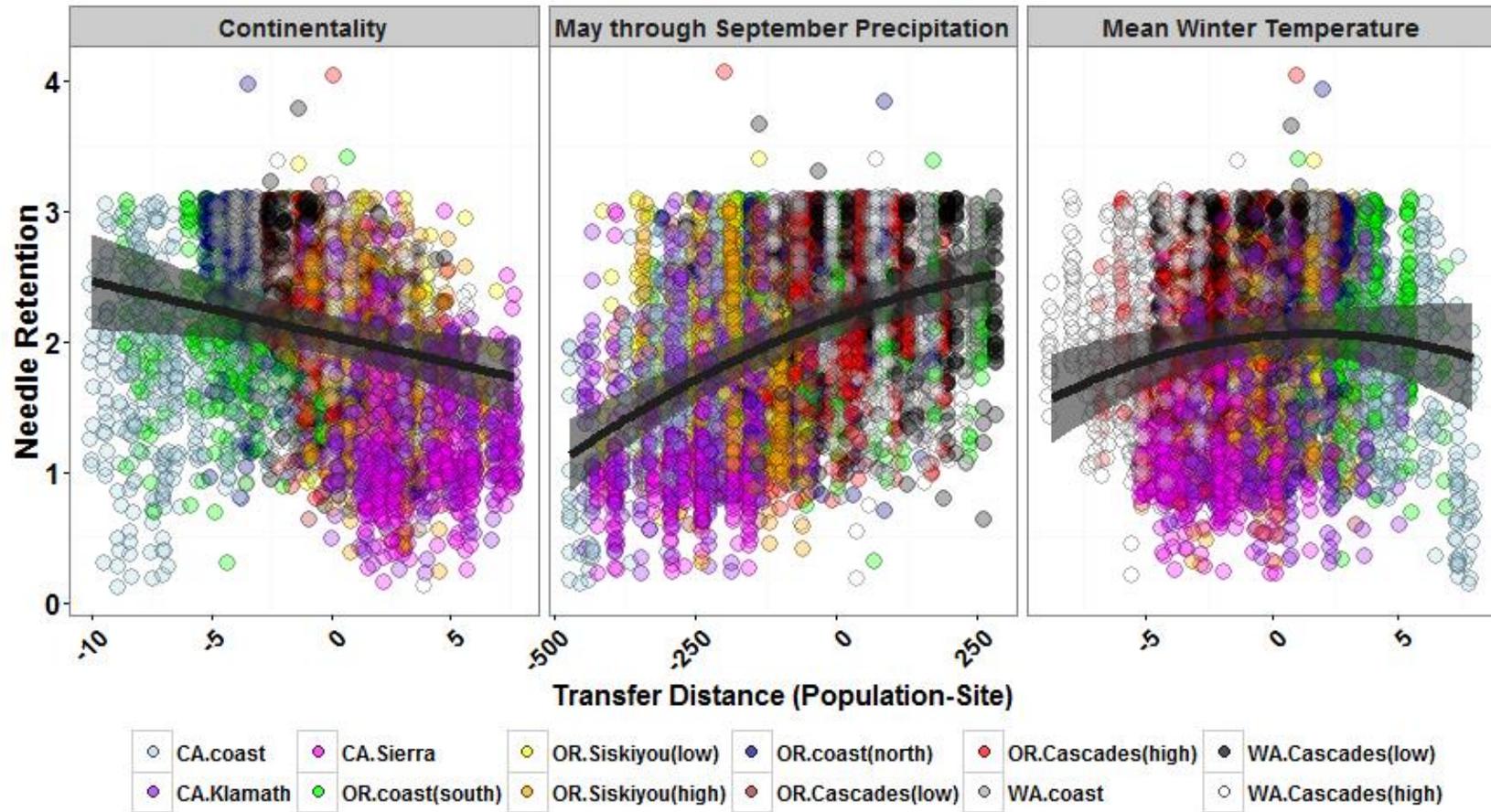


Figure 4.7 Estimated needle retention (all disease present) versus climate transfer distance and 95% confidence intervals with raw data. Data are from all trees in the Douglas-fir Seed Source Movement trials at the seven sites where *Rhabdocline* spp. and *P. gaeumannii* were identified as present. Each predicted line holds the other climate transfer distances to their mean.

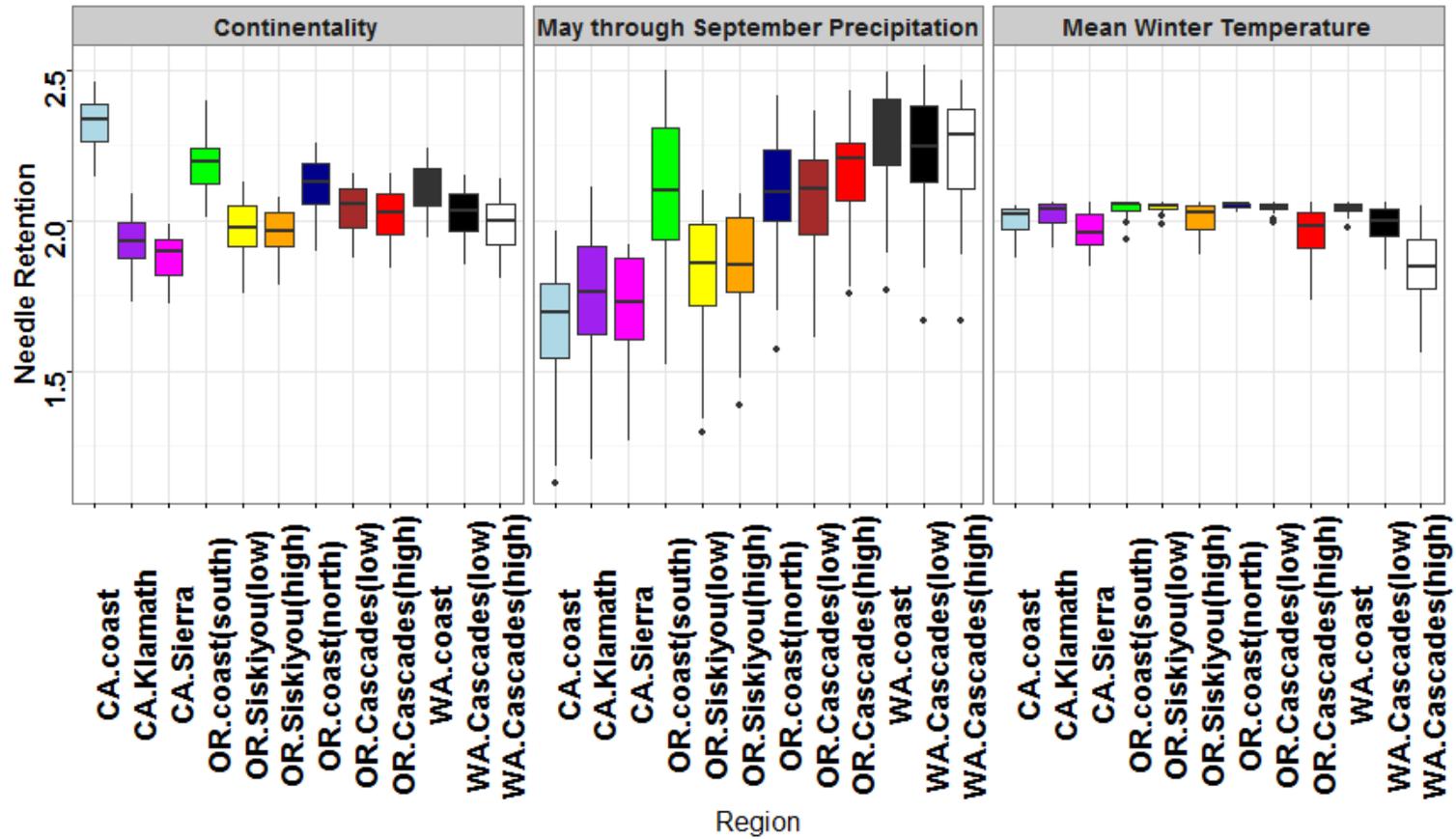


Figure 4.8 Estimated distribution of needle retention (all disease present) in relation to each climate transfer distance holding the other climate transfer distance to its mean. Data are in relation to all 12 regions at all seven sites of the Douglas-fir Seed Source Movement Trials which displayed signs of *Rhabdochline* spp. and *P. gaeumannii*. The x axis displays the regions and is labeled by band of latitude (three regions per band) in order from north to south and from coast to high elevation within each band.

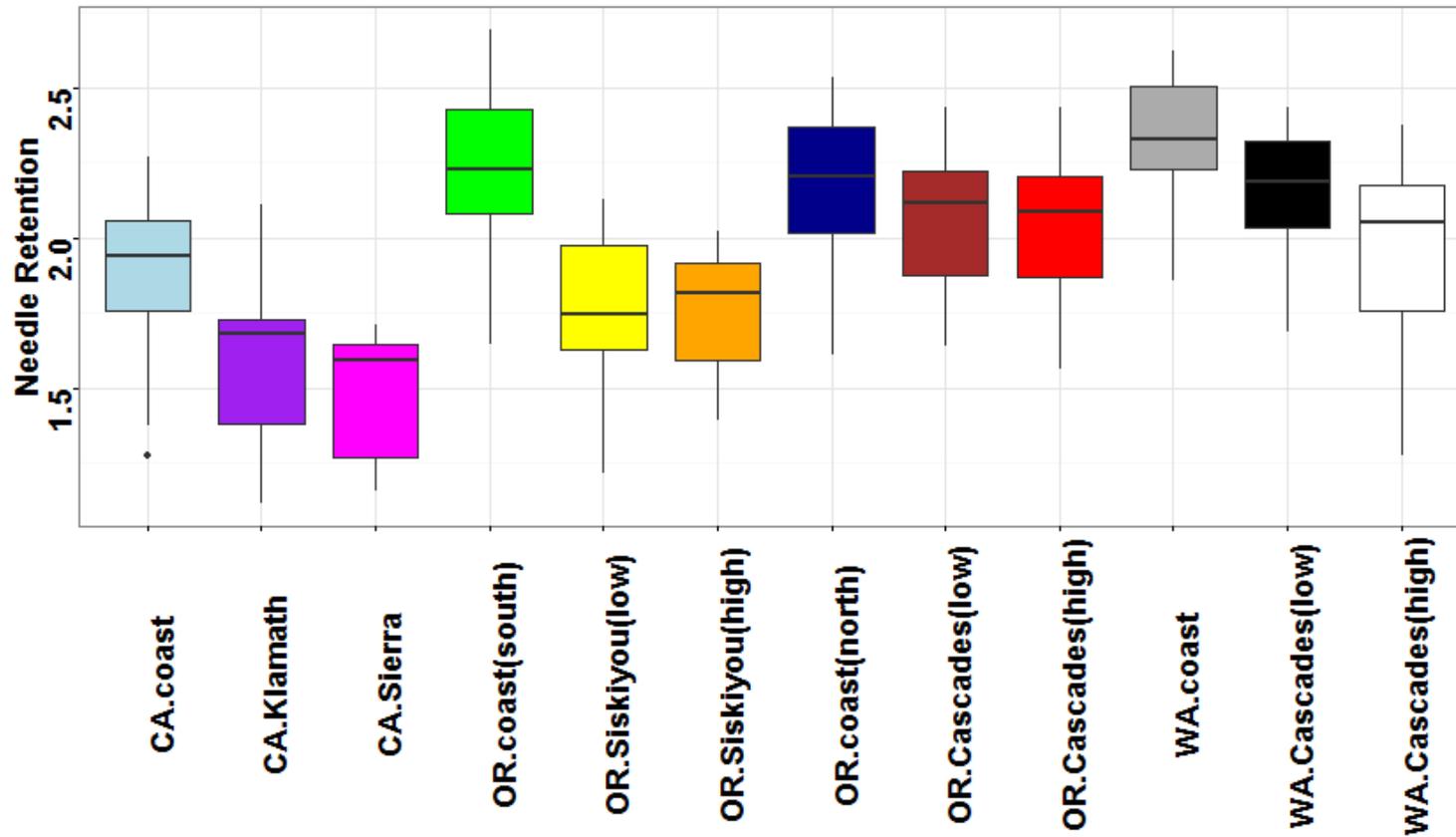


Figure 4.9 Distribution of the estimated needle retention (all disease present) with all explanatory variables varying over their entire range in the dataset. Data are in relation to all 12 regions at all seven sites of the Douglas-fir Seed Source Movement Trials which displayed signs of *Rhabdocline* spp. and *P. gaeumannii*. The x axis is labeled by band of latitude in order from north to south and from coast to high elevation within each band. The x axis displays the 12 regions and is labeled by band of latitude (three regions per band) in order from north to south and from coast to high elevation within each band.

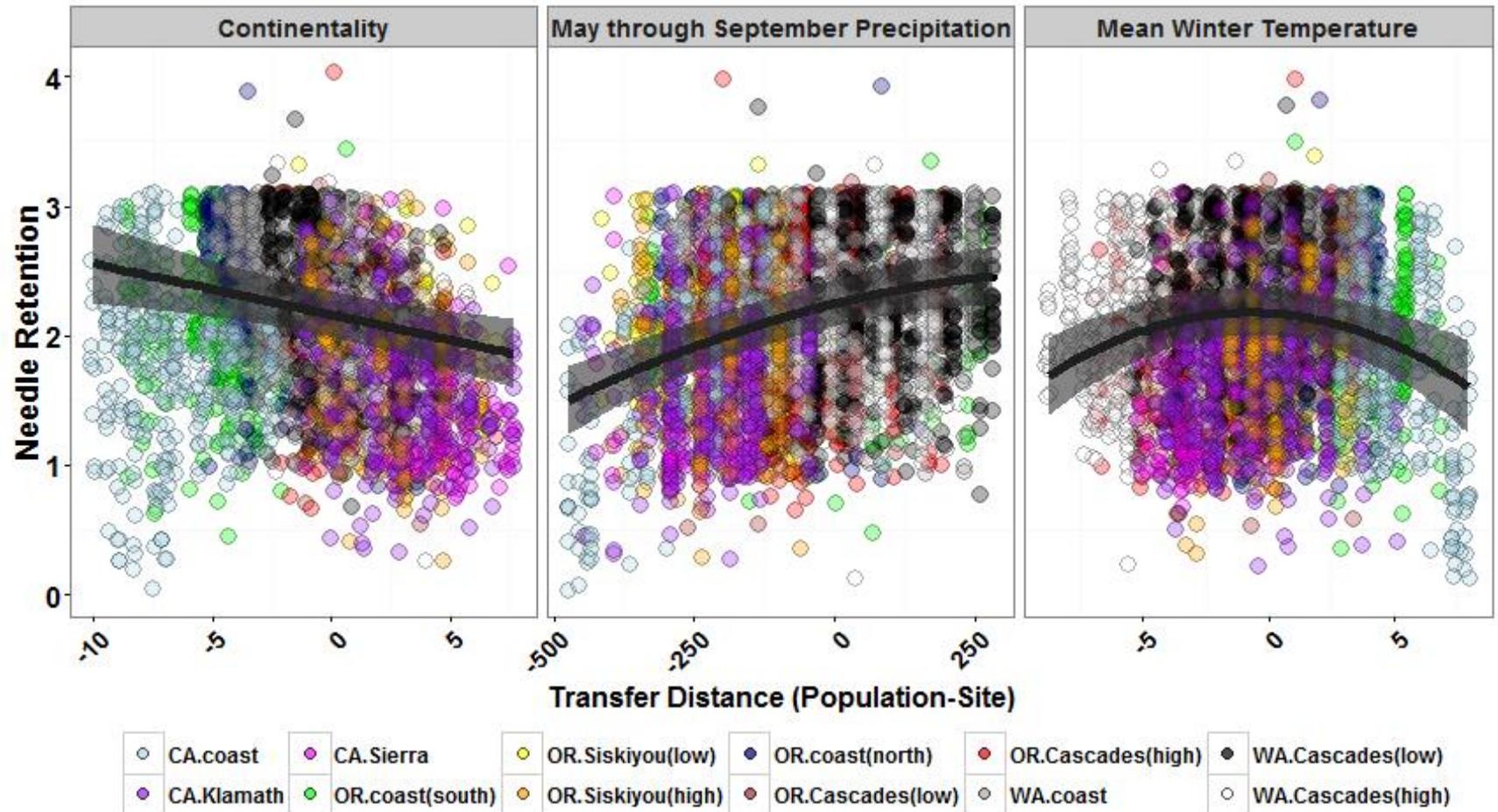


Figure 4.10 Estimated needle retention (trees susceptible to *Rhabdocline* spp. removed) versus climate transfer distance and 95% confidence intervals with raw data. Data are from all trees in the Douglas-fir Seed Source Movement trials at the seven sites where *Rhabdocline* spp. and *P. gaumannii* were identified as present. Each predicted line holds the other climate transfer distances to their mean.

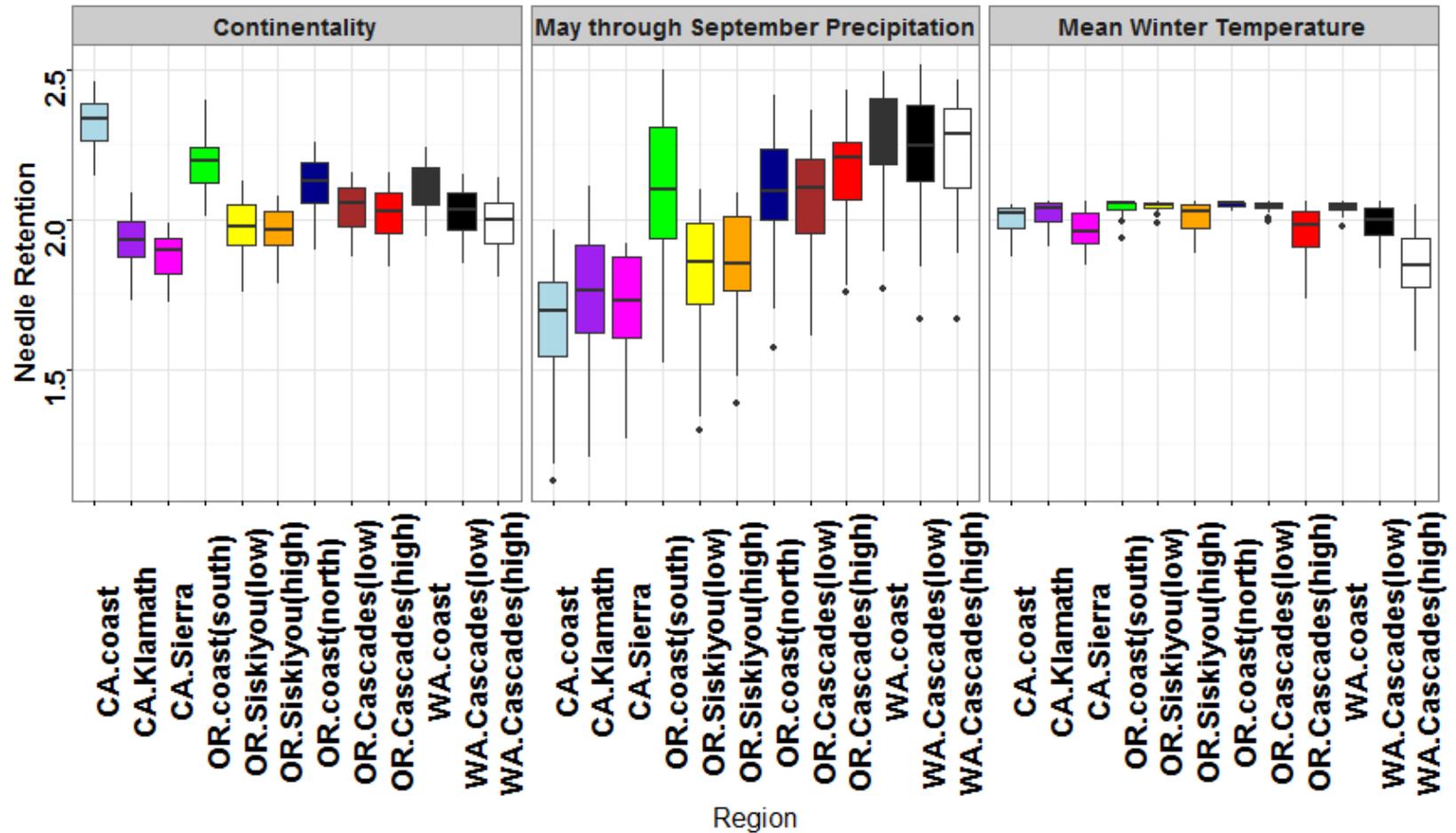


Figure 4.11 Estimated distribution of needle retention (trees susceptible to *Rhabdocline* spp. removed) in relation to each climate transfer distance holding the other climate transfer distance to its mean. Data are in relation to all 12 regions at all seven sites of the Douglas-fir Seed Source Movement Trials which displayed signs of *Rhabdocline* spp. and *P. gaeumannii*. The x axis displays the regions and is labeled by band of latitude (three regions per band) in order from north to south and from coast to high elevation within each band.

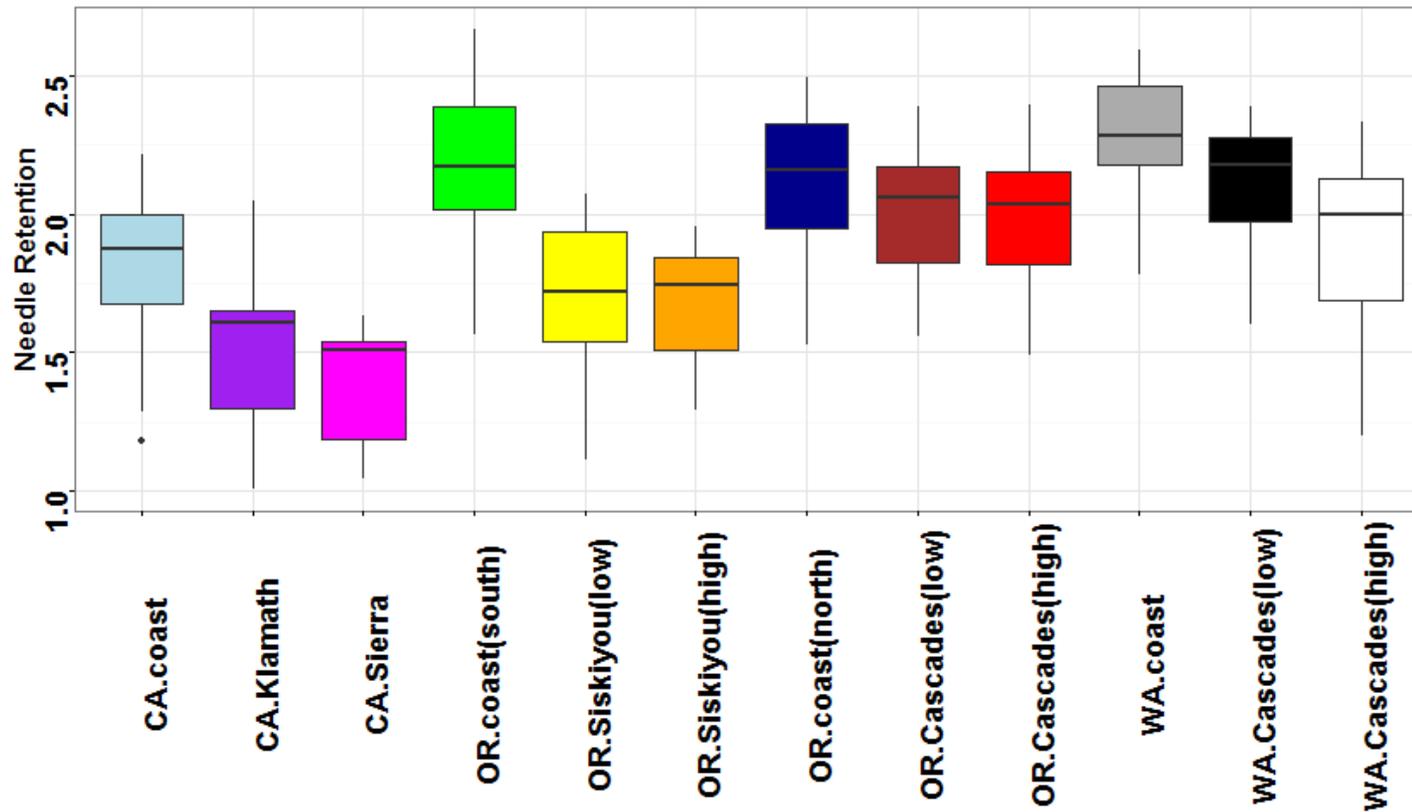


Figure 4.12 Distribution of the estimated needle retention (trees susceptible to *Rhabdocline* spp. removed) with all explanatory variables varying over their entire range in the dataset. Data are in relation to all 12 regions at all seven sites of the Douglas-fir Seed Source Movement Trials which displayed signs of *Rhabdocline* spp. and *P. gaeumannii*. The x axis is labeled by band of latitude in order from north to south and from coast to high elevation within each band. The x axis displays the 12 regions and is labeled by band of latitude (three regions per band) in order from north to south and from coast to high elevation within each band.

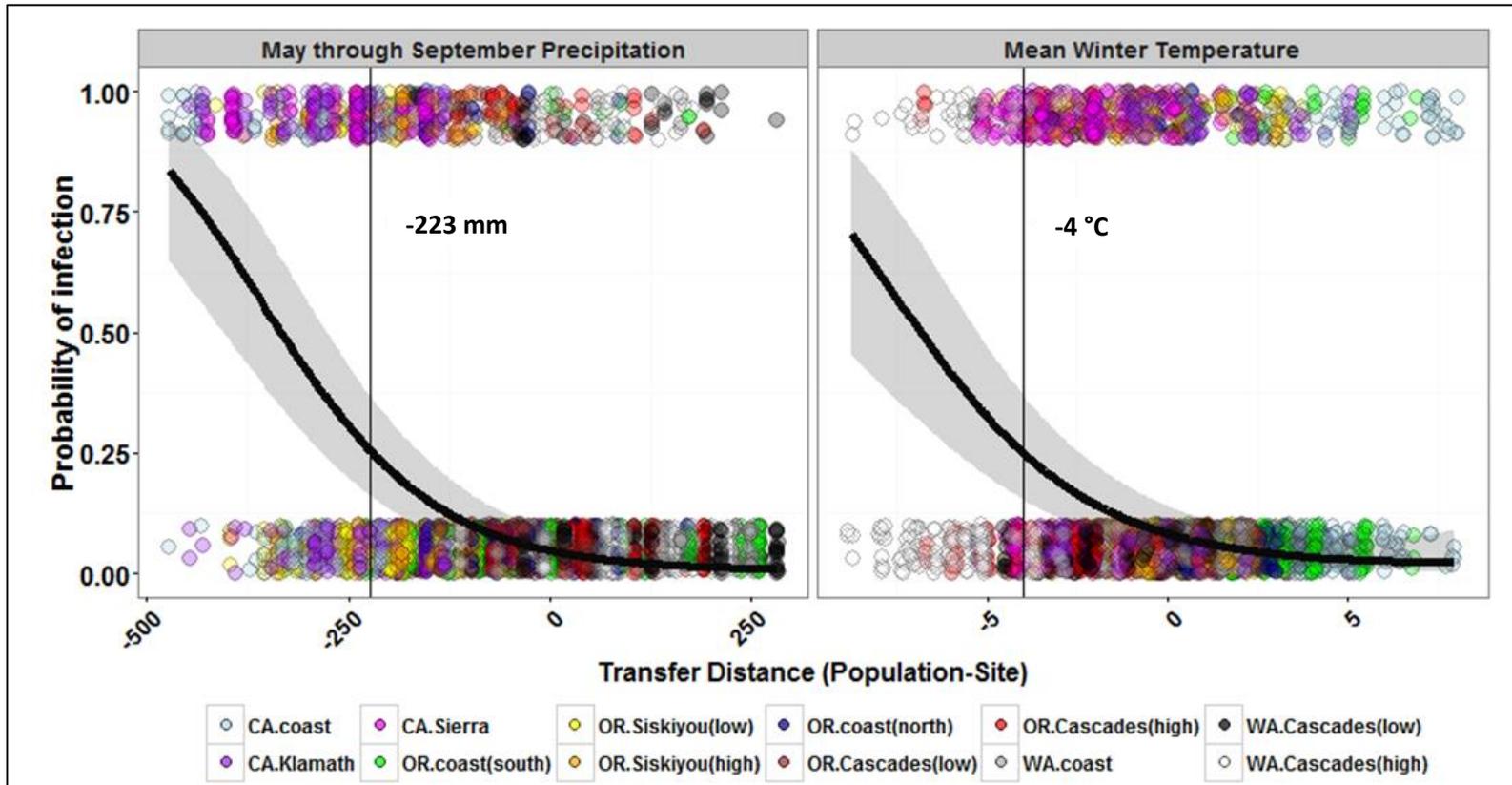


Figure 4.13 Estimated probabilities of low crown density (all disease present) versus climate transfer distances and 95% confidence intervals with the raw data. Each plot holds the other climate transfer distance to its mean. Data are from all trees in the Douglas-fir Seed Source Movement trials at the seven sites where *Rhabdocline* spp. and *P. gaeumannii* were identified as present. The vertical line indicates the threshold after which probabilities are estimated to be greater than 25%.

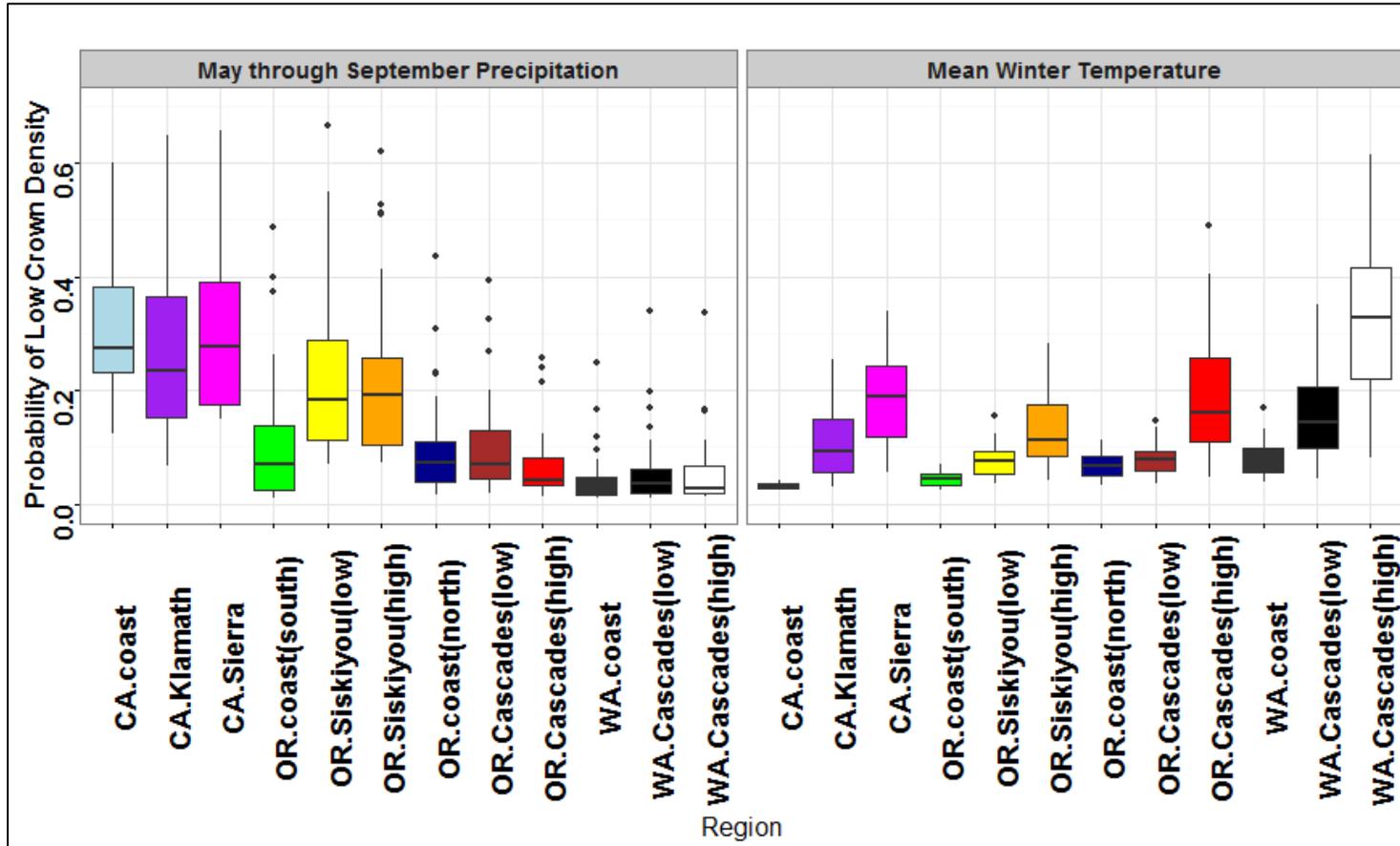


Figure 4.14 Estimated distribution of probabilities of low crown density (all disease present) in relation to each climate variable transfer distance holding the transfer distance to its mean. Probabilities are in relation to each region in the Douglas-fir Seed Source Movement Trials to all seven sites which displayed signs of *P. gaeumannii* and *Rhabdocline* spp.. The x axis displays the regions and is labeled by band of latitude (three regions per band) in order from north to south and from coast to high elevation within each band.

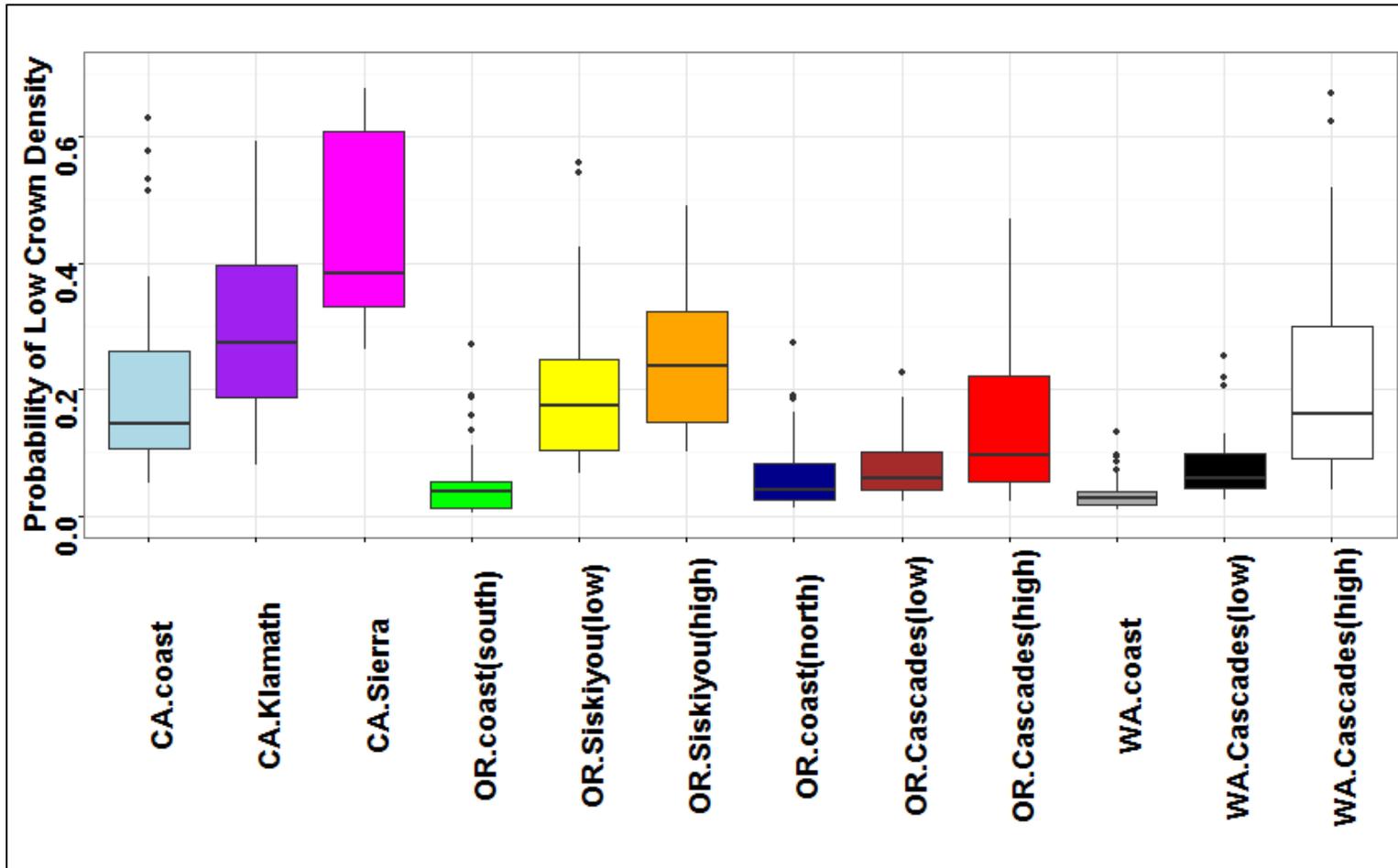


Figure 4.15 Distribution of the estimated probabilities of low crown density (all disease present) with all explanatory variables varying over their entire range in the dataset. Data are in relation to all 12 regions at all seven sites of the Douglas-fir Seed Source Movement Trials which displayed signs of *Rhabdocline* spp. and *P.gaeumannii*. The x axis is labeled by band of latitude in order from north to south and from coast to high elevation within each band. The x axis displays the 12 regions and is labeled by band of latitude (three regions per band) in order from north to south and from coast to high elevation within each band.

APPENDIX TABLES

Table 4.1 AIC and delta AIC scores for each model tested to estimate probabilities related to disease symptoms and infection by *P. gaeumannii* in the absence of trees susceptible to *Rhabdocline*. Scores in bold indicate the chosen model (SNC impacts and *P. gaeumannii* infection analysis). Data are from all twelve regions and all seven test sites in the Douglas-fir Seed Source Movement Trials which displayed signs of *P. gaeumannii* and *Rhabdocline* spp..

Model Fixed Effects	<i>P. gaeumannii</i> Inf.		Crown Density		Crown Color		Needle Retention	
	AICc	Delta AICc	AICc	Delta AICc	AICc	Delta AICc	AICc	Delta AICc
Random effects model	1740.4	4.4	3333.3	97.5	6447.9	58.9	6237.9	121.6
MSP	1742.1	6.1	3312.4	76.6	6436.5	47.5	6194.1	77.8
MSP + MSP ²	1743.6	7.6	3288.4	52.5	6436.4	47.5	6174.5	58.1
TD	1738.7	2.7	3329.6	93.8	6432.0	43.0	6231.5	115.2
TD + TD ²	1736.3	0.3	3293.2	57.3	6403.7	14.7	6204.3	87.9
MWT	1737.2	1.2	3333.0	97.1	6443.8	54.8	6239.8	123.4
MWT+MWT ²	1738.0	1.9	3276.3	40.4	6420.5	31.5	6179.7	63.4
TD + MSP	1740.4	4.4	3308.4	72.6	6419.8	30.8	6186.5	70.2
MWT + MSP	1739.1	3.1	3298.2	62.3	6417.8	28.9	6183.8	67.5
TD + MWT	1739.1	3.1	3331.5	95.7	6433.4	44.4	6226.5	110.1
TD + MWT + MSP	1741.1	5.1	3298.0	62.1	6418.2	29.2	6185.6	69.3
TD + TD ² + MWT	1736.0	0.0	3295.0	59.2	6405.7	16.7	6199.5	83.1
TD + TD ² + MSP	1736.1	0.1	3281.7	45.9	6401.5	12.5	6164.0	47.7
MWT + MWT ² + TD	1739.2	3.2	3262.6	26.8	6394.5	5.5	6148.3	32.0
MSP + MSP ² + TD	1741.6	5.6	3282.1	46.3	6401.4	12.4	6132.2	15.9
MSP + MSP ² + MWT	1740.1	4.1	3267.8	31.9	6418.0	29.0	6164.2	47.8
MSP + MSP ² + TD + TD ²	1737.7	1.7	3257.9	22.1	7069.0	680.1	8103.2	1986.9
MSP + MSP ² + MWT + MWT ²	1741.4	5.3	3237.8	2.0	6400.8	11.8	6142.6	26.2

MWT + MWT ² + TD + MSP	1740.9	4.9	3247.9	12.0	6391.7	2.7	6123.8	7.4
TD + TD ² + MWT + MSP	1737.5	1.4	3271.9	36.1	6401.3	12.3	6164.0	47.7
MSP + MSP ² + TD + MWT	1742.1	6.1	3266.9	31.0	6415.8	26.8	6161.5	45.2
MSP + MSP ² +MWT+ MWT ² + TD	1742.6	6.5	3238.9	3.1	6393.5	4.5	6117.6	1.2
MSP + MSP ² +TD + TD ² + MWT	1739.0	2.9	3244.1	8.3	6400.2	11.2	6141.2	24.8
TD + TD ² + MWT +MWT ² + MSP	1739.3	3.3	3247.5	11.6	6389.0	0.0	6123.8	7.4
TD + TD ² + MWT+ MWT ² + MSP + MSP ²	1740.9	4.9	3235.8	0.0	6390.6	1.6	6116.3	0.0

Table 4.2 AIC and delta AIC scores for each model tested to estimate probabilities related to disease symptoms and infection by *P. gaeumannii* in the absence of trees susceptible to *Rhabdocline*. Scores in bold indicate the chosen model (SNC impacts and *P. gaeumannii* infection analysis). Data are from all twelve regions and all seven test sites in the Douglas-fir Seed Source Movement Trials which displayed signs of *P. gaeumannii* and *Rhabdocline* spp..

Model Fixed Effects	Rhabdocline spp. Inf.		Crown Density		Crown Color		Needle Retention	
	AICc	Delta AICc	AICc	Delta AICc	AICc	Delta AICc	AICc	Delta AICc
Random effects model	3709.3	56.6	4772.4	71.1	7067.2	65.4	6237.9	121.6
MSP	3685.2	32.5	4744.0	42.7	7051.0	49.2	6194.1	77.8
MSP + MSP ²	3687.1	34.4	4736.3	35.0	7050.9	49.1	6174.5	58.1
TD	3691.1	38.3	4760.6	59.3	7048.3	46.4	6231.5	115.2
TD + TD ²	3691.1	38.3	4761.6	60.3	7019.1	17.2	6204.3	87.9
MWT	3709.9	57.1	4770.9	69.6	7063.5	61.6	6239.8	123.4
MWT+MWT ²	3709.9	57.2	4757.0	55.8	7044.0	42.2	6179.7	63.4
TD + MSP	3656.6	3.9	4729.1	27.8	7030.1	28.2	6186.5	70.2
MWT + MSP	3658.9	6.2	4719.6	18.3	7028.5	26.6	6183.8	67.5
TD + MWT	3689.0	36.2	4761.0	59.7	7049.0	47.2	6226.5	110.1
TD + MWT + MSP	3654.8	2.0	4721.5	20.3	7028.1	26.2	6185.6	69.3
TD + TD ² + MWT	3688.8	36.1	4762.2	60.9	7020.7	18.8	6199.5	83.1
TD + TD ² + MSP	3655.1	2.3	4730.9	29.6	7010.8	8.9	6164.0	47.7
MWT + MWT ² + TD	3690.8	38.0	4738.2	36.9	7015.7	13.8	6148.3	32.0
MSP + MSP ² + TD	3658.5	5.8	4718.7	17.4	7028.2	26.4	6132.2	15.9
MSP + MSP ² + MWT	3660.8	8.1	4706.1	4.8	7026.0	24.1	6164.2	47.8
MSP + MSP ² + TD + TD ²	3657.0	4.2	4720.6	19.3	7009.7	7.8	8103.2	1986.9
MSP + MSP ² + MWT + MWT ²	3658.6	5.8	4701.3	0.0	7016.4	14.5	6142.6	26.2
MWT + MWT ² + TD + MSP	3655.4	2.6	4708.8	7.5	7006.8	4.9	6123.8	7.4
TD + TD ² + MWT + MSP	3652.8	0.0	4723.4	22.1	7010.1	8.2	6164.0	47.7

MSP + MSP ² + TD + MWT	3656.6	3.8	4708.1	6.8	7025.5	23.6	6161.5	45.2
MSP + MSP ² +MWT+ MWT ² + TD	3656.8	4.0	4701.8	0.5	7007.9	6.0	6117.6	1.2
MSP + MSP ² +TD + TD ² + MWT	3654.6	1.8	4709.9	8.6	7008.4	6.5	6141.2	24.8
TD + TD ² + MWT +MWT ² + MSP	3654.6	1.8	4707.2	5.9	7001.9	0.0	6123.8	7.4
TD + TD ² + MWT+ MWT ² + MSP + MSP ²	3656.2	3.5	4701.8	0.5	7002.6	0.7	6116.3	0.0

Table 4.3 Percentage of trees in each of the 12 regions of the Douglas-fir Seed Source Movement Trials (SSMT) rated as having healthy crown color at each test site of the SSMT in the presence of all disease. Regions are ordered according to band of latitude (three regions per band) from south to north, from coast to high elevation within each band. Sites are ordered in the same manner.

Region	FLORAS	STONE NURSERY	EVANS CREEK	NORTONS	SLICE BUTTE	SODA320	JAMMER3	BUCKHORN2	DOORSTOP
CA.coast	59	39	70	65	27	27	55	53	16
CA.Klamath	15	35	80	34	20	12	13	21	18
CA.Sierra	3	28	95	12	23	1	4	9	16
OR.coast(south)	45	29	64	72	30	32	50	53	25
OR.Siskiyou(low)	42	29	70	49	21	42	34	29	32
OR.Siskiyou(high)	20	47	71	40	16	8	14	20	26
OR.coast(north)	26	31	64	76	35	38	63	61	28
OR.Cascades(low)	31	21	76	71	46	33	58	54	35
OR.Cascades(high)	33	20	72	51	23	30	51	24	28
WA.coast	30	19	76	91	39	41	56	61	30
WA.Cascades(low)	35	29	66	78	38	32	54	50	18
WA.Cascades(high)	25	19	73	40	23	33	24	31	31

Table 4.4 Variance components associated with the random effects model (no fixed effects) and the selected crown color model (all disease present). Data are from all test trees at the 7 test sites which displayed signs of *Rhabdocline* spp. and *P.gaeumannii* in the Douglas-fir Seed Source Movement Trials.

Source	Random effects model			Source	Selected model		
	Variance	SD	Proportion		Variance	SD	Proportion
Site:Population	0.08	0.28	17%	Site:Population	0.07	0.26	20%
Family	0.05	0.23	10%	Family	0.06	0.23	17%
Population	0.24	0.49	50%	Population	0.06	0.24	17%
Site	0.11	0.34	23%	Site	0.16	0.4	46%
Total	0.48		100%	Total	0.35		100%

Table 4.5 Furthest climate transfer distances and the transfer distance of zero (local) with associated probabilities of chlorotic crown color (all disease present) and 95% confidence intervals. Data are from all test trees at the seven test sites which displayed signs of *Rhabdocline* spp. and *P.gaeumannii* in the Douglas-fir Seed Source Movement Trials. Climate variables: MSP-May through September Precipitation, MWT. - mean winter temperature, and continentality.

Prediction Variable	Climate Variable (units)	Direction of Transfer	Distance	Probability (95% CI)
Chlorotic Crown Density	MSP (mm)	Low to High	472.83	68% (50% - 83%)
		Local	0.33	57% (44% - 69%)
		High to Low	282.99	49% (33% - 65%)
	MWT. (°C)	Low to High	-8.75	84% (66% - 95%)
		Local	0	58% (46% - 70%)
		High to Low	7.93	87% (62% - 97%)
	Continentality (°C)	Low to High	10	38% (14%-68%)
		Local	0	59% (47%-71%)
		High to Low	7.68	92% (78%-97%)

Table 4.6 Percentage of trees in each of the 12 regions of the Douglas-fir Seed Source Movement Trials (SSMT) rated as having healthy crown color at each test site of the SSMT (trees susceptible to *Rhabdocline* spp removed). Regions are ordered according to band of latitude (three regions per band) from south to north, from coast to high elevation within each band. Sites are ordered in the same manner.

Region	FLORAS	STONE NURSERY	EVANS CREEK	NORTONS	SLICE BUTTE	SODA320	JAMMER3	BUCKHORN2	DOORSTOP
CA.coast	61	52	75	71	27	29	57	61	16
CA.Klamath	21	35	80	44	29	12	18	38	31
CA.Sierra	0	28	95	24	50	13	12	33	71
OR.coast(south)	46	30	64	74	30	33	51	52	25
OR.Siskiyou(low)	49	30	70	52	23	47	37	33	40
OR.Siskiyou(high)	22	47	72	47	18	10	15	29	32
OR.coast(north)	27	31	64	77	35	38	64	63	28
OR.Cascades(low)	32	21	76	74	46	35	58	55	39
OR.Cascades(high)	34	20	73	56	25	34	54	29	29
WA.coast	30	19	76	91	40	42	58	61	32
WA.Cascades(low)	36	29	66	80	38	32	54	51	19
WA.Cascades(high)	25	19	73	43	24	36	28	32	34

Table 4.7 Variance components associated with the random effects model (no fixed effects) and the selected crown color model (trees susceptible to *Rhabdocline* spp removed). Data are from all test trees at the 7 test sites which displayed signs of *Rhabdocline* spp. and *P.gaeumannii* in the Douglas-fir Seed Source Movement Trials.

Random effects model				Selected model			
Source	Variance	SD	Model Variance Explained	Source	Variance	SD	Model Variance Explained
Population:Site	0.07	0.26	17%	Population:Site	0.06	0.24	19%
Family	0.06	0.23	14%	Family	0.05	0.24	16%
Population	0.13	0.37	35%	Population	0.04	0.18	13%
Site	0.13	0.36	34%	Site	0.16	0.4	52%
Total	0.388		100%	Total	0.31		100%

Table 4.8 Furthest climate transfer distances and the transfer distance of zero (local) with associated probabilities of chlorotic crown color (trees susceptible to *Rhabdocline* spp. removed) and 95% confidence intervals. Data are from all test trees at the seven test sites which displayed signs of *Rhabdocline* spp. and *P.gaeumannii* in the Douglas-fir Seed Source Movement Trials. Climate variables: MSP-May through September Precipitation, MWT. - mean winter temperature, and continentality.

Prediction Variable	Climate Variable (units)	Direction of Transfer	Distance	Probability (95% CI)
Chlorotic Crown Color	MSP (mm)	Low to High	472.83	68% (50% - 83%)
		Local	0.33	57% (44% - 69%)
		High to Low	282.99	49% (33% - 65%)
	MWT. (°C)	Low to High	-8.75	84% (66% - 95%)
		Local	0	58% (46% - 70%)
		High to Low	7.93	87% (62% - 97%)
	Continentality (°C)	Low to High	10	38% (14%-68%)
		Local	0	59% (47%-71%)
		High to Low	7.68	92% (78%-97%)

Needle Retention Analysis

Table 4.9 Average needle retention of trees in each regions at each test site of the Douglas-fir Seed Source Movement Trials (all disease presence). Regions are ordered according to band of latitude (three regions per band) from south to north, from coast to high elevation within each band. Sites are ordered in the same manner.

Region	FLORA S	STONE NURSERY	EVANS CREEK	NORTONS	SLICE BUTTE	SODA320	JAMMER3	BUCKHORN2	DOORSTOP
CA.coast	1.8	2.5	2.6	1.9	2.3	2.1	1.7	1.8	1.0
CA.Klamath	1.4	2.7	2.8	1.7	2.0	2.0	1.5	1.4	1.6
CA.Sierra	1.3	2.7	2.8	1.5	2.1	1.8	1.2	1.1	1.7
OR.coast(south)	1.9	2.7	2.8	2.2	2.3	2.6	2.0	2.0	2.1
OR.Siskiyou(low)	1.7	2.7	2.7	2.1	2.2	2.7	1.9	1.6	2.0
OR.Siskiyou(high)	1.7	2.8	2.8	2.0	2.0	2.4	1.5	1.5	1.9
OR.coast(north)	1.9	2.7	2.8	2.2	2.6	2.8	2.0	2.1	2.4
OR.Cascades(low)	1.9	2.7	2.9	2.3	2.6	2.8	2.0	2.1	2.4
OR.Cascades(high)	1.7	2.7	2.9	2.1	2.4	2.6	1.8	1.9	2.2
WA.coast	1.9	2.5	2.9	2.4	2.7	2.8	2.1	2.2	2.3
WA.Cascades(low)	1.8	2.7	2.9	2.2	2.7	2.8	1.9	2.1	2.3
WA.Cascades(high)	1.8	2.5	2.8	2.2	2.5	2.6	1.8	1.9	2.3

Table 4.10 Variance components associated with the random effects model (no fixed effects) and the selected needle retention model (all disease present). Data are from all test trees at the seven test sites which displayed signs of *Rhabdocline* spp. and *P. gaueumannii* in the Douglas-fir Seed Source Movement Trials

Source	Random effects model			Source	Selected model		
	Variance	SD	Proportion		Variance	SD	Proportion
Site:Population	0.03	0.16	7%	Site:Population	0.02	0.15	7%
Family	0.01	0.09	2%	Family	0.01	0.09	4%
Population	0.13	0.36	31%	Population	0.03	0.22	11%
Site	0.07	0.26	17%	Site	0.04	0.21	14%
Residual	0.18	0.43	43%	Residual	0.18	0.43	64%
Total	0.42		100%	Total	0.28		100

Table 4.11 Furthest climate transfer distances and the transfer distance of zero (local) with estimated needle retention (all disease present) and 95% confidence intervals. Data are from all test trees at the 7 test sites which displayed signs of *Rhabdocline* spp and *P.gaeumannii* in the Douglas-fir Seed Source Movement Trials. Climate variables: MSP-May through September Precipitation, MWT. - mean winter temperature, and continentality.

Prediction Variable	Climate Variable (units)	Direction of Transfer	Distance	Estimated Needle Retention (95% CI)
Needle Retention	MSP (mm)	Low to High	-472	1.13 (.85 - 1.41)
		Local	-0.33	2.18 (2.02-2.34)
		High to Low	282.99	2.5 (2.27-2.75)
	MWT. (°C)	Low to High	8.75	1.56 (1.22-1.91)
		Local	0.33	2.05 (1.90-2.2)
		High to Low	7.93	1.9 (1.5-2.29)
	Continentality (°C)	Low to High	10	2.46 (2.09 -2.83)
		Local	0	2.04(1.9-2.2)
		High to Low	7.68	1.72 (1.44-2.02)

Needle Retention SNC analysis

Table 4.12 Average needle retention of trees in each regions at each test site of the Douglas-fir Seed Source Movement Trials (trees susceptible to *Rhabdocline* spp. removed). Regions are ordered according to band of latitude (three regions per band) from south to north, from coast to high elevation within each band. Sites are ordered in the same manner.

Region	FLORA S	STONE NURSERY	EVANS CREEK	NORTONS	SLICE BUTTE	SODA320	JAMMER3	BUCKHORN2	DOORSTOP
CA.coast	1.8	2.5	2.6	1.9	2.3	2.1	1.7	1.8	1.0
CA.Klamath	1.4	2.7	2.8	1.7	2.0	2.0	1.5	1.4	1.6
CA.Sierra	1.3	2.7	2.8	1.5	2.1	1.8	1.2	1.1	1.7
OR.coast(south)	1.9	2.7	2.8	2.2	2.3	2.6	2.0	2.0	2.1
OR.Siskiyou(low)	1.7	2.7	2.7	2.1	2.2	2.7	1.9	1.6	2.0
OR.Siskiyou(high)	1.7	2.8	2.8	2.0	2.0	2.4	1.5	1.5	1.9
OR.coast(north)	1.9	2.7	2.8	2.2	2.6	2.8	2.0	2.1	2.4
OR.Cascades(low)	1.9	2.7	2.9	2.3	2.6	2.8	2.0	2.1	2.4
OR.Cascades(high)	1.7	2.7	2.9	2.1	2.4	2.6	1.8	1.9	2.2
WA.coast	1.9	2.5	2.9	2.4	2.7	2.8	2.1	2.2	2.3
WA.Cascades(low)	1.8	2.7	2.9	2.2	2.7	2.8	1.9	2.1	2.3
WA.Cascades(high)	1.8	2.5	2.8	2.2	2.5	2.6	1.8	1.9	2.3

Table 4.13 Variance components associated with the random effects model (no fixed effects) and the selected needle retention model (trees susceptible to *Rhabdocline* spp removed). Data are from all test trees at the 7 test sites which displayed signs of *Rhabdocline* spp. and *P.gaeumannii* in the Douglas-fir Seed Source Movement Trials

Source	Random effects model			Source	Selected model		
	Variance	SD	Model Variance Explained		Variance	SD	Model Variance Explained
Site:Population	0.02	0.13	6%	Site:Population	0.01	0.11	4%
Family	0.01	0.08	3%	Family	0.01	0.08	4%
Population	0.07	0.26	19%	Population	0.02	0.13	7%
Site	0.09	0.29	25%	Site	0.06	0.25	22%
Residual	0.17	0.41	47%	Residual	0.17	0.41	63%
Total	0.36		100%	Total	0.27		100%

Table 4.14 Furthest climate transfer distances and the transfer distance of zero (local) with estimated needle retention (trees susceptible to *Rhabdocline* spp. removed) and 95% confidence intervals. Data are from all test trees at the seven test sites which displayed signs of *Rhabdocline* spp and *P.gaeumannii* in the Douglas-fir Seed Source Movement Trials. Climate variables: MSP-May through September Precipitation, MWT. - mean winter temperature, and continentality.

Prediction Variable	Climate Variable (units)	Direction of Transfer	Distance	Probability of Low Crown Density (95% CI)
Needle Retention	MSP (mm)	Low to High	472	1.5 (1.24-1.8)
		local	-0.33	2.25 (2.07-2.43)
		High to Low	282	2.5 (2.23-2.69)
	MWT (°C)	Low to High	8.75	1.68 (1.39 - 1.98)
		local	0	2.18 (1.99 - 2.35)
		High to Low	7.93	1.61 (1.25 - 1.96)
	Continentality (°C)	Low to High	-10	2.55 (2.25 - 2.86)
		local	0	2.10 (1.99 - 2.34)
		High to Low	7.68	1.86 (1.59 - 2.12)

Crown Density Analysis

All disease

Table 4.15 Percentage of trees in each of the 12 regions in the Douglas-fir Seed Source Movement Trials (SSMT) with healthy crown density at each test site in the SSMT (all disease present). Regions are ordered according to band of latitude from south to north (three regions per band), from coast to high elevation within each band. Sites are ordered in the same manner.

Region	FLORAS	STONE NURSERY	EVANS CREEK	NORTONS	SLICE BUTTE	SODA 320	JAMMER 3	BUCK HORN 2	DOOR STOP	Region Ave.
CA.coast	81	83	99	85	94	67	80	89	33	79
CA.Klamath	41	98	100	95	84	51	51	73	52	72
CA.Sierra	42	100	99	77	15	8	21	28	20	46
OR.coast(south)	90	94	97	99	99	92	94	98	77	93
OR.Siskiyou(low)	82	100	99	96	92	90	85	93	70	90
OR.Siskiyou(high)	60	100	97	92	90	77	64	79	61	80
OR.coast(north)	79	99	98	99	100	94	93	96	90	94
OR.Cascades(low)	73	96	98	100	96	96	98	99	95	95
OR.Cascades(high)	53	97	100	99	96	85	86	91	79	87
WA.coast	70	93	99	100	99	97	96	98	86	93
WA.Cascades(low)	58	98	100	97	99	94	85	95	84	90
WA.Cascades(high)	65	90	95	96	95	78	74	90	84	85
Site Ave.	66	96	98	95	88	77	77	86	69	

Table 4.16 Variance components associated with the random effects model (no fixed effects) and the selected crown density model (all disease present). Data are from all test trees at the seven test sites which displayed signs of *Rhabdocline* spp. and *P.gaeumannii* in the Douglas-fir Seed Source Movement Trials.

Source	Random effects model			Source	Selected model		
	Variance	SD	Proportion Explained		Variance	SD	Proportion Explained
Site:Population	0.16	0.40	15%	Site:Population	0.14	0.38	30%
Family	0.07	0.27	7%	Family	0.07	0.27	15%
Population	0.52	0.72	49%	Population	0.13	0.36	28%
Site	0.32	0.56	29%	Site	0.13	0.36	28%
Total	1.07		100%	Total	0.47		100%

Table 4.17 Furthest climate transfer distances and the transfer distance of zero (local) with associated probabilities of low crown density (all disease present) and 95% confidence intervals. Data are from all test trees at the 7 test sites which displayed signs of *Rhabdocline* spp. and *P.gaeumannii* in the Douglas-fir Seed Source Movement Trials. Climate variables: MSP-May through September Precipitation, MWT. - mean winter temperature, and continentality.

Prediction Variable	Climate Variable (units)	Direction of Transfer	Distance	Probability (95% CI)
Crown Density	MSP (mm)	Low to High	472.83	84% (65%-94%)
		Local	0	5% (2%-9%)
		High to Low	282.99	0.9% (0.2%-4%)
	MWT (°C)	Low to High	8.75°	70% (46%-88%)
		Local	0	8% (4%-14%)
		High to Low	7.93°	2% (.4%-9%)

