Douglas-fir Seedlings in the Pacific Northwest: The Genetics of Drought Adaptation

by
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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Erda Celer, Author

I dedicate this thesis to my grandparents Fikri and Fikriye Demirer.

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AN ABSTRACT OF THE THESIS OF

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Douglas-fir (*Pseudotsuga menziesii*) is a widely distributed, ecologically important, and commercially valuable tree species in North America. However, climate change is expected to adversely impact Douglas-fir trees, and assisted migration may become necessary to lessen the effects of climate change. Because drought stress is one of the projected effects of climate change in the western U.S., it is increasingly important to include drought adaptation traits in breeding programs and in reforestation decisions.

This study assesses genetic variation in drought adaptation traits in Douglas-fir as part of the Drought Hardiness Study that was initiated by the Bureau of Land Management (BLM). Currently, it is being managed as collaboration among the BLM, Pacific Northwest Tree Improvement Research Cooperative (PNWTIRC), Northwest Tree Improvement Cooperative (NWTIC), Weyerhaeuser, Silver Butte Timber Company, and Washington Department of Natural Resources.

In this study, I addressed the following objectives: (1) obtain baseline measurements and climate data to help in the analysis and interpretation of future measurements in the

Drought Hardiness Study; (2) characterize the quantitative genetics of drought adaptation traits; and (3) determine whether drought adaptation traits are associated with the climatic origin of Douglas-fir seedlings.

To achieve these objectives, data were collected from about 10,000 Douglas-fir seedlings from 429 families from western Oregon and Washington that were planted at two sites (Sprague and Lost Creek) in southern Oregon. Measured variables, which I refer to as drought adaptation traits, included height, second flushing, spring bud flush, damage (foliage, stems, and leaders), and survival.

Each drought adaptation trait was subjected to an analysis of variance (ANOVA) to obtain variance components. Then, these components were used to estimate quantitative genetic parameters, including genetic variances, heritabilities, family-level breeding values (BLUPs), and genetic correlations. Climate variables (1961-1990 normals) from the female parent source locations were estimated using the ClimateNA software program. Simple correlations and lasso regressions were calculated between drought adaptation traits (family BLUPs) and climate variables.

Based on ClimateNA models and weather station data collected in the year of the study (2015-2016), the Sprague site is typically hotter and drier than Lost Creek. Results also indicate that the trees at the Sprague site grew less, were more damaged, and had greater mortality than the trees at Lost Creek. Therefore, differences in climate and seedling growth between the two sites indicate that this experiment should be effective for

screening families for drought adaptation. In later analyses of the Drought Hardiness Study, early height measurements will be helpful for the analysis and interpretation of later measurements. For instance, either height in the greenhouse or height in the field can be used as an “initial height” for comparison with later height measurements to remove the confounding effects of family height variation resulting from early seedling growth in the greenhouse.

In the first growing season, heritabilities and genetic variances differed widely among traits. I also found that estimated genetic gains were large for drought adaptation traits, primarily because of the large number of families tested (i.e., high selection differentials). For example, large potential genetic gains were observed for flushing (Flush), second flushing (SFlush), and height increment (Htinc). Although genetic correlations were found among drought adaptation traits, low correlations were found between growth in the greenhouse and other drought adaptation traits, flushing versus height growth, and flushing versus mortality. Additionally, genotype-by-environment interactions at the family level are reported.

Drought adaptation traits were significantly correlated with some parental climate variables. Large and significant correlations were found between growth in the greenhouse and parent source climates. However, I did not find any correlations with growth in the field. I found moderate correlations for spring bud flush, and low correlations between other drought adaptation traits and climate. For instance, I found

early bud flush was associated with warmer and drier climates, suggesting that early bud flush is a drought avoidance strategy.

Selection of climate variables associated with drought adaptation traits was investigated using genecological-modeling techniques. I found that the end of the frost-free period (eFFP) was the most relevant variable, based on the data from the Sprague site. However, eFFP only explained a low amount of variation in second flushing (SFlush). The same procedure identified growing degree-days below 18°C (DD_18) as the most relevant variable based on the Lost Creek data.

My results help increase the understanding about the importance of climatic-driven genetic differences for drought adaptation traits in Douglas-fir. The results of this study and later analyses of the Drought Hardiness Study will provide useful information for understanding drought, enhancing breeding programs, and potentially adjusting forest management to climate change impacts.

DOUGLAS-FIR SEEDLINGS IN THE PACIFIC NORTHWEST:
THE GENETICS OF DROUGHT ADAPTATION

1 Introduction

1.1 Douglas-fir (*Pseudotsuga menziesii*)

Douglas-fir (*Pseudotsuga menziesii*) is ecologically and commercially one of the most significant conifer tree species in North America. The species ranges over 4500 km from British Columbia (BC) to Mexico, and covers 20 million ha (Hermann and Lavender 1990; Hermann and Lavender 1999) (Figure 1.1). In the coastal range Douglas-fir can be found up to 750 m in elevation in the north and 1700 m in the south of North America, as well as 3300 m east of the Cascades and in the Sierra Nevada (Kleinschmit and Bastien 1992). The species is well established and highly productive, being one of the leading timber species of North America. Douglas-fir benefits from silvicultural practices, such as thinning, that can increase wood productivity. In fact, coastal Douglas-fir mean annual increment (MAI) in managed areas can be above the 14 m^3/ha observed in unmanaged areas (Hermann and Lavender 1999). Recent studies have revealed that a total of 26.6 billion board feet (77.9 million m^3) of lumber was produced in 2011 in the U.S. (Howard and Westby 2013). About 11.9 billion board feet (43.7%) comes from the West. For instance, in 2011, larch and Douglas-fir lumber production in the inland regions of Washington, Oregon, California, plus the inland west from Nevada to South Dakota was over one billion board feet, and in the coast regions of western Washington and western

Oregon was over four billion board feet (Zhou and Warren 2012). From 2010 to 2011, the exports of Douglas-fir logs increased about 63% (Howard and Westby 2013), and during the second quarter of 2011, Douglas-fir exports accounted for 40.5% of softwood lumber (U.S. Department of Agriculture 2011).

Like other conifers, Douglas-fir has a very large genome (18.7 GB) (see http://dendrome.ucdavis.edu/NealeLab/crsp/overview.php). Douglas-fir differs genetically from other Pinaceae species in the number of chromosomes. Specifically, Douglas-fir has 2N=26 chromosomes instead of the 2N=24 chromosomes for the rest of the Pinaceae family. Douglas-fir is a monoecious species, and flowering and the production of seeds rarely starts before age seven. After that, seed production varies from year to year, with good seed production every two to eleven years (U.S. Department of Agriculture 2002). For growth characteristics, there is a clear association between the amount of inbreeding depression (i.e., reduced fitness or vigor due to mating between close relatives) and the magnitude of the inbreeding coefficient. For example, researchers have found that an estimate of inbreeding depression in height of 1-1.5% is associated with an inbreeding coefficient of 0.025 (reviewed in Howe et al. 2006; U.S. Department of Agriculture 2002).

Douglas-fir trees are evolutionarily adapted to their natural environments (Rehfeldt, 1994; St.Clair et al. 2005). That is, natural selection to the local environment is typically

reflected in Douglas-fir populations. Most reciprocal transplant studies, which compare the performance of local and nonlocal genotypes to determine how genotypes are adapted to climate in common gardens, have documented that native populations are typically well adapted to their native environments (St.Clair et al. 2013). Here, local adaptation refers to the process followed by local populations in order to increase their fitness (i.e., ability to survive and reproduce) in their native habitats (Kawecki and Ebert 2004; Gibson et al. 2016). For instance, Kawecki and Ebert (2004) found that populations that are grown in their natural environments are better able to withstand extreme conditions and grow better than when they are grown under different environmental conditions. Douglas-fir has a high degree of genetic variation in its natural habitat, which enables evolution and adaptation to climate. However, physiology and development change as Douglas-fir trees mature. For example, young Douglas-fir trees set bud later, are likely to have a second flush, and are typically less tolerant to low temperatures in the fall or spring (reviewed in Howe et al. 2006).

Looking at the environments where Douglas-fir naturally grows, the importance of drought and cold hardiness is evident (Howe et al. 2006). Cold temperatures and low soil moisture are the major constraining factors in the northern and southern areas of the species range, respectively (Hermann and Lavender 1990). Some populations from warm and dry environments are more resistant to drought. This suggests that some southerly and low elevation populations have greater drought resistance than previously believed. For populations growing at lower elevations, summer aridity is considered to be the most

important driver of natural selection (Bansal et al. 2015). Some Douglas-fir studies have shown correlations between adaptive traits and the climate at the seed source locations, indicating climate-related natural selection. For Douglas-fir, drought hardiness and productivity are associated with the location of the population from which the seed was obtained. Differences in productivity and drought tolerance are observed among coastal Douglas-fir populations (Bansal e al. 2015; Eilmann et al. 2013; St.Clair and Howe 2007). The relationship between drought hardiness and cold hardiness also appears to depend on the environment in which natural selection for these traits occurred. Families that originate from areas with cold winters at relatively high elevations exhibit high tolerance to drought and cold. Conversely, families from areas with dry summers have higher tolerance to drought, but exhibit lower tolerance to cold (Bansal et al. 2015; 2016).

1.2 Genecological approach

The geographic configuration of genetically diverse populations is associated with temperature, water availability, and other environmental variables (Howe et al. 2006). Genecological methods have been used to understand the evolution of adaptive characteristics in Douglas-fir (St.Clair et al. 2005). Here, we use genecology to refer to the study of genetic differences in relation to local environments (St.Clair et al. 2013). In this context, genetic variation can be determined in terms of geographic coordinates (e.g., latitude, longitude, elevation) that are associated with environmental variables. However,

recently developed climate interpolation models can predict climate variables, making them valuable for understanding the genetics of adaptation (Howe et al. 2006).

Genecological studies can be used to assess genetic variation in relation to local environments (Aitken 2004, St.Clair and Howe 2007). As the climate changes, genecological prediction can be used based on possible future climate conditions. That is, to predict the effects of climate change on seedling performance (St.Clair et al. 2013). Thus, we can map geographically based genetic variation based on current and projected future climates. This approach can be used to predict whether the existing populations of Douglas-fir will adapt to upcoming climates (Rehfeldt et al. 1999; Wang et al. 2006; Howe et al. 2006; Thomson et al. 2009; Leites et al. 2012).

Genecological models can also be used to predict the risk of genetic maladaptation so that the seeds can be used safely for reforestation (Adams and Campbell 1981; Aitken 2004; St. Clair, and Howe 2007; Gould et al. 2010). The main benefit of genecological studies is that they provide opportunity to efficiently sample and test a large number of populations (Kilkenny 2015). For example, genecological studies can be used to outline seed transfer areas and select appropriate seed sources for reforestation (Campbell 1986, Beaulieu et al. 2004). Thus, genecological studies can be used to enhance the successful regeneration of Douglas-fir (Adams and Campbell 1981; Aitken 2004; St. Clair and Howe 2007; Gould et al. 2012).

Genecological studies can also be used to determine appropriate seed transfer distances to determine how far populations can be moved to new planting environments (Gibson et al. 2016). These studies allow the assessment of a large number of populations from extensive seed source locations through the establishment of a few common garden tests. This facilitates the mapping of the adaptive traits across the landscape. For instance, genecological models developed from field data are useful to determine the adaptability of Douglas-fir trees to future climate conditions, measure genetic variation, and map geographic genetic variability (Howe et al. 2006). These maps can be used to develop recommendations for deploying genotypes and for practicing assisted migration (St.Clair et al. 2013).

Reciprocal transplant tests can also be used to infer how forests will respond to future climates. However, these studies have important limitations. For instance, even though reciprocal transplant studies are effective for testing adaptability to native habitats (Kawecki and Ebert 2004), testing several sources across many locations may be expensive and unfeasible (O'Neill et al. 2008). Consequently, they are typically established on a limited number of sites (which limits inferences). Furthermore, they do not clearly identify which traits are critical for adaptation. Because the trees are planted, they cannot assess the processes of seed production, germination, and seedling establishment. To find relationships between genetic traits and source environments, field trials and nursery trials have been used in common garden tests and reciprocal studies.

However, few of the trials were established broadly enough to demonstrate robust relationships (St.Clair et al. 2013).

In Douglas-fir, genecology studies have been centered on adaptive traits that increase the fitness of the tree in a given environment. These adaptive traits include survival, height growth, bud phenology (e.g., timing of bud set or bud flush), fall and spring frost hardiness, drought hardiness, and the frequency of second flushing.

To advance understanding of the environmental drivers of natural selection, relationships between trait variation and environmental variables can be assessed. For example, temperature and the availability of water are both important drivers of natural selection, resulting in genetic adaptation of trees to their environment (Howe et al. 2003). In their natural environments, early growth of Douglas-fir is important to avoid being overtopped or being browsed by animals (Hermann and Lavender 1990). Juvenile Douglas-fir trees in natural stands grow poorly in shady conditions. By the sapling stage, sufficient height is needed to survive and produce seed in their environment (Howe et al. 2006).

Drought hardiness and cold hardiness are among the most important adaptive traits. Although the timing of fall bud set and second flushing have relatively small genetic correlations with drought and cold hardiness, the timing of spring bud flush is highly correlated with spring frost hardiness (Howe et al. 2003; O'Neill et al. 2000). Vegetative bud phenology is associated with annual height growth and tolerance to frosts and

drought. For example, the timing of bud set is positively related to annual height growth, although it may also increase the chances of fall frost damage (e.g., a compromise between frost hardiness and height growth) (Howe et al. 2006). Early bud set and growth cessation (Rohde et al. 2010) limit annual shoot elongation and increase drought and cold hardiness. For instance, Campbell and Sorensen (1973) reported that delays in bud set could raise chances for the trees to be damaged by cold by up to 25%. On the other hand, warmer temperatures encourage cold de-acclimation and bud flush in the spring (Harrington et al. 2010). Second flushing promotes the resumption of shoot growth if water is available in the same growing period, even though they have already set bud (Howe et al. 2006).

1.3 Research questions

The main focus of my study is on drought adaptation traits. Specifically, I consider the following traits: survival, height growth, resistance to sunscald, resistance to foliage damage, resistance to leader damage, timing of bud flush, and frequency of second flushing. The most important questions of this study are:

1. Are Douglas-fir drought adaptation traits heritable?
2. Is there an association between drought adaptation traits and seedling characteristics at the time of planting and subsequent growth and survival?
3. Is early bud flush associated with other drought adaptation traits?

4. Are drought adaptation traits associated with the climatic origin of the Douglas-fir families?

In relation to these research questions, the hypotheses about the genetics of drought adaptation traits in young Douglas-fir seedlings were examined: (1) Drought adaptation traits of Douglas-fir seedlings is partly determined by genetics; (2) Natural selection for drought adaptation traits has been stronger in areas that are warmer and drier; (3) Because of high leaf areas, tall Douglas-fir seedlings are more prone to damage from drought; and (4) Early bud flush in Douglas-fir is a genetically controlled drought avoidance strategy.

1.4 Goals and objectives

1.4.1 Goals

The overarching goal of this study was to understand the effects of drought on the growth and survival of Douglas-fir seedlings. The long term goal of this study is to increase the understanding of the genetic capacity of Douglas-fir trees to tolerate drought stress, obtain useful information to enhance approaches for genetically improving drought adaptation traits, and enhance approaches for appropriately deploying genotypes from breeding programs. Adding to our understanding of the potential effects of climate change will help provide information for practicing effective assisted migration.

1.4.2 Objectives

In this work, I used an ongoing study that seeks to understand the genetics of drought adaptation. This study will provide information on how forest genetic resources might be better managed to deal with the potential impacts of climate change. The objectives of this study are to: (1) Obtain baseline measurements and climate data to help in the analysis and interpretation of future measurements in the Drought Hardiness Study; (2) Characterize the quantitative genetics of drought adaptation traits; and (3) Determine whether drought adaptation traits are associated with the climatic origin of Douglas-fir seedlings.

1.5 Climate change

1.5.1 Climate change in Western North America

According to the latest Assessment Report 5 (AR5) of the Intergovernmental Panel on Climate Change (IPCC 2013) and the 2014 U.S. National Climate Assessment (NCA), western North America is expected to experience an increase in atmospheric carbon dioxide, higher temperatures, and changes in both precipitation and moisture regimes during this century. The National Climate Assessment (NCA) shows that global warming is unequivocal and is already occurring. Changes in precipitation patterns with extreme weather conditions are happening simultaneously, and there is a high probability that

temperatures will continue to increase. Winter warming is also highly likely to increase in the northern latitudes, and summer warming will increase in intensity in the southwestern U.S. (Christensen et al. 2007). Since 1895 (when mean annual temperature records in the U.S. are available), temperatures have risen an average of 1.3 to 1.9 °F, and the warmest temperatures on record have been observed in the 21st century (U.S. Global Change Research Program 2014). In fact, long-term weather stations in the Northwestern U.S. indicate that temperatures have increased since the beginning of the 21st century (Abatzoglou et al. 2014). A number of climate change profiles predict that temperatures in the Pacific Northwest may increase an average of 3.5 °C over the period from 2070 to 2099 (St.Clair and Howe 2007). As warming temperatures continue to climb all over the world, it is highly possible that there will be negative impacts on the frequency, duration, and intensity of disturbances such as forest fires, insect epidemics, and drought (Luce and Holden 2009; St.Clair and Howe 2007). For example, in western forests, even a slight increase in temperatures (less than 1 °C) is likely to affect the extent and occurrence of forest disturbances (Hamann and Wang 2006).

Climate change should be understood as a multivariate process, in which several components are changing and interacting simultaneously. In this context, drought has been an important threat affecting forests in the U.S. The western U.S. has recently faced a period of extensive drought (Melillo et al. 2014; Van Mantgem and Stephenson 2007). Below average precipitation and high temperatures have led to the most extreme drought in the last 1200 years in California, USA (Bansal et al. 2016). In contrast to the

northwestern U.S., which is experiencing an increase in precipitation, the southern U.S. is expected to observe a decline in precipitation due to increasing summer temperatures (Mote and Salathé 2010). Temperature and moisture regimes are the natural selective pressures that affect genetic differentiation in adaptive traits. For example, especially in southern areas where climatic conditions are drier and hotter, moisture regimes are the major climatic drivers of genetic variation in adaptive traits (Howe et al. 2006).

1.5.2 Effects of climate change on Douglas-fir

Climate change is likely to adversely impact the growth and productivity of Douglas-fir forests in the American west (Dale et al. 2000). Specifically, trees may become maladapted to new climatic conditions (Howe et. al. 2006; Aitken and Whitlock, 2013; Montwe et al. 2016). For example, Eilmann et al. (2013) concluded that the northern Douglas-fir provenances typically show a higher productivity in northern regions than those from the south. However, tolerance to drought increases in provenances from the south. This explains why it is difficult to identify provenances that combine both high productivity and drought tolerance. Because of climate change, local populations may not be genetically optimized; human intervention may be required to move Douglas-fir populations from low to high elevations. Taking seeds outside geographic limits leads to maladaptation of the populations (e.g., cold injury, drought, insects, disease, and mortality) because seeds from different geographic origins grow differently in different environments. To avoid maladaptation new seed transfer guidelines are needed.

Maladaptation may not only adversely affect populations in the south and at low elevations, but may also negatively impact the distribution of wide-ranging species because of the climate adaptation of local subpopulations (Aitken and Whitlock 2013; Montwe et al. 2016). Species may be negatively impacted by extreme drought conditions in western forests, specifically in warm and xeric conditions at low altitudes. Therefore, increasing intensity and frequency of drought may cause the loss of some species (Bell et al. 2014; Kelly and Goulden 2008).

1.5.3 Effects of drought on forest trees

Drought is a shortage of precipitation over a period of time, which can have a lasting and adverse effect on forest structure and function. Plant populations can cope with droughty conditions by using dormancy or by physiological mechanisms that promote acclimation to the dry conditions (Poorter and Markesteijn 2008). In regions where drought is uncommon, and species have not developed adaptive mechanisms, substantial management actions may be necessary to create forests better adapted to future drought. As drought patterns change, the ability to accurately estimate the impact of drought on forests is crucial for taking the necessary actions that will increase resistance, resilience, and adaptation. Because thinned stands require less water to promote growth, managers conduct silvicultural activities such as thinning or density management, and can plant quality seedlings with high survivability under drought conditions (Vose et al. 2016).

Populations exposed to cold winters and dry summers may be particularly drought hardy, and may be valuable sources of seed for regenerating forests in the upcoming decades (Bansal et al. 2015). Increasing our understanding of how trees respond to drought-prone sites (i.e., sites with a probability of drought > 20%) would have a positive impact on managing seedling stocks for drought conditions. It is, therefore, vital to achieve a better understanding of how species and genotypes will react in different areas to make better decisions on how to manage forests to improve drought hardiness in future climates (Erickson et al. 2012).

Temperature and availability of water are fundamental environmental constraints limiting growth and survival. They also act as environmental signals to induce necessary physiological adjustments in trees (Howe et al. 2006). Currently, reduced tree productivity and survival are known as the greatest threats in northern areas (Allen et al. 2010; Montwe et al. 2016) due to variations in water supply by decreasing precipitation and warming temperatures (Cayan et al. 2001; Stewart et al. 2005). Increased temperatures often result in a faster depletion of soil water (Kerr et al. 2015). Low levels of soil moisture adversely affect seedling survival and growth by reducing leaf water potential and gas exchange (Poorter and Markesteijn 2008). High temperatures contribute to high evaporative demand, and this combines with low soil moisture to give rise to drought stress. Therefore, trees are vulnerable to summer droughts, which could damage and kill them (Howe et al. 2006; Allen et al. 2010). Spring and fall frosts adversely affect seedlings, causing damage and even death (Poorter and Markesteijn 2008). For example,

trees that flush early due to warming temperatures in the spring, or that grow particularly late into the fall are more likely to suffer damage from drought or frost (Campbell and Sorensen 1973; Howe et al. 2003; Howe et al. 2006). The frequency, severity, and intensity, of both cold and drought stressors may be altered under a changed climate (e.g., changing precipitation and temperature regime) (Bansal et al. 2016; Allen et al. 2015). Tree productivity is also closely related to soil moisture conditions. Kimmins (2004) found that drought-induced damage negatively impacts the juvenile seedling's ability to reach deeper water, which could cause them to have stunted growth and disease. Seedlings are typically more vulnerable to abiotic stresses than mature trees. Even when sufficient moisture is available, climate change-associated mortality rates are increasing more in younger forests than older ones (Luo and Chen 2013).

Martinez-Maier et al. (2008) state that a decrease in transpiration leads to stomatal closure. This is typically followed by reduced growth, and this growth loss is also related to a reduction in wood density. Increasing the biomass and length of roots improves water uptake in plants, helping them to survive under extreme dry conditions. At the same time, reducing water loss from leaves and stomata can also allow plants to withstand dry periods (Poorter and Markesteijn 2008). Drought has increased in the last two decades through combined warming and decreased precipitation, and this may reduce tree growth and cause mortality (Bansal et al. 2016, Allen et al. 2015, Millar and Stephenson 2015, Allen et al. 2010, Williams and Dumroese 2013). At the same time, the most relevant physiological process being affected by drought is photosynthesis. Soil

water stress may result in reduced photosynthesis. Low soil moisture restricts the mass movement of key nutrients, reduces litter decomposition and mineralization, and under extreme conditions, plants can lose biomass (Kimmins 2004). For example, Lomas (1999) found that drought stress in coastal Douglas-fir reduces photosynthesis and transpiration, and causes shoot damage, limiting the growth potential. Likewise, exposure of Douglas-fir seedlings to drought may reduce seedling height and diameter growth (Timmis and Tanaka 1976). Seasonal shifts in precipitation and temperature regimes affect the timing and intensity of drought. The increasing occurrence and intensity of drought may dramatically affect natural and artificial regeneration of seedlings. It may also increase the vulnerability of seedlings to environmental stress, animal grazing, disease, and other factors (Hobbs et al.1980; Kerr et al. 2015). With increasing intensity and extent of drought, increasing evaporative demand and low soil moisture may cause xylem conduits to embolize (Dalla-Salda et al. 2009; Domec and Gartner 2002; Martinez-Maier et al. 2008). Ultimately, continued intense and frequent drought events can cause mortality of roots and twigs (Martinez-Maier et al. 2008).

To enhance approaches for reforestation by appropriately deploying genotypes, provenances, or clones (Rosner et al. 2008), it is important to understand the concept of hydraulic sensitivity (McDowell et al. 2008; Rosner et al. 2014). Hydraulic balances may change due to deficits of water in the soil and high evaporation demands. Lomas (1999) found that the proportion of cavitation is directly linked to physiological mechanisms which influence drought-survival ability. Cavitation is defined as the breaking of the

water column that may limit water flow in trees (Dalda-Salda et al. 2013; Sperry et al. 1998; Hacke et al. 2001). Water column breaks may interrupt the flow of water to leaves and roots (Vilagrosa et al. 2012). Air bubbles in tracheids or vessels may cause embolisms (Domec et al. 2002). According to Rosner et al. (2014), vulnerability to cavitation would determine the hydraulic performance of sapwood under high temperatures and water deficit, and will enhance the risk of drought stress. Hydraulic vulnerability curves express the percent loss of conductivity. According to Dalda-Salda et al. (2013), cavitation begins in the xylem cells and propagates through the inter-tracheid pits. Dalda-Salda et al. (2013) describe the cavitation process in Douglas-fir tree-rings as a two-part event: (1) at the beginning of a water shortage, cavitation starts and quickly spreads in the latewood; (2) when the water deficit continues and rises, a second cavitation commences and propagates in the earlywood, and ultimately spreads to the transition wood. The transition wood is the last conductive portion of the growth ring. There are two different stages of development in a tree ring. Each ring has earlywood, produced towards the beginning of the growing season. Earlywood cells have thin walls and wide-diameter lumens. Near the end of the growing period, tracheids with thicker walls and small-diameter lumens are produced. These are called latewood cells (Martinez-Maier et al. 2008). Latewood is generally produced when the soil water content is exhausted, photoperiod decreases, and carbon dioxide demand increases (Dalda-Salda et al. 2013). In this context, the authors were able to establish an association between resistance to cavitation and wood density. According to Domec et al. (2002), the transition from earlywood to latewood is associated with changes in soil moisture.

Earlywood is more likely to use stored water compared to latewood in dry environments (< -2.0 MPa). In moderately wet environments (> -2.0 MPa), latewood is more susceptible to cavitation compared to earlywood, and has a greater water storage capacity because the cavitation begins early, reaching more than 80% of the nonconductive area. Therefore, embolism seems to start in the latewood and eventually affects earlywood. In dry conditions (< -2.0 MPa), to improve resistance to embolism, latewood may have a lower limit of specific conductivity (ks) (Domec et al. 2002).

Rosner et al. (2014) studied the "smart sampling" approach, which means that the data collected for assessing conductivity, susceptibility to cavitation, and density were obtained from the same ring, increasing the probability of highlighting significant relationships and differences. They studied drought stress due to heat waves during the summer of 2003 and during July 2006 in Europe. They investigated the relationship between vulnerability to cavitation and wood density, and compared healthy trees and declining trees. Trees decline because of a combination of stress factors that weaken the tree. This occurred in southern Norway during 1990 to 2010. They found that annual diameter increment was beginning to decrease due to drought and heat waves during the summer of 2003, and during July 2006 in Europe. Vigorous trees had a rising trend in annual wood increment. In addition, declining trees tended to have more cavitation following drought stress, which is the major factor that distinguishes declining trees from vigorous trees. In 2007, after extreme heat waves, the declining trees produced narrow annual rings. Martinez-Maier et al. (2008) showed that earlywood had a higher density,

whereas latewood had a lower density. This explains a reduction in within-ring density in the drought year of 2003 in Europe. For example, Martinez-Maier et al. (2008) noted that changes in wood density may adversely affect the hydraulic system of trees, impact their fitness, and reduce growth in a changing climate. Rosner et al. (2014) also suggested that wood density was strongly related to both growth and vulnerability to cavitation.

1.5.4 Morphological adaptations related to drought hardiness

Drought hardiness is defined as the ability to survive and grow well on droughty sites. Drought hardiness is a combination of several traits that can be classified as either drought avoidance traits or drought tolerance traits (Kramer and Kozlowski 1979). Drought avoidance traits often involve timing growth to avoid active growth during periods of drought. Other drought avoidance strategies involve greater allocation of biomass to roots to increase access to soil water, increased stomatal resistance, thicker cuticle on leaves, changes in leaf area (e.g., needle shaped leaves), and changes in leaf orientation (e.g., leaves that can roll or fold). These traits help trees avoid transpiration or limit water losses from leaves in hotter and drier conditions. Drought tolerance is related to the ability to survive very low (e.g., extremely negative) plant water potentials. These include traits that reduce vulnerability to cavitation (e.g., breaking water columns in tracheids or vessels) (Jones and Corlett 1992; Touchette et al. 2007).

There is a compromise between obtaining CO_2 for photosynthesis and preventing water loss (Vilagrosa et al. 2012). Facing continued risk of water scarcity in the soil, plants may decrease the number of leaves on each plant and their leaf size (Anjum et al. 2011). Hadley and Smith (1990) found that lower water loss from high cuticular wax in conifers is directly linked to drought hardiness. An extreme drought condition would alter the structure of the wood rings. This might cause alterations in the hydraulic design of seedlings, with resulting impacts on the water distribution to the leaves necessary for tree growth and survival (Martinez-Meier et al. 2008; Dalda-Salda et al. 2013). Wood produced during spring and later in the growing season may have various hydraulic architectures (Domec and Gartner, 2001; Martinez-Maier et al. 2008). In Douglas-fir, more than 80% of the water flow occurs in the earlywood of the sapwood (Domec and Gartner 2002; Martinez-Maier et al. 2008). In annual rings produced two years after extreme drought in Europe, wood density was significantly higher in vigorous trees in the middle part of earlywood, and in the main part of the latewood (Rosner et al. 2014). One year after the drought in Europe, however, wood density was remarkably higher in declining trees in the first 15% of ring width, and was lower in the latewood. This can be explained as a reaction to severe drought stress. For example, Martinez-Maier et al. (2008) found that denser cell walls and reduced diameter lumens (which correspond to higher mean ring density wood) might be associated with drought tolerance. Therefore, the authors suggested that the mean ring density might be an indicator of increased tolerance to drought.

Likewise, Douglas-fir trees that survived an extreme heat wave had significantly higher mean ring densities in annual rings, but also higher latewood densities in annual rings produced prior to the drought (Martinez-Meier et al. 2008; Rosner et al. 2014). For example, Domec et al. (2002) concluded that Douglas-fir trees with higher wood density and increased amounts of latewood are likely to prevail under strong drought conditions. Dalda-Salda et al. (2009) claimed that trees with thick cell walls and smaller diameter lumens might be better able to maintain their hydraulic architecture. In addition, these features would also impact water transport and wall collapse (Dalda-Salda et al. 2009). Domec et al. (2002) concluded that earlywood and latewood may maintain water flow under drought stress. In addition, earlywood water transport is more effective and less susceptible to xylem embolism than is latewood water transport. According to St.Clair et al. (2005), the ratio between the second-year diameter and height may be associated with summer drought tolerance. They also suggested that seedlings with greater diameters would have better drought tolerance. Some researchers state that the latewood/earlywood ratio would be an adaptive hydraulic character in conifer trees. Others emphasize that the water storage capacity of latewood could allow it to conduct water after earlywood becomes non-conductive (Martinez-Maier et al. 2008). According to Dalda-Salda et al. (2009) there is an association between wood density and wood hydraulic properties, which indicates that more resistance to cavitation is linked to the greatest mean and minimum ring density. Dalda-Salda et al. (2013) suggested that transition wood must be well understood when studying adaptation to drought because the transition wood

(between the earlywood and latewood) might have significance in the between-tree variation of cavitation resistance.

1.5.5 Physiological adaptations to drought hardiness

Water availability is critical for survival of all living organisms. Trees require water to photosynthesize, support biochemical processes, and transport nutrients, minerals, organic compounds, and hormones (Pfautsch et al. 2016). Kerr et al. (2015) point out that the availability of water is an important issue in seedling survival and establishment.

Lomas (1999) states that drought hardiness is related to the xylem conductivity in droughty environments. Favorable measures of drought hardiness or sensitivity to drought are xylem cavitation (e.g., caused by tension on the water column), which is connected to several physiological mechanisms. Populations that have acclimated to droughty conditions are more resistant to cavitation than those that have acclimated to mesic conditions (Lomas 1999). Since high temperature and low precipitation trigger water deficits in plants, plants respond to this situation by closing their stomata (Kimmins 2004; Vose et al. 2016). For example, compared to other conifers, Douglas-fir has more effective stomatal control mechanisms, which may help save water in droughty environments. Because of this, Douglas-fir trees may have the ability to maintain productivity under extreme drought (Eilmann et al. 2013). Plants can regulate water transport by closing their stomata and decreasing stomatal conductance during high vapor

pressure deficits (VPD) (Vose et al. 2016). Elevated atmospheric CO_2 may reduce plant water stress (Franks et al. 2013) and significantly increase root growth (Iversen 2010), which may help species with deeper roots get water from the soil. Thus, these species may remain productive under moisture stress.

1.5.6 Genetics of drought hardiness

Drought tolerance or other stress tolerance genes are probably influenced by natural selection. Tolerance to one single stressor may adversely affect or reduce tolerance to other stressors (Bansal et al. 2016). Species with high genetic variation (such as Douglas-fir) are more likely to have the capacity to adjust to future climate conditions (Ackerly et al. 2000). Therefore, breeding programs may help trees cope with changing climate conditions (Howe et al. 2006). Tree breeders should select genotypes appropriately because genotypes with fast diameter growth will be more prone to drought stress (Rosner et al. 2014). Martinez-Maier et al. (2008) studied heritabilities of some adaptive traits. They point out that although ring density has a high heritability, ring width has a low heritability. According to Anekonda et al. (2002), foliage damage and xylem cavitation increased, whereas xylem hydraulic conductivity decreased under drought stress. There is considerable environmental variability influencing drought hardiness traits and estimates of heritabilities are modest, with an average of 0.19. They reported that early testing for drought hardiness is possible. In addition, growth in moist conditions was nearly uncorrelated with drought hardiness. The traits favorable for

drought resistance of juvenile seedlings could advance understanding for predicting how ongoing climate driven variation in surface moisture availability will impact species' distributions (Kerr et al. 2015). As climates continue to warm, tolerance of forest trees to drought may be surpassed (St.Clair and Howe 2007; Allen et al. 2010). In this study, I address these issues by considering sites in southern Oregon. I considered a different set of variables and took into account the effect of seedling origin on drought adaptation.

1.5.7 Molecular adaptations to drought hardiness

At the molecular level, many genes control drought-induced responses and reactions to other abiotic stresses (Perdiguero et al. 2013). According to Guevara et al. (2005), the current knowledge of genomic tools (e.g., genome sequencing, RNA-sequencing, SNP genotyping, genetic maps, quantitative trait loci, association mapping, and genetic transformation techniques) could aid in the interpretation of the complex structure of tree genomes and provide us with the ability to understand the genetic basis of adaptation.

Molecular markers are markers that display heritable differences in DNA sequence among individuals. The main advantages of DNA markers are that (1) an almost unlimited number of molecular markers are available (e.g., SNPs) and (2) they are stably inherited and detectable in all tissues. There are different kinds of molecular markers, including base pair changes (SNPs), rearrangements (translocations or inversions), insertions or deletions, and variations in the quantity of tandem repeats. For instance,

Muller et al. (2012) identified 1,000 genes associated with stress due to drought. Transcriptome analysis provides significant advantages for identifying genes controlling adaptive traits in the genome. However, analyses of seed sources should contribute to identification of genes for adaptation. Comparative genomics combined with suitable sampling strategies make it possible to comprehend the form of these genomes (Guevara et al. 2005)

1.6 Consequences of climate change

Forest tree species may respond to climate change by phenotypic plasticity, evolving in place, migrating, or becoming locally extinct (Aitken et al. 2008). Phenotypic plasticity is the ability of plants to acclimate by modifying their physiology or development in response to alterations in the environment (Martinez-Maier et al. 2008). Phenotypic plasticity can enhance the trees' capacity to cope with their environment in the short-term, and this may allow long-term evolutionary adaptation (Nicotra et al. 2010). However, phenotypic plasticity may be insufficient to meet the demands of rapid climate change (Morin et al. 2009).

There is a critical need to know whether phenotypic plasticity will be sufficient to effectively deal with climate change (Kawecki and Ebert 2004). Assisted migration may be required if phenotypic plasticity is not sufficient to acclimate or adapt to future climates (Aitken et al. 2008). Rehfeld et al. (2002) expressed that a conifer population

would take 12 generations to adapt to projected climate change. However, other studies claim that phenotypic plasticity can help populations cope with climate change (Aitken et al. 2008). Genetic diversity of a population benefits the evolution of traits that lead to the local phenotypic adaptation. Thus, adaptive phenotypic plasticity, which increases the ability to survive and reproduce, allows further evolutionary adaptation to occur. It is important to note that populations typically show adaptation to their environment by changing genetic composition as a result of natural selection (Kawecki and Ebert 2004). Adaptation to a local environment relies on genetic variation within populations, and can be improved by introducing new alleles that confer a higher fitness (Kremer et al. 2012). Hence, small populations are expected to be more vulnerable to rapid changes in climate. However, even though large populations may be more capable of adapting to climate change, populations are expected to experience significant adaptation lag. That is, populations take a long time to respond to climate change via evolutionary adaptation (Rehfeldt et al. 2002; Frank 2017a). Thus, it is important to determine the sensitivity of forest trees to climate change (Frank 2017a).

1.7 Tree breeding

Breeding programs for Douglas-fir aim to increase growth and wood quality, while maintaining adaptability for frost and drought hardiness. Breeding zones are defined as geographical areas with well-determined boundaries and altitudinal limits into which genetic material can be planted without risk of maladaptation (Howe et al. 2006).

Populations that are growing rapidly and producing greater yield are the main focus of breeding programs (Blum 2005). However, selection for increased growth may lessen the ability to tolerate frost and drought (Chapin 1980). Therefore, it is critical to include adaptive traits in Douglas-fir breeding programs. Tree breeding strategies are mainly focused on growth (Rosner et al. 2014). Genetics advances in forest trees typically focus on improving vegetative growth, tolerance of abiotic and biotic stresses, and increasing wood and stem quality (Howe et al. 2006). As mentioned earlier, due to changing climate, tree breeders should consider genetic variation and adaptability.

1.7.1 Quantitative genetics and inheritance

Quantitative genetics is the study of quantitative traits that are characterized by a continuum of phenotypes and are controlled by many genes. For quantitative traits, the effect that every gene locus has on the phenotypic expression of the trait is minor. In addition, the environment has a substantial influence on quantitative traits (White et al. 2007). Genotypes respond differently across a wide range of different environments. To design successful breeding strategies, it is crucial to consider the relative magnitude of variation that depends on the choice of genotypes and environments (Howe et al. 2006). Furthermore, Howe et al. (2006) argue that most information about quantitative genetics is derived from analysis of families collected from natural populations. For example, traits that are measured in this study (e.g., height, timing of bud flush, foliage damage, and stem damage) are quantitative traits. In this context, the use of statistical methods

allows us to quantify the phenotypic variation of the traits of interest; calculate the effects of genetic and environmental factors; and predict desired genetic values under certain conditions (White et al. 2007).

1.7.2 Additive genetic variation

Additive genetic variation (i.e., variance of breeding values) is the performance of a parent's sexually produced offspring, which explains how progeny (offspring) resemble their parents. Breeding values can be used to describe the variation in the effects that are transmitted from one generation to the next (White et al. 2007). The mean additive genetic value of a tree's offspring is called the tree's breeding value. For open-pollinated trees, the female parent provides only half of the genes in the progeny, with the other half coming from multiple male parents. Thus, a single female parent is naturally mated to a larger group of individuals in the population (White et al. 2007). In general, breeding strategies depend on improving populations through recurrent selection, as well obtaining superior genotypes from open-pollinated seed orchards. Recurrent selection improves breeding populations by increasing the frequencies of the alleles that are preferable. Because of this, breeders of Douglas-fir trees focus on the variance of breeding values (additive genetic variance) (Howe et al. 2006).

1.7.3 Heritabilities

Narrow-sense heritability (h^2) is defined as the ratio of additive genetic variation to total phenotypic variation; that is

$h^2 = (\sigma^2_{\text{additive}})/(\sigma^2_{\text{additive}} + \sigma^2_{\text{non-additive}} + \sigma^2_{\text{environment}})$ (White et al. 2007).

Observe that, by definition, h^2 ranges from 0 to 1. Breeders of forest trees mainly focus on the additive genetic variance. For instance, heritabilities close to 1 imply that the phenotypic value completely reflects the breeding value of the corresponding trait for that tree (White et al. 2007). Cornelius (1994) reviewed 67 published papers, including more than 500 estimates of h^2 for different species (conifers and hardwoods), traits, and ages. Cornelius (1994) concluded that estimates of narrow sense heritability are between 0.19 and 0.26 for most traits, except for wood specific gravity (h^2=0.48). Narrow-sense heritabilities for many growth and form traits range between 0.10 and 0.30, whereas wood specific gravity ranges from 0.3 to 0.6. This indicates that wood specific gravity is under stronger genetic control (White et al. 2007; Howe et al. 2006). Trait heritabilities are important for estimating genetic gains. Increasing family heritabilities (e.g., both by decreasing environmental variability and increasing family size) would increase genetic gains (Howe et al. 2006). According to Howe et al. (2006), the heritabilities of Douglas-fir differ between traits of interest. For instance, heritabilities for growth and cold hardiness, branch size, and stem defects are low to moderate, whereas heritabilities for

wood density, branch angle, spring cold hardiness, bud flush, and bud set are moderate to high. Bud flush has the highest heritability compared to other measured traits in some studies. The magnitude of the heritability is the key criterion in tree improvement programs that allows us to understand the amount, structure, and form of field trials and selection methods that are suitable (White et al. 2007).

1.7.4 Genetic correlations

The correlations between the breeding values of two traits, known as additive genetic correlations, are important. They can be used to select for traits that are more expensive or difficult to quantify than other genetically correlated traits. For example, if the genetic correlation between two traits is positive and high, the parent with a large breeding value for the first trait will tend to have a large breeding value for the second trait, producing superior offspring for both traits. On the other hand, negative genetic correlations have been well documented for growth versus cold hardiness, bud set, and wood density (Howe et al. 2006). Growth is directly related to second flushing, bud set, and frost damage in the fall. However, within populations, there is no consistent association between growth versus spring frost damage and bud flush (Howe et al 2003). Some important associations between vegetative bud phenology and cold hardiness have been established. For instance, trees that flush later in the spring are more tolerant of frost (positive genetic correlation). Therefore, bud phenology can be used to indirectly select for frost hardiness in the fall and spring. However, these correlations may vary among

populations. In Douglas-fir seedlings and saplings, the correlation between fall and spring cold hardiness goes from very weak to moderately negative (Howe et al. 2006).

1.7.5 Genetic gain

Genetic gain expected for each trait is predicted using genetic variances and heritabilities in tree improvement programs (White et al. (2007). Estimates of genetic gain are important for determining breeding strategies and the economic value of breeding programs (Howe et al. 2006). Genetic gain can be estimated as:

$$gain = ih\sigma_{additive}$$

where i is selection intensity, h is the square-root of the narrow sense heritability, and $\sigma_{additive}$ is the square-root of the additive genetic variance.

Mixed model methods are often used to predict breeding values and create selection indices that may help increase genetic gain (White et al. 2007).

1.7.6 Genotype-by-environment interactions

Genotype-by-environment interactions typically take place at several different genetic levels. Having genotype-by-environment interactions near zero implies that genotypes

have the same relative performance everywhere, which is expected to occur within the optimal breeding zone. The presence of genotype-by-environment interactions implies that genotypes act differently throughout a range of environments. This suggests that the relative performance of varieties depends on the environment (White et al. 2007).

1.8 Genetics and forest management

1.8.1 Seed transfer guidelines and climate change

One of the advantages of using local seedlots is that they are probably adapted to the climate conditions of the planting site (Kilkenny 2015). Results from provenance tests in the 1900 concluded that “local is best” (O’Neill et al. 2017), and this guided the first restrictions on seed transfer. For example, Thrupp (1927), a Canadian forest scientist, claimed that seeds should not be used from different geographic origins due to differences in hardiness and growth. Bates (1928) also recommended regulating seed movement in reforestation. However, the scientific and biological processes behind policies are not clear to forest managers. Furthermore, local seed sources may be suitable for the planting site, but they may not be available because of economic, ecological, or logistical constraints. One possibility is to plant genetically high quality seed sources (possibly non-local) that are more likely to have a favorable response to selection (Kilkenny 2015).

Seeds from different sources grow differently in different environments. Seeds cannot be moved to areas where they cannot survive due to maladaptation. Seed movement should be limited to ensure that planted trees are appropriate (e.g., adapted, competitive, or able to reproduce) in given environment. Taking seeds outside appropriate geographic limits may lead to maladaptation, such as death or injury from cold, drought, insects, or disease (Ying et al. 2006; O'Neill et al. 2017). That is why climate change impacts need to be incorporated into seed transfer recommendations (Ying et al. 2006). Managing for genetic diversity is also important. Hence, forest managers need to know how to select seed sources that are both genetically variable and adapted (Adams and Campbell 1981; Kilkenny 2015). The main purpose of reforestation is to produce plantations that maximize genetic potential within local environmental constraints (e.g., soils, climate etc.). To reach this goal, seeds must match the climatic environments in which they grow.

To match seeds with suitable environments, two types of zones are used in seed transfer systems: fixed and focal point zones (O'Neill et al. 2017). Seed transfer guidelines, which help identify seed sources that are suitable for planting at a particular location, are fundamental to forestry operations (Ying et al. 2006; O'Neill et al. 2017). These guidelines seek to minimize the risk of seed transfer for specific species. Optimally, they are derived from genecological models developed from provenance tests (St. Clair et al. 2013). Earlier guidelines for seed transfer were based on geographic and topographic variables. Now, however, these guidelines can be based on climate rather than latitude, longitude, and elevation (Kilkenny 2015). Rehfeldt (1983) introduced the "floating

principle" into seed transfer. Rehfeldt (1983) also used regression models like Campbell's (1974) model to determine limits or boundaries of seed zones. Floating boundaries (focal point zones), which intend to maximize fitness in seed transfers (Hamann et al. 2011; Kilkenny 2015), can be discontinuous (e.g., not connected) and flexible. Floating seed transfer systems are based on predictive models, and transfers are always limited at the same geographic or climatic distance (Ying et al 2006). Focal point zones and seed transfer guidelines are often developed from reciprocal transplant studies (Kawecki and Ebert 2004).

Fixed seed zones consist of contiguous areas delimited by fixed boundaries (Morgenstern 1996; Kilkenny 2015). Fixed zone systems were introduced in America in 1969 (O'Neill et al. 2017). Fixed zones delimit large, relatively uniform environments. Fixed zones are static and do not change in space or time. However, transfer in different geographic directions may be limited at different climatic distances if the seed sources are located near a fixed zone boundary. That is, seeds cannot be moved across the seed zone boundaries (Kilkenny 2015). Fixed zones are more common than focal point zones because of their simplicity (Kilkenny 2015). In fact, nursery genecological studies can be used when large reciprocal studies are not feasible. In such cases, the effect of climate change on seed transfer guidelines can be estimated from common gardens (Kilkenny 2015).

In the Pacific Northwest, seed zone delineation shifted after Campbell (1974) described his regression approach. Campbell's approach was a quantitative and predictive approach for inferring the effects of seed transfer (Ying et al 2006). The basis of the regression approach is that local adaptation varies clinally (e.g., there is a gradual change in a character or feature in relation to the environment) across the landscape. Natural selection is assumed to be the major force in causing this pattern of adaptive variation (Ying et al 2006). In general, genetic control of the adaptive variation can be associated with past natural selection. Unfortunately, this assumption is not always verifiable, and may not even be valid, making, the adaptability of a trait across different environment sometimes unpredictable. However, we can still determine the associations between phenotypic traits and environmental conditions, which ultimately allows us to delineate zones that minimize the risk of maladaptation (Kilkenny 2015).

The scientific basis for seed transfer guidelines is provenance testing (Ying et al 2006). A provenance test of forest trees is an experiment in which seeds are collected from different regions of the same species and planted in a common environment to assess genetic differences. Provenance tests enable forest breeders to choose the best available seed source for reforestation. To establish the most successful tree improvement program, it is important to use provenance tests prior to building an intensive breeding population (Wright 1976). In the absence of data from provenance trials for some populations, areas are typically divided into zones that have a similar geography, climate, or ecology where they can be observed and measured to uncover patterns of genetic variation. Thus,

geographic, climate, and ecological variables can substitute for information on the genetics of populations (O'Neill et al. 2017).

Biogeoclimatic classification (BEC) systems delineate zones based on geography, climate, and vegetation patterns (Ying et al 2006), and these can be used as generalized seed zones in situations where genetic data are missing (Kilkenny 2015). BEC classification enables the wise use of assisted migration to lower the effects of climate change. A set of BEC variants that are climatically similar to the BEC of the seed source can be identified for planting. Climate transfer functions can be developed and climate distances can be measured between the sets of BEC variants (O'Neill et al. 2017).

Paker (1992; 2000) used a geographic information system (GIS) to develop seed zones, which allows a very effective management and planning of seed transfer to be done because of its strong visual access (Ying et al 2006). General Circulation Models (GCM) can be used to delineate future seed zones. These climate variables can be obtained using ClimateNA software (O'Neill et al. 2017).

1.8.2 Seedlot selection

Seedlot selection is critical in order to achieve healthy and productive reforestation. To this end, novel technologies, analysis techniques, and genetic data have been used in British Columbia (BC) (O'Neil et al. 2015). The Seedlot Selection Tool was developed

from a joint effort between the US Forest Service, Oregon State University, and the Conservation Biology Institute. The Seedlot Selection Tool is a geographic information system (GIS) mapping program that matches seed sources and future planting climate. This tool covers a broad range of areas such as the Western U.S., Alaska, and British Columbia (see *https://seedlotselectiontool.org/sst/*).

1.8.3 Seed transfer

Moving seeds safely without fear of maladaptation is the main approach of any seed transfer system. The critical seed transfer distance (CSTD), is the maximum distance seed can be safely deployed (Ukranetz et al. 2011) and CSTDs are used to guide the size of fixed zones and the width of seed transfer limits (e.g., the size of focal point seed zones) (O'Neill et al. 2017). It is important to determine the CSTD. This can be done by using provenance data to associate the climatic origin of the seed with the growth or health of forest trees (O'Neill et al. 2017).

For naturally regenerated forests, it would be best to develop seed transfer guidelines based directly on fitness. Even though height may not be completely correlated with fitness, it is still more useful than other measures to reflect fitness (St. Clair et al. 2005; O'Neill et al. 2017).

1.8.4 Assisted migration

Assisted migration is the human-aided movement of populations (provenances) to new sites where they are expected to be better adapted to future climates. Human aided movement (e.g., assisted migration) is an important approach to mitigate the effects of climate change. Because climate change will likely lessen forest productivity, assisted migration is an important tool to facilitate or reduce the adverse effect of climate change (O'Neill et al. 2017). The main goal of assisted migration is to ensure productive forests in the future.

Populations take time to adapt to new climatic conditions. Therefore, it is necessary to know both past and future climate change in order to identify the projected climate for seeds for a given plantation. Shifting the target procurement climate from current climate by a climate distance is defined as migration distance. The migration distance can be used to achieve assisted migration, as it offers a quantification method that it is easy to interpret and can be adjusted over time (O'Neill et al. 2017). Forest restoration will also benefit from climate-based selection.

Assisted migration may be required to maintain the adaptability of Douglas-fir forests. Seed zones are geographical areas of defined boundaries and altitudinal limits from which seeds can be collected, and into which genetic material can be moved to suitable locations. Seed zones can help enhance seedling survivability by indicating where they

are best adapted to current and future climates. Moving seeds outside of their local climate conditions may lead to maladaptation (e.g., cold injury, drought injury, insects, disease, and mortality) (Campbell 1991; Morgenstern 1996). Because of climate change, local populations may not be genetically optimized. Therefore, it may be necessary to move Douglas-fir populations from lower to high elevations by human intervention (Ledig and Kitzmiller 1992).

Although assisted migration has been controversial, it may become crucial due to increasing climate change. Some approaches that take into consideration the maladaptation and susceptibility of species in a given area have been proposed. In this context, common garden studies are critical to assess the necessity of assisted migration (Kilkenny 2015).

Data collected from common garden studies is extremely important to assess the necessity and usefulness of assisted migration under climate change scenarios. The development of new transfer guidelines demands a careful examination in terms of planning horizon, transfer distances, and acceptable risks (Howe et al. 2003; Bansal et al. 2016). Assisted migration is the best tool in the areas where seed zones are currently in place, suggesting it can be very effective for potential future climate change conditions. The objective of any seed zone delineation is to minimize the adaptive genetic differences among populations within seed zones (Ying et al 2006).

Assisted migration can be achieved using climate variables to delineate seed zones, allowing a smaller number of seed sources to be safely placed in specific areas (O'Neill et al. 2017). To prepare for climate change, seed transfer guidelines can be modified to move species, populations, or genotypes from lower elevations and warmer climates to higher elevations and cooler climates (Balduman et al. 1999; St.Clair and Howe 2007), or even shift the species or population outside of its known historical distribution. Douglas-fir populations may need to migrate 450 m-1330 m higher in elevation and 1.8-4.9 degree higher in latitude, which is approximately 200 km to 540 km northward to match expected climates by the end of the this century (St.Clair 2005). In addition, studies show that to avoid maladaptation of current Douglas-fir populations, populations may be placed 500-1000 m higher in their current location, and up to 5 degrees higher in latitude to successfully adapt to future climates (St.Clair and Howe 2007).

Figure 1.1. Natural range of Douglas-fir (*Pseudotsuga menziesii*) in the U.S. and Canada. The map was downloaded from Geosciences and Environmental Change Science Center web site http://gec.cr.usgs.gov/data/little/pseumenz.pdf (Little 1971).

2 Materials and Methods

2.1 Overview of the Drought Hardiness Study

The Drought Hardiness Study is a collaboration between the Department of Forest Ecosystems and Society at Oregon State University, Northwest Tree Improvement Cooperative (NWTIC), Pacific Northwest Tree Improvement Research Cooperative (PNWTIRC), Bureau of Land Management (BLM), Plum Creek Timber Company (now Weyerhaeuser), and Silver Butte Timber Company. The original project was initiated by Jeannette Griese at the BLM in 2008-2009.

The genetics of drought adaptation is being investigated using Douglas-fir seedlings from 429 families from western Oregon and Washington (Pacific Northwest, PNW). The seedlings were grown in the BLM Sprague greenhouse for two years, and then planted at three sites (Lost Creek, Sprague, and Mill Pond) in southern Oregon. Each plantation site had a weather station that was installed for recording detailed weather data.

For this study, I measured about 10,000 seedlings distributed across two sites. I used these data to answer my researchable questions.

The information in the following sections comes from Crawford (2015): “Nursery Phase, Field Layout and Experimental Design, and Planting and Mapping.”

2.2 Plant materials

The Douglas-fir seedlings used in the experiment were obtained from the following seed orchards: Horning, Tyrrell, Schroeder, Provolt, DNR Meridian, and Plum Creek in the Pacific Northwest. The genetics of drought adaptation is being investigated using 429 elite families produced in these orchards. Families were selected based on performance in first-generation tests and (where available) second-cycle tests in the PNW.

Most seedlots (n = 409) are open pollinated seed from first-generation parents in these orchards. These first-generation parents originated from western Oregon (Figure 2.1). Another 20 families were provided by the Washington DNR (WDNR). The WDNR families are half-sib families created by pooling full-sib families produced in the Meridian Seed Orchard. The WDNR families were designed to imitate open-pollinated seedlots. Because the WDNR did not have suitable open-pollinated seedlots, they mixed the seeds from a number of full-sib families that have the same female parent, resulting in a half-sib family. Two additional woods-run seedlots from southern Oregon were also included. Each family is represented by up to 60 Douglas-fir trees. Due to herbicide damage at the Millpond plantation site, this thesis includes only the Lost Creek and Sprague plantation sites.

2.3 Nursery phase

Four hundred and twenty nine families were sown into Q-plugs in January 2013 (up to 60 cells/family), and then transferred to Styro-40 blocks in May 2013. Seedlings were watered irregularly early in the spring. There were large height differences observed in the greenhouse, ranging from 1.27 to 17.8 cm in July 2013 (Figure 2.2).

Seedling roots started to grow while in the Q-plugs, and then continued growing after the seedlings were transplanted into the Styro-40 blocks. Bottom heat was used to induce and speed the root development. Most seedlings in blocks (about 23,520 filled cells) survived. However, a small number of seedlings (about 15) did not survive after they started root development. In September 2013, seedlings were transported to the shade house where they continued growing under good airing and irrigation conditions. By June 2014, the seedlings reached heights ranging from 20.32 to 45.72 cm (Figure 2.3).

Seedlings were labeled with high quality coated paper tags in December of 2014. Seedlings were moved from the greenhouse to the J.H. Stone Nursery in Central Point, OR for cooler storage in the beginning of 2015 to keep them from growing again after release from dormancy. Lifting and packing was finished on January 29, 2015. Seedlings showing severe damage were not packed (Figure 2.4).

2.4 Field layout and experimental design

Layout and pinning work was done at all sites during the fall of 2014. Each site has fences to exclude deer and elk (Figure 2.5). The Sprague site was already surrounded by a seed orchard, so no additional fencing was required.

Herbaceous competition was controlled by herbicides at Lost Creek, and by weedmats and mowing at Sprague (Jayawickrama and Crawford 2016).

At the Sprague site, a total of 6480 Douglas-fir seedlings (2-year-old individuals) from 427 families were planted at 8 x 8 ft. spacing in March 2015. Trees were planted in single-tree plots in a randomized block design with 22 blocks.

At the Lost Creek site, a total of 3449 Douglas-fir seedlings (2-year-old individuals) from 293 families were planted at 8 x 8 ft. spacing in March 2015. Trees were planted in single-tree plots in a randomized block design with 17 blocks.

2.5 Planting sites

The Lost Creek site belongs to Plum Creek Timber Company (now Weyerhaeuser). The Sprague site is owned by the Bureau of Land Management. The Mill Pond site is owned by Silver Butte Timber Company (Figure 2.6).

2.6 Sprague site

The Sprague seed orchard site is located near Merlin on BLM land in southwestern Oregon (42°32'45.6612"N, 123°25'16.1508"W). The elevation is about 1067 m with a moderate slope (0-10%). The site faces southeast, and the site was previously covered by a sugar pine seed orchard. Adjacent stands occur on dry sites and include scattered Douglas-fir and ponderosa pine mixed with Oregon white oak and madrone. Soil structure at the Sprague site is a sandy loamy (Figure 2.7).

The Sprague site is relatively hot and dry. The mean annual temperature is 9.8 °C and the coldest month has an average temperature of 2.4 °C. The precipitation is about 875 mm per year.

2.7 Lost Creek site

The Lost Creek is located near Shady Cove on Weyerhaeuser land in southern Oregon (42°40'06.5496"N, 122°36'19.6704"W). It is about 64.37 km north of Sprague, and at a higher elevation of 2920 m. This site has moderately uniform slopes (10-40%). The site has areas facing in both the northeast and southeast directions and has good air drainage. The land was formerly covered with Douglas-fir and grand-fir. Soil structure is a deep, rocky loam, and the weather is cooler and wetter than at Sprague (Figure 2.8).

The mean annual temperature at Lost Creek is 4.6 °C, with an average temperature of 1.3 °C in the coldest month. The precipitation is about 1677 mm per year.

2.8 Millpond site

The Millpond site is located near Merlin on Silver Butte Timber Company land in southern Oregon (42°32'45.6056"N, 123°25'16.1508"W). It has an elevation of about 1777 m and a moderately uniform slope (20-40%). The site is facing in a southeast direction. The forest is mostly covered by Douglas-fir, with less grand-fir. Soil structure at the Millpond site is a deep clay loam soil with no rock (Figure 2.9).

The mean annual temperature is 9.4 °C, and the coldest month has an average temperature of 5.9 °C. The precipitation is about 1264 mm per year. Because of the herbicide damage at Millpond, we were not able to include this site in our study.

2.9 Planting and mapping

Seedlings were transplanted from J.H Stone Nursery to coolers at Merlin and Roseburg using a BLM refrigerated semi-truck (Figure 2.10). Planting site conditions were favorable (e.g., cool, moist, and overcast) at both sites. Border trees were not planted at the Sprague site due to limited space. At Lost Creek, Douglas-fir seedlings were not

planted along the fence lines. Instead, 351 ponderosa pine buffer trees were planted in areas where test trees were not planted to the fence lines.

Southwestern Oregon experienced prolonged drought and high temperatures in 2015. These conditions were particularly severe in Sprague, with temperatures exceeding 38 °C over several days. For this reason, seedlings at the Sprague site were irrigated on one occasion to ensure survival during the first year. Irrigation at Lost Creek was not considered necessary, and first year survival was close to 90% (Jayawickrama and Crawford 2016). The plantations were established in March 2015 at the three test sites: Sprague, Lost Creek, and Mill Pond (Fig 2.11).

2.10 Measured and derived variables

In the fall of 2015 (i.e., at the end of the first growing season in the field), we measured height of the seedlings, presence of second flushing, foliage damage, stem damage, leader damage, and mortality. In the spring of 2016, we measured the timing of bud flush.

2.10.1 Height

We measured 2014 height (Ht14, centimeters), which are the heights of the seedlings in the year 2014 when they were planted. We measured Ht14 at the end of the first growing season in the field. Ht14 was measured from the ground to the terminal bud scale scars

using a meter stick. This corresponds to the growth of the seedlings while they were in the greenhouse. The 2015 height (Ht15, centimeters) is the height of the seedlings at the end of the first growing season in the field. Ht15 was measured from the ground on the uphill side of the tree to the tip of the bud on the terminal leader using a meter stick, if the leader was damaged or missing, we measured to the top of the tallest branch if the branch was upright and more than 50% of the height of the damaged leader.

2.10.2 Height increment

I calculated the height increment (Htinc, centimeters) as the difference between Ht15 and Ht14.

2.10.3 Second flush

We measured the presence or absence of second flushing (SFlush) in the fall of 2015. We scored second flush visually (1= presence of second flushing, 0=absence of second flushing).

2.10.4 Foliage damage

We assessed the percentage of dead foliage (FD) at the end of the 2015 growing season in mid September. Green foliage was considered to be alive, whereas yellow or brown

foliage was considered to be dead. Foliage damage was scored using a 1 to 10 scale, which represents 10% damage classes (10-100 %), and assessment was done visually.

2.10.5 Foliage damage (binary variable)

I calculated the presence or absence of dead foliage (FD_bin). Using the FD measurements, FD_bin was scored 0, if the tree was not damaged, and 1 if the tree was damaged.

2.10.6 Stem damage from sunscald

We assessed the percentage of stem damage (SD) in the fall of 2015. Stem tissue that was brown to black was considered to have resulted from sunscald. Seedlings with less dark color on the stem were scored into lower classes of damage. Stem damage was scored using a 1 to 10 scale, which represents 10% damage classes (10-100%).

2.10.7 Stem damage (binary variable)

I calculated the presence or absence of sunscald damage (SD_bin) on the stem. Using the SD measurements, SD_bin was scored 0, if the tree was not damaged, and 1 if the tree was damaged.

2.10.8 Leader damage

We assessed the presence or absence of leader damage (LD) in the fall of 2015. LD was scored 0, if the tree was alive, 1 if the leader was missing, and 2 if the leader was present, but dead.

2.10.9 Leader damage (binary variable)

I calculated the presence or absence of leader damage (LD_bin). Using the LD measurements, LD_bin was scored 0, if the tree was not damaged, and 1 if the tree was damaged.

2.10.10 Fall mortality

We measured whether the tree was alive (0) or dead (1) in the fall of 2015 (Mort_F). This is an indicator variable to indicate whether the seedling is dead.

2.10.11 Spring mortality

We measured whether the tree was alive (0) or dead (1) in the spring of 2016 (Mort_S). This is an indicator variable to indicate whether the seedling is dead.

2.10.12 Bud flush

We measured the stage of bud flush (Flush) in April of 2016. Bud flush was scored in categories from 1 to 5 (1= the bud was closed, tight and dark; 2= the bud was closed, swollen, light colored; 3= the bud was just beginning to burst through tip (slight green showing); 4= the bud was open, needles around 1 cm long; and 5= the bud was fully open with needles fully elongated).

2.10.13 Bud flush (binary variable)

I calculated the presence or absence of bud flush (Flush_bin) on 2016. Using the Flush measurements, Flush_bin was scored 0, if the tree was not flushed, and 1, if the tree was flushed.

2.11 Data analysis

2.11.1 Obtain baseline measurements and climate data to help in the analysis and interpretation of future measurements in the Drought Hardiness Study

I summarized the drought adaptation measurements within and across plantations. I also obtained geographic (i.e., latitude, longitude, and elevation) and climatic information for the female parents of the families (i.e., parent source locations). I generated climate variables (1961-1990 normals) using the ClimateNA (Climate North America) software

program (Wang et al. 2006). ClimateNA is a software package that can predict climate variables for given site based on latitude, longitude, and elevation. I produced summary statistics from the quantitative trait and climate information. These statistics include mean, median, minimum, maximum, and standard deviations for families and individual trees at each site.

Comparisons of quantitative traits between planting sites

I compared quantitative trait means between the Sprague and Lost Creek plantations. I used a two-sample t-test to test the hypothesis H0: $\mu X - \mu Y = 0$ (i.e., the two means are equal). These tests were conducted assuming the population variances were unknown and not necessarily equal. The statistical significance level was set to 5% probability.

Two-sample t-test for comparing normally distributed traits

$$t = \frac{(\bar{X} - \bar{Y})}{\sqrt{\frac{s_x^2}{m} + \frac{s_y^2}{n}}}$$

where t is the two-sample test statistic for testing differences in means ; $\bar{X}$ is the sample mean at Sprague; $\bar{Y}$ is the sample mean at Lost Creek; s_x^2 is the sample variance at Sprague; s_y^2 is the sample variance at Lost Creek; m is the total number of seedlings at Sprague; and n is the total number of seedlings at Lost Creek.

Two-sample z-test for comparing proportions

To compare proportions (i.e., for binary traits) I used the z-test based on the normal approximation.

$$z = \frac{(p_1 - p_2)}{\sqrt{\tilde{p}(1-\tilde{p})\left(\frac{1}{m}+\frac{1}{n}\right)}}$$

where z is the two-sample test statistic based on normal approximation; $p_1$is the proportion the of binary variable at Sprague site; p_2 is the proportion of binary variable at Lost Creek site; $\tilde{p}$ is the overall sample proportion of binary variable at Lost Creek and Sprague $\tilde{p} = X + Y/(m+n)$, X and Y are the sums of the binary variable at Sprague and Lost Creek, and m and n are as described above.

2.11.2 Characterize the quantitative genetics of drought adaptation traits

I conducted quantitative genetic analysis for each drought adaptation trait as described below.

Linear models

I used random effects linear models to estimate variance components and obtain population and family-within-population random effects (BLUPs for populations and family-within-populations). The statistical analyses were performed in two steps.

Single-site analyses

For each site, I used a linear random effects model of the form:

$$y = Mean + Block(Site) + Family + Family \times Block(Site)$$

where y is the response of interest (e.g., height or other drought adaptation traits); Mean is the experiment mean; Block(Site) is the random effect of block-within-site; Family is the random effect of family, and Family x Block(Site) is the random effect of the family by block-within-site interaction.

Across-site analyses

I analyzed both sites together using a multi-environment trial (MET) analysis. The MET analysis was conducted using a linear random effects model of the form:

$$y = Mean + Site + Block(Site) + Family + Family \times Site + Family \times Block(Site)$$

where y, Mean, Block(Site), Family, and Family x Block(Site) are as described above, Site is the random effect of sites, and Family x Site is the random effect of family-by-site interaction.

Variance components

I used analyses of variance of single sites and across sites to obtain variance components. I estimated variance components using SAS PROC GLIMMIX, version 9.2 (SAS Institute). I then used the variance components to estimate genetic, environmental, and phenotypic variances; plus heritabilities.

σ_s^2 is the variance component for site.

$\sigma_{b(s)}^2$ is the variance component for block-within-site.

σ_f^2 is the variance component for family.

σ_{f*s}^2 is the variance component for the interaction between family and site.

$\sigma_{f*b(s)}^2$ is the variance component for the interaction between family and block-within-site (experimental error).

For individual trees, genetic, environmental, and phenotypic variances were estimated as follows:

1. Phenotypic variance for the single-site analysis:

$$\sigma^2_{P(s)} = \sigma^2_f + \sigma^2_{f*b(s)}$$

2. Phenotypic variance for the among-site analysis:

$$\sigma^2_{P(m)} = \sigma^2_f + \sigma^2_{f*s} + \sigma^2_{f*b(s)}$$

3. Additive genetic variance (variance of breeding values):

$$\sigma^2_A = 3\sigma^2_f$$

4. Error variance:

$$\sigma^2_e = \sigma^2_P - \sigma^2_A$$

Heritabilities

I estimated individual-tree heritabilities and family heritabilities for single sites and multiple sites. Then, I estimated breeding values, genetic correlations, and genetic gains as described below.

1. Individual-tree heritability, $h^2_i(s)$, for a single site:

$$h^2_i(s) = \frac{\sigma^2_A}{\sigma^2_{P(i,s)}} = \frac{3\sigma^2_f}{\sigma^2_f + \sigma^2_{f*b(s)}}$$

2. Family heritability, $h_f^2(s)$, for a single site:

$$h_f^2(s) = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_{f*b(s)}^2/b}$$

where b is the geometric mean number of replications (trees) per family.

3. Individual-tree heritabilities, $h_i^2(m)$, for multiple sites:

$$h_i^2(m) = \frac{\sigma_A^2}{\sigma_{P(i,m)}^2} = \frac{3\sigma_f^2}{\sigma_f^2 + \sigma_{f*s}^2 + \sigma_{f*b(s)}^2}$$

4. Family heritabilities, $h_f^2(m)$, for multiple sites:

$$h_f^2(m) = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_{f*s}^2/s + \sigma_{f*b(s)}^2/bs}$$

where s is the number of sites and b is the average geometric mean number of replications (trees) per family.

Breeding values

I estimated family-level breeding values for drought adaptation traits using BLUP (best linear unbiased prediction) and SAS PROC GLIMMIX, version 9.2 (SAS Institute). This was done for each site and across sites.

Genetic correlations

I estimated genetic correlations among drought adaptation traits as:

$$r_{g(1,2)} = Corr(BV_1 : BV_2)$$

where $r_{g(1,2)}$ is the genetic correlation between traits 1 and 2, BV_1 are the family-level breeding values for trait 1, and BV_2 are the family-level breeding values for trait 2. Breeding values were estimated as described above.

Type B genetic correlations were also measured for the same trait measured at Sprague and Lost Creek using the equation:

$$r_{g(Sp,Lc)} = \sigma_f^2 / (\sigma_f^2 + \sigma_{f*s}^2)$$

where $r_{g(Sp,Lc)}$ is the genetic correlation between sites. Variance components were described above (Johnson 1997).

Genetic gains

I estimated genetic gains for each trait. The expected genetic gain (ΔG) for each drought adaptation trait was calculated as:

$$\Delta G(\%) = 2\left[\frac{i_f \sigma_{P(f)} h_f^2}{\overline{X}}\right]100$$

where (1) the best 25 of 200 parents (12.5% selection intensity; i_f = 1.636 for n=200) or (2) the best 25 of 1000 parents (2.5% selection intensity; i_f = 2.338 for n=1000) (Falconer and Mackay 1996). h_f^2 is the family heritability, $\sigma_{P(f)}$ is the phenotypic standard deviation of family means, and $\overline{X}$ is the family mean for each trait.

2.11.3 Determine whether drought adaptation traits are associated with the climatic origin of Douglas-fir seedlings

I used ClimateNA variables from Objective 1 to achieve Objective 3. Then, I used climate estimates to calculate correlations and develop genecological models. A genecological model is a model that describes how genetic variation is related to environmental factors, such as climate. I related seedling performance to the climate of the female parent location. Then, I calculated (1) simple correlations between drought adaptation traits (family-level breeding values) versus individual climate variables and (2) multiple Lasso regressions between selected drought adaptation traits and multiple climate variables.

Simple correlation

I calculated simple correlations between across-site, family-level breeding values (BLUPs) for drought adaptation traits and individual climate variables.

Genecological models

To develop multivariate genecological models, I used Lasso regression analysis of drought adaptation traits versus parent source climate data. Lasso regressions were performed using SAS PROC GLMSELECT, version 9.2 (SAS Institute) and the default (SBC) stop criterion for model selection.

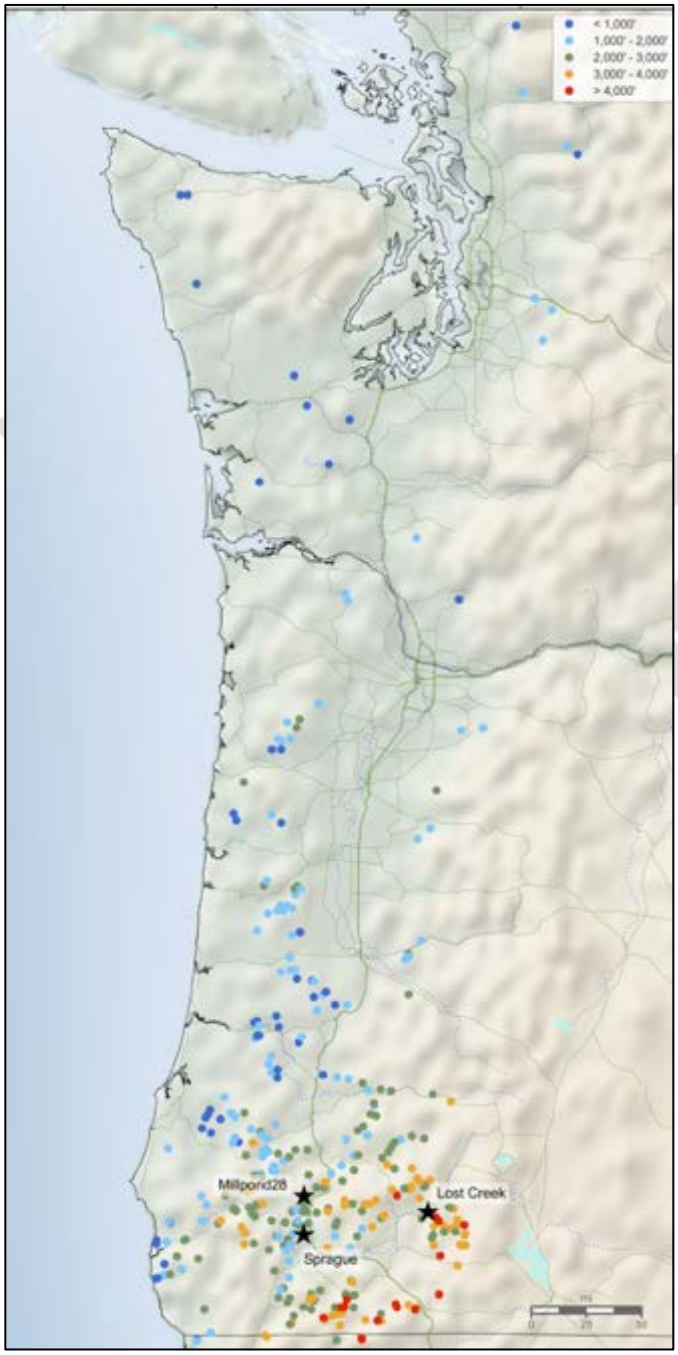


Figure 2.1. Locations of test sites and origins of parents used in BLM's Douglas-fir Drought Hardiness Study planted in 2015 (Jayawickrama and Crawford 2016). Stars show the locations of test sites. Dots show the original locations of the female parents.

Figure 2.2. Seedling height differences in the greenhouse (left) and root growth of seedlings in the greenhouse (right) (photos by Michael Crawford).

Figure 2.3. Seedlings in the greenhouse (photo by Michael Crawford).

Figure 2.4. Seedling packing arrangement (photo by Michael Crawford).

Figure 2.5. Fences were constructed at the Lost Creek site (photo by Michael Crawford).

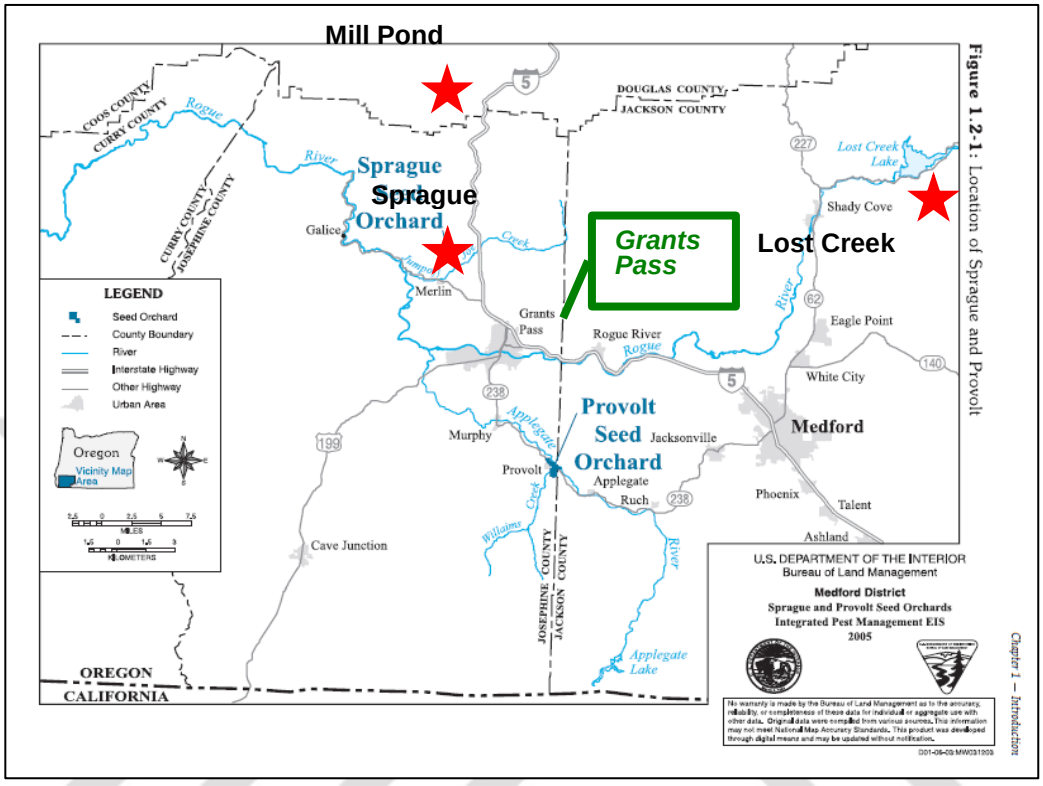


Figure 2.6. Field site location where the seedlings were planted.

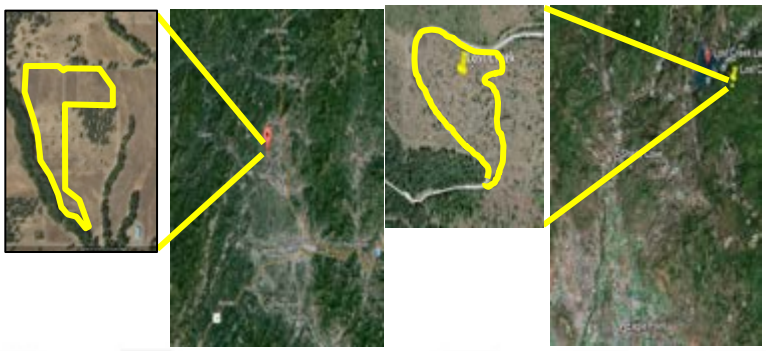
Figure 2.7. Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii)* seedlings at the Sprague site in 2015.

Figure 2.8. Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) seedlings at Lost Creek in 2015.

Figure 2.9. Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) seedlings with herbicide damage at Millpond in 2015.

Figure 2.10. Seedling planting in Sprague (left panel) and Lost Creek (right panel) (photos by Michael Crawford).

Sprague Lost Creek



Mill Pond

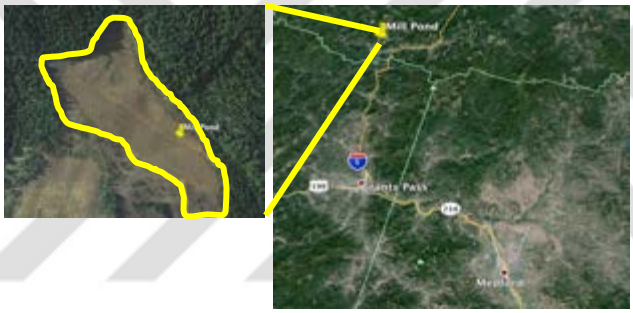


Figure 2.11. High-resolution satellite imaginary of the test sites.

Table 2.1. Descriptions of geographic and climate variables and their abbreviations. Climate variables were derived from ClimateNA (Wang et al. 2012).

Category	Source	Abbreviation	Description	Unit
Geography		LAT	Latitude based on the grid system	M
		LONG	Longitude based on the grid system	M
		ELEV	Elevation	Ft
Climate	ClimateNA	MAT	Mean annual temperature	°C
		MWMT	Mean warmest month temperature	°C
		MCMT	Mean coldest month temperature	°C
		TD	Temperature difference between MWMT and MCMT,	°C
		MAP	Mean annual precipitation	Mm
		MSP	Mean annual summer precipitation, (May to September)	Mm
		AHM	Annual heat-moisture index (MAT+10)/(MAP/1000)	°C m^{-1}
		SHM	Summer heat-moisture index (MWMT)/(MSP/1000)	°C m^{-1}
		DD_0	Degree-days below 0°C, chilling degree-days	
		DD5	Degree-days above 5°C, growing degree-days	
		DD_18	Degree-days below 18°C, heating degree-days	
		DD18	Degree-days above 18°C, cooling degree-days	
		NFFD	The number of frost-free days	
		FFP	Frost-free period	
		bFFP	The Julian date on which FFP begins	Julian date
		eFFP	The Julian date on which FFP ends	Julian date
		PAS	Proportion of precipitation as snow	Mm
		EMT	Estimated extreme minimum temperature,	°C
		EXT	Estimated extreme maximum temperature	°C
		EREF	Reference atmospheric evaporative demand	mm d^{-1}
		CMD	Climatic moisture deficit	
		MAR	Mean annual solar radiation	MJ m^{-2} d^{-1}
		RH	Mean annual relative humidity	%

Abbreviations: LAT=latitude; LONG=longitude; ELEV=elevation; MAT= mean annual temperature (°C); MWMT= mean warmest month temperature (°C); MCMT= mean coldest month temperature (°C); TD= temperature difference between MWMT and MCMT (°C); MAP=mean annual precipitation (mm); MSP= May to September precipitation (mm); AHM= annual heat-moisture index (MAT+10)/(MAP/1000); SHM= summer heat-moisture index ((MWMT)/(MSP/1000); DD_0= degree-days below 0°C (DD < 0); DD5= degree-days above 5°C (DD > 5); DD_18= degree-days below 18°C (DD < 18); DD_18= degree-days above 18°C (DD > 18); NFFD= number of frost-free days; bFFP= beginning of FFP; eFFP= ending date of FFP; FFP= frost-free period; PAS= proportion of precipitation as snow; EMT= estimated extreme minimum temperature over a 30-yr normal period; EXT= extreme maximum temperature over 30 years; EREF= reference atmospheric evaporative demand; CMD= climatic moisture deficit; MAR= mean annual solar radiation (MJ m-2 d-1); RH= mean annual relative humidity (%).

Table 2.2. Drought adaptation traits measured on Douglas-fir (*Pseudotsuga menziesii*) seedlings grown at Sprague and Lost Creek.

Variables	Drought adaptations trait group	Drought adaptation traits	Abbreviation	Units	Description
Measured Variables					
	Growth	Height	Ht14	cm	2014 height growth
		Height	Ht15	cm	2015 height growth
	Bud Phenology and Second Flushing	Bud flush	Flush	1 to 5	Bud flush score on 2016
		Second flushing	Sflush	1,0	The presence or absence of second flushing
	Damages	Foliage damage	FD	10 to 100%	The percentage of the dead foliage
		Stem damage	SD	10 to 100%	The percentage of sunscald damage on the stem
		Leader damage	LD	2,1,0	An indicator variable to indicate whether the leader (tallest shoot) is damaged
				2	2=dead
				1	1= damages
				0	0=alive and not damaged
	Survivability	Mortality	Mort	1,0	The mortality (1=dead; 0=alive)
Derived variables					
	Growth	Height increment	Htinc	cm	The height increment during the 2015 growing season
	Bud Phenology and Second Flushing	Bud flush binary	Flush_bin	1,0	The presence or absence of bud flush on 2016
	Damages	Foliage damage binary	FD_bin	1,0	The presence or absence of dead foliage
		Stem damage binary	SD_bin	1,0	The percentage of sunscald damage on the stem
		Leader damage binary	LD_bin	1,0	The leader condition (1=damaged; 0=not damaged)
	Survivability	Fall mortality	Mort_F	1,0	The mortality in the fall of 2015 (1=dead; 0=alive)
		Spring mortality	Mort_S	1,0	The mortality in the fall of 2016 (1=dead; 0=alive)

3 Results

3.1 Obtain baseline measurements and climate data to help in the analysis and interpretation of future measurements in the Drought Hardiness Study

3.1.1 The Sprague site is typically hotter and drier than the Lost Creek site

According to ClimateNA, the mean annual temperature (MAT) at Sprague has been 9.8 °C versus 4.6 °C at Lost Creek (Table 3.1). Thus, the MAT at Sprague has been about 5 °C higher than at Lost Creek. The beginning of the frost-free period (bFFP) appeared 22 days earlier at Sprague than at Lost Creek, but it ended at nearly the same time at both plantations. Therefore, Lost Creek extended the FPP for about 20 days compared to Sprague. For example, the frost-free period (FFP) at Sprague has been 184 days versus 164 days at Lost Creek. The mean coldest month temperature (MCMT) at Sprague has been 2.4 °C versus -1.3 °C at Lost Creek, and the mean warmest month temperature (MWMT) has been about 4 °C warmer at Sprague than at Lost Creek, with MWMT of 18.7 °C and 14.5 °C, respectively. The mean annual precipitation (MAP) at Sprague has been 875 mm versus 1677 mm at Lost Creek, a difference that is much more pronounced than the difference in temperature. In fact, the amount of rainfall at Lost Creek has been almost double the amount at Sprague. Similarly, the mean summer precipitation (MSP) at Sprague has been about three times less than at Lost Creek, with 114 mm at Sprague and 389 mm at Lost Creek. The summer heat moisture (SHM) index at Sprague has been 163.4 °C m^{-1} versus 37.2 °C m^{-1} at Lost Creek, and the climatic moisture deficit (CMD)

was nearly 10 times larger at Sprague (512 mm) than at Lost Creek (62 mm). However, the longer growing season and larger CMD at Sprague could still lead to growth if sufficient moisture is available. In addition, RH has been greater at Lost Creek (85%) than at Sprague (67%) (Table 3.1).

Based on weather station data, there has been a daily average high temperature maximum of 42.94 °C and low temperature minimum of -9.66 °C at Sprague over the period March 2015 to October 2016. At Lost Creek, the reported daily average high temperature maximum was 39.33 °C and the low temperature minimum was -8.50 °C over the same period. Daily average rain at Sprague was 0.03 mm versus 0.10 mm at Lost Creek over the 2015-16 period (Figures 3.1, 3.2, and 3.3).

3.1.2 The trees at the Sprague site grew less, were more damaged, and had greater mortality than the trees at the Lost Creek Site

Ht15, Htinc, Flush, and SFlush were significantly greater at the Lost Creek site compared to the Sprague site (Table 3.2). Thus, Douglas-fir seedlings at the Sprague site were shorter than those at the Lost Creek site in 2015 (Ht15). Also, Douglas-fir seedlings at Sprague grew less than those at Lost Creek. Htinc was 9.28 cm at Sprague versus 9.76 cm at Lost Creek. In contrast, FD_bin, SD_bin, LD_bin, and Mort were significantly greater at the Sprague site (Tables 3.2 and 3.3; $p < 0.001$). For example, foliage damage (FD_bin) was present in about 53% of the trees at Sprague, but only present in 16% of the trees at Lost Creek. SD_bin and LD_bin were also greater at Sprague. Likewise,

Sprague also had a higher mortality rate (31%) compared to Lost Creek (12%) during the first year of growth in the field (Table 3.2).

3.1.3 Early height measurements will be helpful for the analysis and interpretation of later measurements

There were large differences in height among families in the greenhouse. Variation in height after one year in the field largely reflects differences in growth that occurred in the greenhouse. That is, there was a significant and high correlation between Ht14 and Ht15 (r = 0.97) at both Sprague and Lost Creek (Tables 3.9 and 3.10). For example, at Sprague, the mean Ht14 was 39.97 cm and the standard deviation among family means was 7.407 (SE= 0.358), and this variability obscured family performance in the field based on Ht15 (Table 3.3). Likewise, at Lost Creek, the mean Ht14 was 42.71 and the standard deviation among family means was 6.532 (SE=0.381), and this variability obscured family performance in the field based on Ht15 (Table 3.3). Thus, Ht14 and Ht15 were used to calculate height increment to get a better assessment of growth in the field (Table 3.3). There was a moderate positive genetic correlation between Ht14 and Htinc at Lost Creek (r = 0.23) (Table 3.10). The correlation across both plantations was also moderate and positive (r = 0.18) (Table 3.11). These results suggest that initial height (Ht14) should be used as a covariate in analyses of growth, damage, and survival in the field (see Objective 2).

3.2 Characterize the quantitative genetics of drought adaptation traits

3.2.1 Heritability and genetic variance differed widely among traits

We found clear evidence for heritability of Flush. Individual-tree heritability for Flush was 0.62 at Sprague versus 0.83 at Lost Creek (Table 3.5). In the first growing season, we also found the frequency of SFlush was under weak genetic control($h_i^2 = 0.13$) at Lost Creek. At Sprague, however, the frequency of SFlush and the heritability were very low ($h_i^2 = 0.05$) (Table 3.5). Individual-tree heritabilities were high for Ht14 and Ht15 at both sites ($h_i^2 =$ 0.91-0.96 at Sprague versus 0.93-0.99 at Lost Creek) (Table 3.5). However, individual tree-heritabilities for Htinc were low for both sites. For instance, individual-tree heritability was 0.13 at Sprague versus 0.20 at Lost Creek. Individual tree-heritability was even lower across sites ($h_i^2 = 0.08$). Likewise**,** individual-tree heritabilities were near zero for FD_bin, SD_bin, LD_bin, and Mort at both sites ($0.02 \leq h_i^2 \leq 0.12$) (Table 3.5). The descriptions of variance components and quantitative genetic statistics are explained in Table 3.4.

Furthermore, additive genetic coefficients of variation (AGCV) were very high for SD_bin (50%) and LD_bin (49%), high for Flush (32%), SFlush (30%), and Mort (27%); moderate for Ht14, Ht15, and Htinc (14% - 23%); and lowest for FD_bin (0.00) (Table 3.8).

3.2.2 Estimated genetic gains were large for drought adaptation traits

Family heritabilities can be used to estimate genetic gains. Here, I consider two different gains: *gain 1*, where the best 25 of 200 parents are selected (12.5% selection intensity; i_f = 1.636 for n = 200) and *gain 2*, where the best 25 of 1000 parents are selected (2.5% selection intensity; i_f = 2.338 for n = 1000). Due to the high heritability and genetic variability for Htinc, Flush, SFlush, and LD_bin, the estimated genetic gains were also large. For example, gain 1 was 20% for Htinc, 53% for Flush, 95% for SFlush, 57% for LD_bin, and 35% for Mort. Gain 2 was 29% for Htinc, 75% for Flush, 87% for SFlush, 82% for LD_bin, and 50% for Mort at Sprague. At Lost Creek, gain 1 was 26% for Htinc, 57% for Flush, 50% for SFlush, 108% for LD_bin, and 95% for Mort, and gain 2 was 37% Htinc, 81% for Flush, 71% for SFlush, 155% LD_bin, and 135% for Mort. Gains from the across-site analysis for these traits were also large compared to gains for other drought adaptation traits. For instance, gain 1 was 25% for Htinc, 65% for Flush, 29% for SFlush, 82% for LD_bin, and 35% for Mort, and gain 2 was 36% for Htinc, 92% for Flush, 42% for SFlush, 117% LD_bin, and 50% for Mort across both plantations (Table 3.5). These results show that with more intensive selection for drought adaptation traits, genetic gain increases both at single sites and across sites.

3.2.3 Genetic correlations among drought adaptation traits

There were significant genetic correlations among drought adaptation traits for each single site and across sites ($p < 0.001$; Tables 3.9, 3.10, and 3.11). Ht14 does not reflect family differences in drought adaptation. Ht15 largely reflects family differences in growth that occurred in the greenhouse. That is, the large family differences in greenhouse growth obscured possible variation among families in the field. Therefore, Ht14 and Ht15 cannot be used as a measure of how the seedlings are growing under field conditions, or responding to drought. This conclusion is further supported by a high genetic correlation between height measurements at both plantations ($r = 0.97$) (Tables 3.9 and 3.10). I focused my attention on Htinc because it is more relevant for understanding the genetics of field growth and drought adaptation. For example, Htinc was correlated with Mort at both sites ($r = -0.57$ at Lost Creek and $r = 0.10$ at Sprague). Htinc was negatively correlated with FD_bin at both sites ($r = -0.48$ at Lost Creek and $r = -0.19$ at Sprague) (Tables 3.9 and 3.10). Likewise, FD_bin was positively correlated with Mort at both sites. For instance, the correlation between FD_bin and Mort was 0.62 at Sprague, versus 0.81 at Lost Creek (Tables 3.9 and 3.10). This indicates that the bigger the growth of the trees, the lower the mortality and foliage damage. However**,** there was no association between FD_bin and Mort across both plantations. In addition, Flush and LD_bin were positively correlated at both sites. For example, the correlation was 0.45 at Sprague, versus 0.28 at Lost Creek. Similarly, the correlation between Flush and LD_bin across both plantations was 0.49 (Table 3.11).

Additionally, at Lost Creek, Htinc was positively correlated with SFlush, which indicates that families with SFlush tended to have greater height growth (r = 0.42) (Table 3.10). However, Htinc was not strongly and not significantly correlated with SFlush at Sprague. Additionally, the correlation between Htinc and SFlush was low and negative across the Sprague and the Lost Creek sites (r = -0.19) (Table 3.11).

3.2.4 Low correlation between growth in the greenhouse and drought adaptation traits in the field

There were low negative genetic correlations between Ht14 versus Flush, SFlush, FD_bin, and LD_bin at Sprague (r = -0.25 to -0.13) (Table 3.9). In contrast, the correlations were mostly low to moderate and positive at Lost Creek ($0.03 \geq r \geq 0.34$). The one exception was the correlation between Ht14 and Flush, which was -0.20. The correlations across both plantations were also low, but the direction of the correlations changed depending on the individual sites ($r \leq 0.16$). In addition, there was a weakly positive genetic correlation between Ht14 and Mort, indicating there was a low association between these traits across both plantations (r = 0.08) (Table 3.11). Relationships between other variables are also explained in Tables 3.9, 3.10, and 3.11.

3.2.5 Low genetic correlation between flushing, versus height growth and mortality

There was a moderately low, but statistically significant negative genetic correlation between Htinc and Flush (r = -0.31) at Sprague. In contrast, the correlation was low and positive at Lost Creek; however, it was not statistically significant. In addition, the correlation between Htinc and Flush across both plantations was negative, suggesting that early bud flush may limit the growth of the seedlings in droughty conditions (r = -0.19) (Tables 3.9, 3.10 and 3.11).

In addition, a low negative genetic correlation between Flush and Mort was observed at Sprague (r = -0.18). Likewise, there was a negative genetic correlation between Flush and Mort, measured across locations, indicating that early bud flush may reduce seedling mortality (r = -0.18) (Tables 3.9 and 3.10).

3.2.6 Genotype-by-environment interactions

Genotype-by-environment interactions were very high for SFlush, (V_{GE}=0.86) and FD_bin (V_{GE} = 1.00); high for Htinc (V_{GE} = 0.44) and Mort (V_{GE} = 0.64); moderate for LD_bin (V_{GE} = 0.37), Ht14 (V_{GE} = 0.24), Ht15 (V_{GE} = 0.23), and Flush (V_{GE} = 0.12); and lowest for SD_bin (V_{GE} = 0.00) (Table 3.8). These results suggest that the variation in population effects differ between the Sprague and Lost Creek plantations. For the growth traits, genotype-by-environment interaction was greatest for Ht15 (V_{GE} = 0.44).

That is, a substantial genotype-by-environment interaction was found for Ht15. Genotype-by-environment interaction for FD_bin and SFlush were the highest among other drought adaptation traits (Table 3.8).

Site-to-site genetic correlations were assessed by using Type B genetic correlations (Burdon 1977). Higher Type B genetic correlations correspond with lower genotype-by-environment interactions. The Type B genetic correlations were very high for SD_bin (r_g= 1.00); high for Flush (r_g= 0.88), Ht14 (r_g= 0.76) and Ht15 (r_g= 0.77); moderate for Htinc, (r_g= 0.56) and LD_bin (r_g = 0.63); and lowest for Mort (r_g = 0.36) and SFlush, (r_g = 0.14) (Table 3.8).

3.3 Determine whether drought adaptation traits are associated with the climatic origin of Douglas-fir seedlings

3.3.1 Relationships between drought adaptation traits and source climates

I prepared a summary of geographic and climate variables associated with the location of the female parents. The climate data consisted of historical 30-year normals (1961-1990) from the ClimateNA software program (Wang et al. 2006). The correlations between climate variables and drought adaptation traits across sites were significant ($p < 0.0001$) (Table 3.11). Seeds were collected from female parents ranging in elevation from low elevation (60.96 m) to high elevation (1371.6 m) (Table 3.12). The female parents come from cold to mild areas. For example, MAT ranged between 5 °C and 12 °C, with a mean

of 6.89°C (SE = 0.169). MAP ranged between 565 mm and 6325 mm, with a mean of 2160 mm (SE = 49.04). Other variables are explained in Table 3.12.

3.3.2 Source temperature was positively associated with growth in the greenhouse, but showed no relationship to growth in the field

The relationship between BLUPs for drought adaptation traits and single climate variables across-sites was determined from the correlations between the BLUPs and the geographic and climate variables (Tables 3.13, 3.14, and 3.15). In general, temperature variables, especially MAT, DD5, and EREF, were positively associated with Ht14 at both sites. Ht14 shows higher correlations (above 0.40) with temperature variables in both sites; however, correlations are much lower for Htinc (Table 3.15).

Table 3.13 shows the correlations between BLUPs and climate variables for the Sprague plantation. A moderately positive genetic correlation was found between Ht14 versus MAT, DD5, and EREF ($r \geq 0.41$). In contrast, a negative genetic correlation was observed between Ht14 and DD_18 ($r = -0.41$). For example, the correlation between MAT and Ht14 was 0.41, indicating that about 16% of the variation was explained by MAT. Other variables are described in Table 3.13.

Table 3.14 shows the correlations between BLUPs and climate variables for the Lost Creek plantation. A moderately positive genetic correlation was found between Ht14, versus MAT, DD5, NFFD, EXT, and EREF ($r \geq 0.40$). In contrast, a negative genetic

correlation was observed between Ht14 and DD_18 (r = -0.44). Other variables are described in Table 3.14. The correlation between MAT versus Ht14 and Ht15 was 0.44. This indicates that about 16% of the variation was explained by MAT. EREF was significantly and moderately correlated with Ht14 and Ht15 at Lost Creek (r = 0.44). This indicates that about 19% of the variation was explained by EREF.

For BLUPs calculated across the Sprague and Lost Creek sites, moderately positive genetic correlations were found between Ht14 versus MAT, DD5, and EREF ($r \geq 0.42$). In contrast, a negative genetic correlation was observed between Ht14 and DD_18 (r = -0.42) (Table 3.15).

3.3.3 Moderate relationship between flushing and source climates

At Sprague, there was no significant correlation between TD, MAP, MSP, AHM, SHM and eFFP versus Ht14 and Ht15 (Table 3.13). However, other climate variables were significantly correlated with Flush, with values ranging from -0.25 to 0.28. For example, there is a moderate positive relationship between Flush versus MCMT, AHM, SHM, eFFP, and EMT ($r \geq 0.21$). The strongest negative correlations were between Flush versus TD and MSP. These correlations were both -0.25, indicating that a little more than 6% of the variation was explained by TD or MSP (Table 3.13). This might also show that early bud flush in Douglas-fir can be a drought avoidance mechanism.

At Lost Creek, moderately positive relationships were observed between Flush and MCMT, AHM, SHM, eFFP, and EMT ($r \geq 0.22$). In contrast, negative genetic correlations were found between Flush and TD, MAP, and MSP ($r \leq 0.21$) (Table 3.14).

Compared to Sprague, correlations for SFlush were relatively large at Lost Creek. For example, MAT was correlated with SFlush at Lost Creek. The correlation between MAT and SFlush was 0.32, indicating that about 10% of the variation was explained by MAT.

For BLUPs calculated across the Sprague and Lost Creek sites, moderately positive genetic correlations were found between Flush versus MCMT, AHM, SHM, eFFP, and EMT($r \geq 0.21$; Table 3.15). In contrast, negative genetic correlations were observed between Flush versus TD, MAP, and MSP ($r \leq -0.21$) (Table 3.15).

3.3.4 Across Sprague and Lost Creek, correlations between parental climates and seedling traits were low

In addition to correlations between BLUP values and climate variables, I performed similar analyses using family means ($|r| \geq 0.20$) (Tables 3.16, 3.17, and 3.18). In general, results were similar to those obtained based on BLUPs. In a few instances, relationships were found with Htinc. For example, the strongest observed correlation was -0.20 between Htinc and RH (Table 3.17).

3.3.5 Selection of climate variables

Table 3.19 shows the results for four variable selection methods used to predict Flush, SFlush, and Htinc at Sprague and Lost Creek (forward selection, backward selection, stepwise selection and Lasso). The stepwise selection procedure selects eFFP as the only variable in the prediction equation for SFlush at Sprague, but the same procedure selects DD_18 for Lost Creek. The different procedures lead to models that can explain up to about 26% of the variability in the response of interest, depending on the estimation method. Interestingly, in some cases, Lasso regression does not find any of the variables as being statistically significant, which may be a consequence of the Lasso penalty.

These models seek to predict the mean value of the response variable (e.g., SFlush) as a function of the climate variables (e.g., eFFP). A model with one explanatory variable has two parameters: the intercept parameter and the slope parameter. The interpretation of the model is that the coefficient of eFFP, for example, represents the change in SFlush associated with an increase in eFFP, considering that all other variables are the same. The adjusted R^2 value is interpreted as the percentage of total variance in SFlush that is explained by eFFP.

SBC, the default stop criterion, which is the statistic applied to stop the selection process is the same statistic that is applied to select the sequence of models. Adjusted R^2 is the percentage of total variance in the response that is explained by the model. Table 3.20

shows the estimated coefficients for the models obtained using the Lasso regression approach.

Table 3.1. Geographic and climatic characteristics of the Sprague and Lost Creek plantations. Climate variables were derived from ClimateNA (Wang et al. 2012).

			Test Sites	
Category	**Unit**	**Abbreviation**	**Sprague**	**Lost Creek**
Geography	m	LAT	42°32'45.6612	42°40'06.5496
	m	LONG	123°25'16.1508	122°36'19.6704
	m	ELEV	1067	2920
Climate	°C	MAT	9.8	4.6
	°C	MWMT	18.7	14.5
	°C	MCMT	2.4	-1.3
	°C	TD	16.3	15.8
	mm	MAP	875	1677
	mm	MSP	114	389
	°C m^{-1}	AHM	22.6	8.7
	°C m^{-1}	SHM	163.4	37.2
	°C	DD_0	131	483
	°C	DD5	2106	1069
	°C	DD_18	3136	4878
	°C	DD18	154	23
	day	NFFD	275	210
	Julian date	bFFP	124	146
	Julian date	eFFP	308	310
	Julian date	FFP	184	164
	mm	PAS	52	612
	°C	EMT	-18.6	-27.6
	°C	EXT	37.5	29
	mm d^{-1}	Eref	859	259
	mm	CMD	512	62
	MJ m^{-2} d^{-1}	MAR	16.7	14.4
	%	RH	67	85

Abbreviations: LAT=latitude; LONG=longitude; ELEV=elevation; MAT= mean annual temperature (°C); MWMT= mean warmest month temperature (°C); MCMT= mean coldest month temperature (°C); TD= temperature difference between MWMT and MCMT (°C); MAP=mean annual precipitation (mm); MSP= May to September precipitation (mm); AHM= annual heat-moisture index (MAT+10)/(MAP/1000); SHM= summer heat-moisture index ((MWMT)/(MSP/1000); DD_0= degree-days below 0°C (DD < 0); DD5= degree-days above 5°C ; DD_18= degree-days below 18°C; DD18= degree-days above 18°C; NFFD= number of frost-free days; bFFP= beginning of FFP; eFFP= ending date of FFP; FFP= frost-free period; PAS= proportion of precipitation as snow; EMT= estimated extreme minimum temperature over a 30-yr normal period; EXT= extreme maximum temperature over 30 years; Eref= reference atmospheric evaporative demand; CMD= climatic moisture deficit; MAR= mean annual solar radiation (MJ m^{-2} d^{-1}); RH= mean annual relative humidity (%).

Table 3.2. Statistics for traits measured on individual trees of Douglas-fir seedlings in the Sprague and Lost Creek plantations. P values indicate the probability of a mean difference in the seedling trait between plantations (t-test).

	Sprague								Lost Creek									
	N	**Mean**	**Median**	**StdDev**	**Min**	**Max**	**Range**	**h_i^2**	**N**	**Mean**	**Median**	**StdDev**	**Min**	**Max**	**Range**	**h_i^2**	**Mean Diff**	**p-values**
Ht14	6476	40.53	40	11.142	10	102	92	0.96	3446	42.91	42	10.942	17	92	75	0.93	2.38	< 2.2e-16
Ht15	6476	49.81	50	11.911	12	109	97	0.91	3446	52.67	52	11.629	18	102	84	0.99	2.86	< 2.2e-16
Htinc	6476	9.28	10	4.857	0	38	38	0.13	3446	9.76	10	4.512	0	33	33	0.20	0.48	5.93E-07
Flush	4495	1.71	2	0.720	1	5	4	0.62	3026	2.61	3	0.970	1	5	4	0.83	0.90	< 2.2e-16
Flush_bin	6476	0.09	0	0.290	0	1	1	0.32	3446	0.55	1	0.497	0	1	1	0.57	0.46	1.20E-288
SFlush	6476	0.06	0	0.236	0	1	1	0.05	3446	0.38	0	0.486	0	1	1	0.13	0.32	1.20E-288
FD	6476	33.63	10	43.746	0	100	100	0.06	3446	11.74	0	31.066	0	100	100	0.11	-21.89	< 2.2e-16
FD_bin	6476	0.53	1	0.499	0	1	1	0.05	3446	0.16	0	0.364	0	1	1	0.08	-0.37	1.20E-288
SD	6476	1.28	0	4.224	0	70	70	0.02	3446	0.80	0	4.813	0	100	100	0.03	-0.48	6.87E-07
SD_bin	6476	0.11	0	0.307	0	1	1	0.02	3446	0.04	0	0.203	0	1	1	0.02	-0.07	1.20E-288
LD	6476	0.19	0	0.443	0	2	2	0.07	3446	0.04	0	0.202	0	2	2	0.06	-0.15	< 2.2e-16
LD_bin	6476	0.17	0	0.380	0	1	1	0.09	3446	0.03	0	0.182	0	1	1	0.06	-0.14	1.20E-288
Mort	6476	0.31	0	0.461	0	1	1	0.07	3446	0.12	0	0.327	0	1	1	0.12	-0.19	< 2.2e-16
Mort_F	6476	0.28	0	0.449	0	1	1	0.06	3446	0.11	0	0.307	0	1	1	0.11	-0.17	< 2.2e-16
Mort_S	6476	0.31	0	0.461	0	1	1	0.07	3446	0.12	0	0.327	0	1	1	0.12	-0.19	< 2.2e-16

Abbreviations: h_i^2 is the individual-tree heritability; Ht14 (cm) is the height of the seedlings in 2014, which corresponds to the growth of the seedlings in the greenhouse; Ht15 is the height of the seedlings in 2015 at the end of the first growing season. Htinc is the difference between Ht14 and Ht15. Flush is the bud flush score in the spring of 2016; Flush_bin is the presence or absence of bud flush in March 2016; SFlush is the presence or absence of second flushing in September 2016; FD is the percentage of dead foliage; FD_bin is the presence or absence of dead foliage; SD is the percentage of sunscald damage on the stem; SD_bin is the presence or absence of sunscald damage on the stem; LD is a variable indicating whether the leader (tallest shoot) is damaged (2=dead, 1=damaged, 0=alive and not damages); LD_bin is the leader condition (1=damaged, 0=not damaged); Mort is mortality (1=dead, 0=alive); Mort_F is mortality in the fall of 2015; Mort_S is the mortality in the spring of 2016.

Table 3.3. Statistics for traits measured on families of Douglas-fir seedlings in the Sprague and Lost Creek plantations.

	Sprague								Lost Creek							
	N	**Mean**	**Median**	**StdDev**	**Min**	**Max**	**Range**	**h_f^2**	**N**	**Mean**	**Median**	**StdDev**	**Min**	**Max**	**Range**	**h_f^2**
Ht14	427	39.97	39	7.407	10	74	64	0.85	293	42.71	43	6.532	28	59	31	0.83
Ht15	427	49.19	49	7.837	20	83	63	0.84	293	52.43	53	7.248	29	76	47	0.85
Htinc	427	9.21	9	2.263	0	19	19	0.34	293	9.72	10	1.908	0	20	20	0.45
Flush	415	1.69	2	0.405	1	3	2	0.75	292	2.61	3	0.558	1	4	3	0.81
Flush_bin	427	0.09	0	0.137	0	1	1	0.59	293	0.55	1	0.257	0	1	1	0.73
SFlush	427	0.06	0	0.091	0	1	1	0.16	293	0.38	0	0.182	0	1	1	0.34
FD	427	33.07	32	18.586	0	100	100	0.20	293	12.02	9	12.076	0	100	100	0.30
FD_bin	427	0.53	1	0.217	0	1	1	0.16	293	0.16	0	0.134	0	1	1	0.23
SD	427	1.23	1	1.400	0	10	10	0.07	293	0.80	0	1.526	0	8	8	0.10
SD_bin	427	0.10	0	0.120	0	1	1	0.06	293	0.04	0	0.063	0	0	0	0.06
LD	427	0.21	0	0.212	0	2	2	0.21	293	0.04	0	0.070	0	0	0	0.19
LD_bin	427	0.19	0	0.190	0	1	1	0.26	293	0.03	0	0.061	0	0	0	0.19
Mort	427	0.30	0	0.194	0	1	1	0.21	293	0.12	0	0.126	0	1	1	0.31
Mort_F	427	0.27	0	0.189	0	1	1	0.19	293	0.11	0	0.119	0	1	1	0.30
Mort_S	427	0.30	0	0.194	0	1	1	0.22	293	0.12	0	0.127	0	1	1	0.34

Abbreviations: h_f^2 is the family heritability; Ht14 (cm) is the height of the seedlings in 2014, which corresponds to the growth of the seedlings in the greenhouse; Ht15 is the height of the seedlings in 2015 at the end of the first growing season. Htinc is the difference between Ht14 and Ht15. Flush is the bud flush score in the spring of 2016; Flush_bin is the presence or absence of bud flush in March 2016; SFlush is the presence or absence of second flushing in September 2016; FD is the percentage of dead foliage; FD_bin is the presence or absence of dead foliage; SD is the percentage of sunscald damage on the stem; SD_bin is the presence or absence of sunscald damage on the stem; LD is a variable indicating whether the leader (tallest shoot) is damaged (2=dead, 1=damaged, 0=alive and not damaged); LD_bin is the leader condition (1=damaged, 0=not damaged); Mort is mortality (1=dead, 0=alive); Mort_F is mortality in the fall of 2015; Mort_S is the mortality in the spring of 2016.

Table 3.4. Descriptions of variance components and quantitative genetic statistics

Parameter	Description	Equation
Variance components		
σ^2_s	Site variance component	From SAS PROC GLIMMIX
$\sigma^2_{b(s)}$	Block within site variance component	From SAS PROC GLIMMIX
σ^2_f	Family variance component	From SAS PROC GLIMMIX
$\sigma^2_{f*b(s)}$	Family x Block interaction variance component	From SAS PROC GLIMMIX
Quantitative genetic statistics		
$\sigma^2_{P(s)}$	Phenotypic variance (single-site analyses)	$\sigma^2_{P(s)} = \sigma^2_f + \sigma^2_{f*b(s)}$
$\sigma^2_{P(m)}$	Phenotypic variance (among-site analyses)	$\sigma^2_{P(m)} = \sigma^2_f + \sigma^2_{f*s} + \sigma^2_{f*b(s)}$
σ^2_A	Additive genetic variance	$\sigma^2_A = 3\sigma^2_f$
σ^2_e	Error variance	$\sigma^2_e = \sigma^2_P - \sigma^2_A$
$h^2_i(s)$	Individual-tree heritability for a single site	$h^2_i(s) = \frac{\sigma^2_A}{\sigma^2_{P(i,s)}} = \frac{3 * \sigma^2_f}{\sigma^2_f + \sigma^2_{f*b(s)}}$
$h^2_f(s)$	Family heritability for a single site	$h^2_f(s) = \frac{\sigma^2_A}{\sigma^2_{P(f,s)}} = \frac{\sigma^2_f}{\sigma^2_f + \sigma^2_{f*b(s)}/b}$
$h^2_i(m)$	Individual-tree heritability across multiple sites	$h^2_i(m) = \frac{\sigma^2_A}{\sigma^2_{P(i,m)}} = \frac{3\sigma^2_f}{\sigma^2_f + \sigma^2_{f*s} + \sigma^2_{f*b(s)}}$
$h^2_f(m)$	Family heritability across multiple sites	$h^2_f(m) = \frac{\sigma^2_A}{\sigma^2_{P(f,m)}} = \frac{\sigma^2_f}{\sigma^2_f + \sigma^2_{f*s}/s + \sigma^2_{f*b(s)}/bs}$

Table 3.5. Heritabilities and genetic gains of traits measured at the Sprague plantation, Lost Creek plantation, and across both plantations.

	Ht14	Ht15	Htinc	Flush	Flush_bin	SFlush	FD	FD_bin	SD	SD_bin	LD	LD_bin	Mort	Mort_F	Mort_S
Sprague															
Heritabilities h^2(s)															
Individual heritabilities	0.96	0.91	0.13	0.62	0.32	0.05	0.06	0.05	0.02	0.02	0.07	0.09	0.07	0.06	0.07
Family heritabilities	0.85	0.84	0.34	0.75	0.59	0.16	0.20	0.16	0.07	0.06	0.21	0.26	0.21	0.19	0.22
Genetic gains (%)															
Gain1	47.68	39.87	20.09	52.73	263.75	66.68	27.44	14.44	21.80	16.93	48.55	57.32	34.72	32.10	35.69
Gain2	68.14	56.98	28.71	75.35	376.93	95.30	39.21	20.64	31.16	24.19	69.38	81.91	49.61	45.88	51.00
Lost Creek															
Heritabilities h^2(s)															
Individual heritabilities	0.93	0.99	0.20	0.83	0.57	0.13	0.11	0.08	0.03	0.02	0.06	0.06	0.12	0.11	0.13
Family heritabilities	0.83	0.85	0.45	0.81	0.73	0.34	0.30	0.23	0.10	0.06	0.19	0.19	0.31	0.30	0.34
Genetic gains (%)															
Gain1	42.19	38.32	26.02	56.87	108.63	49.76	89.24	55.84	58.71	27.30	112.37	108.18	94.53	98.55	102.55
Gain2	60.29	54.76	37.18	81.28	155.24	71.11	127.54	79.80	83.91	39.02	160.59	154.59	135.09	140.84	146.55
Sprague and Lost Creek															
Heritabilities h^2(m)															
Individual heritabilities	0.72	0.72	0.08	0.64	0.27	0.02	0.02	0.00	0.03	0.02	0.04	0.05	0.03	0.02	0.03
Family heritabilities	0.78	0.79	0.34	0.82	0.54	0.09	0.14	0.00	0.19	0.16	0.21	0.26	0.15	0.12	0.14
Genetic gains (%)															
Gain1	44.08	38.22	25.31	64.77	160.28	29.09	27.76	0.00	102.88	69.98	69.36	81.88	35.19	28.85	34.14
Gain2	62.99	54.61	36.17	92.57	229.05	41.57	39.67	0.00	147.02	100.00	99.12	117.01	50.29	41.23	48.79

Gain1 is selection of the best 25 of 200 parents (12.5% selection intensity; $i_f = 1.636$ for n = 200)
Gain2 is selection of the best 25 of 1000 parents (2.5% selection intensity; $i_f = 2.338$ for n = 1000)

Table 3.6. Quantitative genetic statistics for seedling traits of Douglas-fir analyzed at the Sprague plantation.

		Variance components			Derived quantitative genetic statistics				
Trait	**No. of obs**	**σ^2_b**	**σ^2_f**	**σ^2_{f*b}**	**σ^2_P**	**σ^2_A**	**σ^2_e**	**h^2_i**	**h^2_f**
Ht14	6476	0.59	40.00	84.37	124.38	120.01	4.36	0.96	0.85
Ht15	6476	0.87	42.94	98.85	141.79	128.82	12.97	0.91	0.84
Htinc	6476	1.08	0.94	21.60	22.54	2.83	19.71	0.13	0.34
Flush	4495	0.04	0.10	0.38	0.47	0.29	0.18	0.62	0.75
Flush_bin	6476	0.00	0.01	0.07	0.08	0.03	0.05	0.32	0.59
SFlush	6476	0.01	0.00	0.05	0.05	0.00	0.05	0.05	0.16
FD	6476	65.88	38.50	1817.48	1855.98	115.49	1740.49	0.06	0.20
FD_bin	6476	0.02	0.00	0.22	0.23	0.01	0.22	0.05	0.16
SD	6476	0.57	0.10	17.19	17.29	0.31	16.98	0.02	0.07
SD_bin	6476	0.00	0.00	0.09	0.09	0.00	0.09	0.02	0.06
LD	6476	0.00	0.00	0.19	0.20	0.01	0.18	0.07	0.21
LD_bin	6476	0.00	0.00	0.14	0.14	0.01	0.13	0.09	0.26
Mort	6476	0.01	0.00	0.20	0.21	0.01	0.19	0.07	0.21
Mort_F	6476	0.01	0.00	0.19	0.20	0.01	0.18	0.06	0.19
Mort_S	6480	0.01	0.00	0.20	0.21	0.01	0.19	0.07	0.22

Abbreviations: σ^2_b, σ^2_f, σ^2_{f*b} are variance components for block, family, and family*block interaction (i.e., the residual error). σ^2_P, σ^2_A, σ^2_e, h^2_i, and h^2_f are the phenotypic variance, additive genetic variance, error variance, individual tree heritability, and family heritability.

Table 3.7. Quantitative genetic statistics for seedling traits of Douglas-fir analyzed at the Lost Creek plantation.

		Variance components			Derived quantitative genetic statistics				
Trait	**No. of obs**	**σ^2_b**	**σ^2_f**	**σ^2_{f*b}**	**σ^2_P**	**σ^2_A**	**σ^2_e**	**h^2_i**	**h^2_f**
Ht14	3446	4.26	36.32	81.41	117.73	108.97	8.77	0.93	0.83
Ht15	3446	4.75	44.42	89.65	134.07	133.27	0.81	0.99	0.85
Htinc	3446	0.37	1.34	18.82	20.16	4.02	16.14	0.20	0.45
Flush	3026	0.04	0.25	0.66	0.91	0.76	0.15	0.83	0.81
Flush_bin	3446	0.00	0.05	0.20	0.24	0.14	0.10	0.57	0.73
SFlush	3446	0.00	0.01	0.22	0.23	0.03	0.20	0.13	0.34
FD	3446	13.07	35.43	921.46	956.89	106.28	850.61	0.11	0.30
FD_bin	3446	0.00	0.00	0.13	0.13	0.01	0.12	0.08	0.23
SD	3446	0.06	0.22	22.89	23.10	0.65	22.46	0.03	0.10
SD_bin	3446	0.00	0.00	0.04	0.04	0.00	0.04	0.02	0.06
LD	3446	0.00	0.00	0.04	0.04	0.00	0.04	0.06	0.19
LD_bin	3446	0.00	0.00	0.03	0.03	0.00	0.03	0.06	0.19
Mort	3446	0.00	0.00	0.10	0.11	0.01	0.09	0.12	0.31
Mort_F	3446	0.00	0.00	0.09	0.09	0.01	0.08	0.11	0.30
Mort_S	3449	0.00	0.00	0.10	0.11	0.01	0.09	0.13	0.34

Abbreviations: σ^2_b, σ^2_f, σ^2_{f*b} are variance components for block, family, and family*block interaction (i.e., the residual error). σ^2_P, σ^2_A, σ^2_e, h^2_i, and h^2_f are the phenotypic variance, additive genetic variance, error variance, individual tree heritability, and family heritability

Table 3.8. Quantitative genetic statistics for seedling traits of Douglas-fir analyzed across the Sprague and Lost Creek plantation.

		Variance components					Derived quantitative genetic statistics						GxE int	
Trait	**No. of obs**	σ^2_f	σ^2_s	σ^2_{f*s}	$\sigma^2_{b(s)}$	$\sigma^2_{f*b(s)}$	σ^2_P	σ^2_A	σ^2_e	h^2_i	h^2_f	**AGCV**	V_{GE}	r_g
Ht14	429	29.44	0.82	9.08	1.90	83.36	121.88	88.33	33.55	0.72	0.78	23.23	0.24	0.76
Ht15	429	33.33	1.11	9.93	2.23	95.73	138.99	99.99	39.00	0.72	0.79	20.08	0.23	0.77
Htinc	429	0.59	0.00	0.47	0.84	20.65	21.71	1.78	19.93	0.08	0.34	14.27	0.44	0.56
Flush	429	0.14	0.52	0.02	0.04	0.49	0.64	0.41	0.23	0.64	0.82	32.28	0.12	0.88
Flush_bin	429	0.01	0.11	0.01	0.00	0.12	0.14	0.04	0.10	0.27	0.54	89.88	0.47	0.53
SFlush	429	0.00	0.05	0.00	0.01	0.11	0.11	0.00	0.11	0.02	0.09	30.19	0.86	0.14
FD	429	11.99	218.59	22.28	45.65	1508.91	1543.18	35.98	1507.20	0.02	0.14	22.25	0.65	0.35
FD_bin	429	0.00	0.06	0.00	0.01	0.19	0.19	0.00	0.19	0.00	0.00	0.00	1.00	0.00
SD	429	0.19	0.05	0.00	0.38	19.12	19.31	0.56	18.74	0.03	0.19	68.16	0.00	1.00
SD_bin	429	0.00	0.00	0.00	0.00	0.07	0.07	0.00	0.07	0.02	0.16	49.54	0.00	1.00
LD	429	0.00	0.01	0.00	0.00	0.14	0.14	0.01	0.14	0.04	0.21	44.81	0.40	0.60
LD_bin	429	0.00	0.01	0.00	0.00	0.10	0.11	0.01	0.10	0.05	0.26	48.99	0.37	0.63
Mort	429	0.00	0.02	0.00	0.00	0.17	0.17	0.00	0.17	0.03	0.15	27.18	0.64	0.36
Mort_F	429	0.00	0.01	0.00	0.00	0.16	0.16	0.00	0.16	0.02	0.12	24.81	0.69	0.31
Mort_S	429	0.00	0.02	0.00	0.00	0.17	0.17	0.00	0.17	0.03	0.14	26.87	0.66	0.34

Abbreviations: σ^2_f, σ^2_s, σ^2_{f*s}, $\sigma^2_{b(s)}$, and $\sigma^2_{f*b(s)}$ are variance components for family, site, family*site interaction, block within site, and family*block within site interaction (i.e., the residual error). σ^2_P, σ^2_A, σ^2_e, h^2_i, and h^2_f are phenotypic variance, additive genetic variance, error variance, individual tree heritability, and family heritability. V_{GE} is the relative amounts of variation explained by the interactions of family x site calculated as $V_{GE} = \sigma^2_{f*s} / (\sigma^2_{f*s} + \sigma^2_f)$. AGCV is the additive genetic coefficient variation calculated as AGCV= sqrt(σ^2_A)/mean *100. r_g is the estimated the Type B genetic correlation of the same trait measured in different trees of the same family on Sprague and Lost Creek sites.

Table 3.9. Correlations among breeding values for Douglas-fir seedling traits measured at Sprague. Pearson correlations are below the diagonal and p-values are above the diagonal.

	Ht14	Ht15	Htinc	Flush	Flush_bin	SFlush	FD	FD_bin	SD	SD_bin	LD	LD_bin	Mort	Mort_F	Mort_S
Ht14		0.00	0.21	0.01	0.02	0.00	0.21	0.01	0.1	0.02	0.00	0.00	0.02	0.01	0.02
Ht15	0.97		0.00	0.00	0.00	0.00	0.57	0.00	0.09	0.03	0.00	0.00	0.08	0.05	0.08
Htinc	0.06	0.28		0.00	0.00	0.34	0.00	0.00	0.65	0.81	0.00	0.00	0.03	0.04	0.03
Flush	-0.13	-0.20	-0.31		0.00	0.00	0.00	0.39	0.41	0.94	0.00	0.00	0.00	0.00	0.00
Flush_bin	-0.11	-0.17	-0.29	0.86		0.00	0.00	0.06	0.33	0.95	0.00	0.00	0;00	0.00	0.00
SFlush	-0.18	-0.18	-0.05	0.29	0.25		0.00	0.08	0.4	0.28	0.00	0.00	0.00	0.00	0.00
FD	0.06	0.03	-0.14	-0.16	-0.23	-0.19		0.00	0.45	0.95	0.31	0.07	0.00	0.00	0.00
FD_bin	-0.13	-0.17	-0.19	-0.04	-0.09	-0.08	0.74		0.30	0.79	0.00	0.06	0.00	0.00	0.00
SD	0.08	0.08	0.02	-0.04	-0.05	-0.04	0.04	0.05		0.00	0.57	0.27	0.37	0.66	0.37
SD_bin	0.11	0.11	-0.01	0.00	0.00	-0.05	0.00	0.01	0.90		0.81	0.54	0.83	0.92	0.83
LD	-0.21	-0.26	-0.23	0.41	0.40	0.26	-0.05	0.14	-0.03	-0.01		0.00	0.02	0.01	0.02
LD_bin	-0.25	-0.3	-0.27	0.45	0.42	0.29	-0.09	0.09	-0.05	-0.03	0.96		0.00	0.00	0.00
Mort	0.11	0.09	-0.10	-0.18	-0.25	-0.20	0.96	0.62	0.04	0.01	-0.11	-0.14		0.00	0.00
Mort_F	0.12	0.09	-0.10	-0.19	-0.25	-0.20	0.96	0.60	0.02	0.00	-0.13	-0.15	0.95		0.00
Mort_S	0.11	0.09	-0.10	-0.18	-0.25	-0.20	0.96	0.62	0.04	0.01	-0.11	-0.14	1.00	0.95	

Abbreviations: Ht14 (cm) is the height of the seedlings in 2014, which corresponds to the growth of the seedlings in the greenhouse. Ht15 is the height of the seedlings in 2015 at the end of the first growing season. Htinc is the difference between Ht14 and Ht15. Flush is the bud flush score in the spring of 2016; Flush_bin is the presence or absence of bud flush on March 2016; SFlush is the presence or absence of second flushing on September 2016; FD is the percentage of dead foliage; FD_bin is the presence or absence of dead foliage; SD is the percentage of sunscald damage on the stem; SD_bin is the presence or absence of sunscald damage on the stem; LD is a variable indicating whether the leader (tallest shoot) is damaged (2=dead, 1=damaged, 0=alive and not damages); LD_bin is the leader condition (1=damaged, 0=not damaged); Mort is mortality (1=dead, 0=alive); Mort_F is mortality in the fall of 2015; Mort_S is the mortality in the spring of 2016.

Table 3.10. Correlations among breeding values for Douglas-fir seedling traits measured at Lost Creek. Pearson correlations are below the diagonal and p-values are above the diagonal.

	Ht14	Ht15	Htinc	Flush	Flush_bin	SFlush	FD	FD_bin	SD	SD_bin	LD	LD_bin	Mort	Mort_F	Mort_S
Ht14		0.00	0.00	0.00	0.03	0.00	0.40	0.29	0.00	0.00	0.81	0.99	0.24	0.17	0.22
Ht15	0.97		0.00	0.00	0.28	0.00	0.00	0.26	0.00	0.00	0.80	0.99	0.00	0.00	0.00
Htinc	0.23	0.45		0.48	0.00	0.00	0.00	0.00	0.06	0.07	0.95	0.99	0.00	0.00	0.00
Flush	-0.20	-0.17	0.04		0.00	0.42	0.76	0.45	0.01	0.01	0.00	0.00	0.69	0.82	0.70
Flush_bin	-0.12	-0.06	0.19	0.90		0.09	0.00	0.00	0.05	0.02	0.00	0.00	0.00	0.00	0.00
SFlush	0.34	0.41	0.42	0.05	0.10		0.00	0.00	0.60	0.90	0.48	0.33	0.00	0.00	0.00
FD	-0.05	-0.20	-0.59	-0.02	-0.28	-0.28		0.00	0.67	0.81	1.00	0.54	0.00	0.00	0.00
FD_bin	0.06	-0.07	-0.48	-0.04	-0.27	-0.23	0.91		0.48	0.34	0.28	0.80	0.00	0.00	0.00
SD	0.21	0.21	0.11	-0.14	-0.12	0.03	-0.03	0.04		0.00	0.58	0.36	0.81	0.45	0.79
SD_bin	0.19	0.20	0.11	-0.16	-0.14	-0.01	-0.01	0.06	0.81		0.61	0.38	0.91	0.49	0.93
LD	0.01	0.01	0.00	0.25	0.22	0.04	0.00	0.06	-0.03	-0.03		0.00	0.42	0.30	0.49
LD_bin	0.00	0.00	0.00	0.28	0.25	0.06	-0.04	0.02	-0.05	-0.05	0.98		0.21	0.20	0.23
Mort	-0.07	-0.21	-0.57	-0.02	-0.30	-0.29	0.94	0.81	-0.01	0.01	-0.05	-0.07		0.00	0.00
Mort_F	-0.08	-0.23	-0.60	-0.01	-0.28	-0.27	0.98	0.84	-0.04	-0.04	-0.06	-0.07	0.93		0.00
Mort_S	-0.07	-0.21	-0.57	-0.02	-0.30	-0.29	0.94	0.82	-0.02	0.01	-0.04	-0.07	1.00	0.93	

Abbreviations: Ht14 (cm) is the height of the seedlings in 2014, which corresponds to the growth of the seedlings in the greenhouse. Ht15 is the height of the seedlings in 2015 at the end of the first growing season. Htinc is the difference between Ht14 and Ht15. Flush is the bud flush score in the spring of 2016; Flush_bin is the presence or absence of bud flush on March 2016; SFlush is the presence or absence of second flushing on September 2016; FD is the percentage of dead foliage; FD_bin is the presence or absence of dead foliage; SD is the percentage of sunscald damage on the stem; SD_bin is the presence or absence of sunscald damage on the stem; LD is a variable indicating whether the leader (tallest shoot) is damaged (2=dead, 1=damaged, 0=alive and not damages); LD_bin is the leader condition (1=damaged, 0=not damaged); Mort is mortality (1=dead, 0=alive); Mort_F is mortality in the fall of 2015; Mort_S is the mortality in the spring of 2016.

Table 3.11. Correlations among breeding values for Douglas-fir seedling traits measured across both plantations. Pearson correlations are below the diagonal and p-values are above the diagonal.

	Ht14	Ht15	Htinc	Flush	Flush_bin	SFlush	FD	FD_bin	SD	SD_bin	LD	LD_bin	Mort	Mort_F	Mort_S
Ht14		0.00	0.00	0.00	0.00	0.00	0.42		0.00	0.00	0.00	0.00	0.10	0.08	0.10
Ht15	0.98		0.00	0.00	0.00	0.00	0.64		0.00	0.00	0.00	0.00	0.70	0.59	0.71
Htinc	0.18	0.40		0.00	0.07	0.00	0.00		0.09	0.09	0.00	0.00	0.00	0.00	0.00
Flush	-0.17		-0.19		0.00	0.00	0.00		0.04	0.25	0.00	0.00	0.00	0.00	0.00
Flush_bin	-0.14		-0.09	0.92		0.00	0.00		0.05	0.26	0.00	0.00	0.00	0.00	0.00
SFlush	0.16	0.20	0.20	0.18	0.20		0.00		0.89	0.97	0.00	0.00	0.00	0.00	0.00
FD	0.04		-0.29	-0.15	-0.29	-0.15			0.31	0.60	0.15	0.04	0.00	0.00	0.00
FD_bin															
SD	0.15	0.20	0.08	-0.10	-0.10	-0.01	0.05			0.00	0.99	0.41	0.20	0.52	0.18
SD_bin	0.16	0.20	0.08	-0.06	-0.05	0.00	-0.03		0.85		0.94	0.56	0.97	0.56	0.98
LD	-0.18		-0.17	0.45	0.45	0.15	-0.07		0.00	0.00		0.00	0.01	0.01	0.01
LD_bin	-0.21		-0.22	0.49	0.47	0.14	-0.10		-0.04	-0.03	0.97		0.00	0.00	0.00
Mort	0.08	0.02	-0.28	-0.18	-0.31	-0.15	0.96		0.06	0.00	-0.12	-0.15		0.00	0.00
Mort_F	0.09	0.03	-0.27	-0.19	-0.32	-0.14	0.96		0.03	-0.03	-0.13	-0.15	0.95		0.00
Mort_S	0.08	0.02	-0.28	-0.17	-0.31	-0.15	0.96		0.07	0.00	-0.12	-0.15	1.00	0.95	

Abbreviations: Ht14 (cm) is the height of the seedlings in 2014, which corresponds to the growth of the seedlings in the greenhouse. Ht15 is the height of the seedlings in 2015 at the end of the first growing season. Htinc is the difference between Ht14 and Ht15. Flush is the bud flush score in the spring of 2016; Flush_bin is the presence or absence of bud flush on March 2016; SFlush is the presence or absence of second flushing on September 2016; FD is the percentage of dead foliage; FD_bin is the presence or absence of dead foliage; SD is the percentage of sunscald damage on the stem; SD_bin is the presence or absence of sunscald damage on the stem; LD is a variable indicating whether the leader (tallest shoot) is damaged (2=dead, 1=damaged, 0=alive and not damages); LD_bin is the leader condition (1=damaged, 0=not damaged); Mort is mortality (1=dead, 0=alive); Mort_F is mortality in the fall of 2015; Mort_S is the mortality in the spring of 2016.

Table 3.12. Statistics for geographic and climate variables of families across plantations associated with the origin of the female parents of Douglas-fir families. Variables were derived from ClimateNA (Wang et al. 2012).

	Variable	N	Mean	Median	StdDev	Min	Max	Range
Geography								
	LAT	408	43.26	43	1.2	42	49	7
	LONG	408	-123.27	-123	0.6	-124	-122	3
	ELEV	408	2139.45	2110	1015.1	200	4500	4300
Climate variables								
	MAT	408	6.89	8	3.433	-5	12	17
	MWMT	408	15.17	16	3.131	6	20	15
	MCMT	408	1.29	2	3.467	-12	7	19
	TD	408	13.89	14	2.786	6	21	16
	MAP	408	2160.50	1932	990.673	565	6325	5760
	MSP	408	297.47	266	135.393	96	933	837
	AHM	408	9.24	9	4.188	2	31	28
	SHM	408	61.12	56	29.37	9	184	175
	DD_0	408	343.49	190	393.064	44	2350	2306
	DD5	408	1484.73	1510	609.365	152	2662	2510
	DD_18	408	4102.80	3836	1204.046	2348	8297	5949
	DD18	408	69.43	50	62.011	0	258	258
	NFFD	408	252.88	264	52.495	61	341	280
	FFP	408	176.61	177	42.181	58	300	242
	bFFP	408	136.16	139	29.346	45	197	152
	eFFP	408	312.76	315	19.081	234	351	117
	PAS	408	448.95	255	500.862	31	3009	2978
	EMT	408	-19.78	-19	5.982	-42	-6	36
	EXT	408	32.24	34	4.932	15	40	25
	Eref	408	568.13	627	250.687	20	995	975
	CMD	408	204.50	201	128.205	0	727	727
	MAR	408	15.40	15	2.582	11	29	18
	RH	408	77.40	76	10.164	46	100	54

Abbreviations: LAT=latitude; LONG=longitude; ELEV=elevation (ft.); MAT= mean annual temperature (°C); MWMT= mean warmest month temperature (°C); MCMT= mean coldest month temperature (°C); TD= temperature difference between MWMT and MCMT (°C); MAP=mean annual precipitation (mm); MSP= May to September precipitation (mm); AHM= annual heat-moisture index (MAT+10)/(MAP/1000); SHM= summer heat-moisture index ((MWMT)/(MSP/1000); DD_0= degree-days below 0°C (DD < 0); DD5= degree-days above 5°C (DD > 5); DD_18= degree-days below 18°C (DD < 8); DD_18= degree-days above 18°C (DD > 18); NFFD= number of frost-free days; bFFP= beginning of FFP; eFFP= ending date of FFP; FFP= frost-free period; PAS= proportion of precipitation as snow; EMT= estimated extreme minimum temperature over a 30-yr normal period; EXT= extreme maximum temperature over 30 years; Eref= reference atmospheric evaporative demand; CMD= climatic moisture deficit; MAR= mean annual solar radiation (MJ m^{-2} d^{-1}); RH= mean annual relative humidity (%).

Table 3.13. Correlations between breeding values and parental climate variables for the Sprague plantation. Variables were derived from ClimateNA (Wang et al. 2012). The shaded areas indicate where correlations are higher (e.g., $|r| \geq 0.20$) and statistically significant.

	Ht14	Ht15	Htinc	Flush	Flush_bin	SFlush	FD	FD_bin	SD	SD_bin	LD	LD_bin	Mort	Mort_F	Mort_S
MAT	0.41	0.40	0.06	0.10	0.09	0.06	0.07	-0.03	0.02	0.07	0.02	-0.01	0.09	0.11	0.09
MWMT	0.36	0.37	0.10	0.05	0.03	0.06	0.05	-0.06	0.00	0.05	0.01	-0.01	0.08	0.09	0.08
MCMT	0.27	0.24	-0.05	0.25	0.22	0.10	0.06	0.01	0.08	0.12	0.06	0.04	0.06	0.08	0.06
TD	0.08	0.12	0.18	-0.25	-0.24	-0.06	-0.01	-0.08	-0.10	-0.10	-0.06	-0.06	0.01	0.00	0.01
MAP	0.01	0.02	0.03	-0.15	-0.14	-0.03	0.10	0.03	-0.06	-0.05	-0.12	-0.14	0.12	0.12	0.12
MSP	0.03	0.06	0.12	-0.25	-0.19	-0.04	0.05	-0.02	-0.14	-0.13	-0.13	-0.14	0.07	0.07	0.07
AHM	0.17	0.16	0.02	0.21	0.20	0.13	-0.10	-0.03	0.03	0.04	0.11	0.12	-0.10	-0.11	-0.10
SHM	0.16	0.14	-0.03	0.23	0.18	0.09	-0.06	0.00	0.07	0.11	0.09	0.10	-0.06	-0.06	-0.06
DD_0	-0.31	-0.30	-0.01	-0.17	-0.15	-0.11	-0.06	0.01	-0.02	-0.07	-0.05	-0.04	-0.07	-0.09	-0.07
DD5	0.43	0.43	0.08	0.04	0.03	0.02	0.07	-0.05	0.01	0.06	-0.01	-0.04	0.10	0.11	0.10
DD_18	-0.41	-0.4	-0.06	-0.10	-0.09	-0.07	-0.07	0.03	-0.02	-0.07	-0.02	0.01	-0.09	-0.11	-0.09
DD18	0.38	0.38	0.06	0.01	-0.03	-0.03	0.08	-0.04	-0.02	0.03	-0.02	-0.04	0.11	0.12	0.11
NFFD	0.35	0.32	-0.03	0.17	0.14	0.07	0.12	0.02	0.06	0.12	0.02	-0.01	0.13	0.15	0.13
bFFP	-0.26	-0.24	0.01	-0.02	-0.06	0.02	-0.14	-0.07	0.06	0.00	0.02	0.04	-0.13	-0.15	-0.13
eFFP	0.14	0.10	-0.14	0.28	0.21	0.08	0.12	0.06	0.11	0.16	0.06	0.06	0.13	0.13	0.13
FFP	0.25	0.21	-0.07	0.14	0.14	0.03	0.16	0.08	0.01	0.07	0.01	0.00	0.15	0.17	0.15
PAS	-0.32	-0.31	-0.03	-0.14	-0.15	-0.08	-0.03	0.02	-0.03	-0.07	-0.06	-0.04	-0.03	-0.05	-0.03
EMT	0.24	0.21	-0.07	0.26	0.22	0.11	0.07	0.02	0.11	0.16	0.04	0.02	0.07	0.09	0.07
EXT	0.38	0.41	0.16	-0.02	-0.02	0.03	0.01	-0.09	-0.02	0.01	-0.01	-0.04	0.04	0.05	0.04
Eref	0.42	0.44	0.16	-0.02	-0.02	0.02	0.02	-0.07	-0.02	0.01	-0.02	-0.05	0.05	0.05	0.05
CMD	0.33	0.34	0.11	0.10	0.06	0.05	-0.06	-0.06	0.03	0.06	0.03	0.02	-0.04	-0.04	-0.04
MAR	-0.27	-0.26	-0.03	0.07	0.02	0.01	-0.09	0.03	0.10	0.05	-0.01	0.00	-0.11	-0.11	-0.11
RH	-0.32	-0.36	-0.21	0.14	0.09	0.03	0.05	0.11	0.07	0.06	0.04	0.06	0.03	0.03	0.03

Abbreviations: Climate variables are described in Table 2.1. Drought adaptation traits are described in Table 2.2.

Table 3.14. Correlations between breeding values and parental climate variables for the Lost Creek plantation. Variables were derived form ClimateNA (Wang et al. 2012). The shaded areas indicate where correlations are higher (e.g., $|r| \geq 0.20$) and statistically significant.

	Ht14	Ht15	Htinc	Flush	Flush_bin	SFlush	FD	FD_bin	SD	SD_bin	LD	LD_bin	Mort	Mort_F	Mort_S
MAT	0.44	0.44	0.13	0.07	0.06	0.32	0.01	0.06	0.12	0.11	0.02	0.02	0.00	0.00	0.00
MWMT	0.39	0.39	0.14	0.07	0.07	0.28	-0.04	0.01	0.09	0.09	-0.01	-0.02	-0.04	-0.04	-0.04
MCMT	0.29	0.27	0.05	0.22	0.18	0.24	0.03	0.07	0.05	0.01	0.07	0.07	0.04	0.03	0.04
TD	0.05	0.07	0.10	-0.22	-0.17	-0.01	-0.09	-0.09	0.04	0.09	-0.10	-0.13	-0.10	-0.10	-0.10
MAP	0.04	0.04	0.02	-0.21	-0.18	0.14	0.00	-0.03	0.06	0.08	0.03	0.02	-0.02	0.00	-0.01
MSP	0.10	0.10	0.03	-0.32	-0.26	0.09	-0.02	-0.03	0.05	0.08	-0.06	-0.06	-0.04	-0.02	-0.03
AHM	0.13	0.13	0.05	0.30	0.27	0.04	-0.01	0.05	-0.01	-0.05	0.01	0.02	0.00	-0.02	-0.01
SHM	0.10	0.10	0.03	0.31	0.27	0.08	0.02	0.04	-0.02	-0.05	0.04	0.03	0.03	0.01	0.03
DD_0	-0.36	-0.35	-0.11	-0.14	-0.12	-0.30	-0.03	-0.08	-0.09	-0.04	-0.03	-0.03	-0.02	-0.03	-0.02
DD5	0.45	0.45	0.13	0.01	0.02	0.30	-0.01	0.04	0.12	0.14	0.01	0.00	-0.01	-0.02	-0.01
DD_18	-0.44	-0.44	-0.13	-0.07	-0.07	-0.32	-0.01	-0.06	-0.12	-0.10	-0.02	-0.02	0.00	0.00	0.00
DD18	0.36	0.35	0.08	-0.01	0.00	0.22	0.00	0.03	0.08	0.11	-0.01	-0.02	0.01	-0.01	0.01
NFFD	0.40	0.38	0.07	0.12	0.10	0.28	0.04	0.09	0.12	0.10	0.07	0.06	0.04	0.03	0.04
bFFP	-0.27	-0.25	-0.04	0.08	0.09	-0.15	-0.05	-0.08	-0.11	-0.14	-0.07	-0.05	-0.06	-0.04	-0.06
eFFP	0.15	0.13	0.01	0.29	0.26	0.17	0.01	0.02	0.05	0.00	0.10	0.11	0.02	0.01	0.02
FFP	0.27	0.25	0.04	0.07	0.05	0.19	0.04	0.07	0.11	0.10	0.09	0.08	0.06	0.03	0.05
PAS	-0.35	-0.35	-0.10	-0.15	-0.12	-0.22	-0.01	-0.06	-0.08	-0.05	0.02	0.01	-0.01	-0.02	-0.01
EMT	0.27	0.26	0.03	0.23	0.20	0.24	0.03	0.07	0.06	0.01	0.08	0.09	0.03	0.03	0.03
EXT	0.45	0.45	0.17	-0.02	0.01	0.30	-0.06	0.01	0.12	0.13	-0.03	-0.03	-0.07	-0.06	-0.07
Eref	0.47	0.47	0.16	-0.04	-0.01	0.31	-0.02	0.04	0.12	0.13	-0.03	-0.03	-0.03	-0.02	-0.03
CMD	0.32	0.32	0.10	0.16	0.16	0.21	0.00	0.04	0.05	0.05	0.01	0.00	-0.01	-0.01	0.00
MAR	-0.31	-0.31	-0.10	0.19	0.16	-0.19	-0.03	-0.08	-0.12	-0.10	0.01	0.01	0.00	-0.03	0.00
RH	-0.39	-0.40	-0.18	0.16	0.11	-0.23	0.06	0.00	-0.08	-0.12	0.08	0.09	0.06	0.05	0.06

Abbreviations: Climate variables are described in Table 2.1. Drought adaptation traits are described in Table 2.2.

Table 3.15. Correlations between breeding values and parental climate variables across the Lost Creek and Sprague plantations. Variables were derived form ClimateNA (Wang et al. 2012). The shaded areas indicate where correlations are higher (e.g., $|r| \geq 0.20$) and statistically significant.

	Ht14	Ht15	Htinc	Flush	Flush_bin	SFlush	FD	FD_bin	SD	SD_bin	LD	LD_bin	Mort	Mort_F	Mort_S
MAT	0.42	0.45	0.11	0.07	0.06	0.27	0.01	0.02	0.08	0.05	0.01	0.01	0.01	0.02	0.01
MWMT	0.37	0.41	0.13	0.06	0.05	0.23	-0.02	-0.04	0.06	0.06	-0.03	-0.03	-0.03	-0.02	-0.03
MCMT	0.27	0.29	0.02	0.21	0.17	0.21	0.03	0.05	0.05	0.03	0.07	0.08	0.03	0.04	0.03
TD	0.08	0.10	0.11	-0.20	-0.16	0.00	-0.06	-0.10	0.01	0.02	-0.13	-0.14	-0.07	-0.07	-0.07
MAP	0.02	0.05	0.04	-0.20	-0.17	0.12	-0.01	-0.04	0.03	0.03	-0.07	-0.08	-0.02	0.00	-0.02
MSP	0.05	0.10	0.07	-0.29	-0.24	0.07	-0.02	-0.04	0.02	0.01	-0.10	-0.11	-0.04	-0.02	-0.04
AHM	0.17	0.13	0.04	0.26	0.23	0.05	-0.01	0.04	-0.01	-0.03	0.08	0.09	-0.01	-0.01	-0.01
SHM	0.16	0.10	0.00	0.27	0.22	0.07	0.01	0.03	0.00	0.00	0.08	0.09	0.02	0.02	0.02
DD_0	-0.33	-0.37	-0.08	-0.14	-0.12	-0.27	-0.02	-0.05	-0.07	-0.03	-0.03	-0.04	-0.01	-0.04	-0.01
DD5	0.45	0.47	0.12	0.01	0.01	0.25	0.00	0.00	0.08	0.06	-0.02	-0.02	0.00	0.01	0.00
DD_18	-0.42	-0.45	-0.11	-0.07	-0.06	-0.27	-0.01	-0.02	-0.08	-0.05	-0.01	-0.01	-0.01	-0.02	0.00
DD18	0.39	0.39	0.08	-0.01	-0.01	0.19	0.01	0.00	0.04	0.04	-0.05	-0.05	0.02	0.02	0.02
NFFD	0.36	0.37	0.05	0.11	0.09	0.24	0.05	0.07	0.09	0.07	0.03	0.03	0.06	0.06	0.05
bFFP	-0.27	-0.26	-0.04	0.06	0.07	-0.14	-0.07	-0.07	-0.07	-0.07	0.00	0.01	-0.08	-0.07	-0.08
eFFP	0.14	0.12	-0.01	0.26	0.23	0.14	0.03	0.02	0.05	0.03	0.06	0.07	0.05	0.04	0.05
FFP	0.26	0.24	0.02	0.07	0.06	0.16	0.06	0.06	0.07	0.06	0.03	0.02	0.08	0.06	0.08
PAS	-0.33	-0.36	-0.07	-0.14	-0.12	-0.18	-0.01	-0.04	-0.06	-0.03	-0.03	-0.04	-0.01	-0.03	-0.01
EMT	0.25	0.24	0.01	0.21	0.18	0.20	0.03	0.06	0.05	0.03	0.07	0.07	0.04	0.04	0.04
EXT	0.39	0.45	0.15	-0.02	0.00	0.24	-0.05	-0.03	0.07	0.04	-0.03	-0.03	-0.06	-0.04	-0.06
Eref	0.43	0.48	0.15	-0.03	-0.02	0.25	-0.02	-0.01	0.07	0.04	-0.02	-0.03	-0.03	0.00	-0.03
CMD	0.34	0.33	0.09	0.13	0.13	0.18	-0.01	0.01	0.02	0.01	0.02	0.02	-0.02	0.00	-0.02
MAR	-0.29	-0.32	-0.08	0.15	0.12	-0.15	-0.04	-0.04	-0.07	-0.01	-0.03	-0.03	-0.03	-0.05	-0.03
RH	-0.34	-0.40	-0.16	0.12	0.10	-0.17	0.05	0.05	-0.03	-0.01	0.05	0.06	0.06	0.04	0.06

Abbreviations: Climate variables are described in Table 2.1. Drought adaptation traits are described in Table 2.2.

Table 3.16. Correlations between family means for Sprague plantation and parental geographic and climate variables. Variables were derived from ClimateNA (Wang et al. 2012). The shaded areas indicate where correlations are higher (e.g., $|r| \geq 0.20$) and statistically significant.

	Ht14	Ht15	Htinc	Flush	Flush_bin	SFlush	FD	FD_bin	SD	SD_bin	LD	LD_bin	Mort	Mort_F	Mort_S
MAT	0.41	0.40	0.06	0.10	0.09	0.06	0.07	-0.03	0.02	0.07	0.02	-0.01	0.09	0.11	0.09
MWMT	0.36	0.37	0.10	0.05	0.03	0.06	0.05	-0.06	0.00	0.05	0.01	-0.01	0.08	0.09	0.08
MCMT	0.27	0.24	-0.05	0.25	0.22	0.10	0.06	0.01	0.08	0.12	0.06	0.04	0.06	0.08	0.06
TD	0.08	0.12	0.18	-0.25	-0.24	-0.06	-0.01	-0.08	-0.10	-0.10	-0.06	-0.06	0.01	0.00	0.01
MAP	0.01	0.02	0.03	-0.15	-0.14	-0.03	0.10	0.03	-0.06	-0.05	-0.12	-0.14	0.12	0.12	0.12
MSP	0.03	0.06	0.12	-0.25	-0.19	-0.04	0.05	-0.02	-0.14	-0.13	-0.13	-0.14	0.07	0.07	0.07
AHM	0.17	0.16	0.02	0.21	0.20	0.13	-0.10	-0.03	0.03	0.04	0.11	0.12	-0.10	-0.11	-0.10
SHM	0.16	0.14	-0.03	0.23	0.18	0.09	-0.06	0.00	0.07	0.11	0.09	0.10	-0.06	-0.06	-0.06
DD_0	-0.31	-0.30	-0.01	-0.17	-0.15	-0.11	-0.06	0.01	-0.02	-0.07	-0.05	-0.04	-0.07	-0.09	-0.07
DD5	0.43	0.43	0.08	0.04	0.03	0.02	0.07	-0.05	0.01	0.06	-0.01	-0.04	0.10	0.11	0.10
DD_18	-0.41	-0.4	-0.06	-0.10	-0.09	-0.07	-0.07	0.03	-0.02	-0.07	-0.02	0.01	-0.09	-0.11	-0.09
DD18	0.38	0.38	0.06	0.01	-0.03	-0.03	0.08	-0.04	-0.02	0.03	-0.02	-0.04	0.11	0.12	0.11
NFFD	0.35	0.32	-0.03	0.17	0.14	0.07	0.12	0.02	0.06	0.12	0.02	-0.01	0.13	0.15	0.13
bFFP	-0.26	-0.24	0.01	-0.02	-0.06	0.02	-0.14	-0.07	0.06	0.00	0.02	0.04	-0.13	-0.15	-0.13
eFFP	0.14	0.10	-0.14	0.28	0.21	0.08	0.12	0.06	0.11	0.16	0.06	0.06	0.13	0.13	0.13
FFP	0.25	0.21	-0.07	0.14	0.14	0.03	0.16	0.08	0.01	0.07	0.01	0.00	0.15	0.17	0.15
PAS	-0.32	-0.31	-0.03	-0.14	-0.15	-0.08	-0.03	0.02	-0.03	-0.07	-0.06	-0.04	-0.03	-0.05	-0.03
EMT	0.24	0.21	-0.07	0.26	0.22	0.11	0.07	0.02	0.11	0.16	0.04	0.02	0.07	0.09	0.07
EXT	0.38	0.41	0.16	-0.02	-0.02	0.03	0.01	-0.09	-0.02	0.01	-0.01	-0.04	0.04	0.05	0.04
Eref	0.42	0.44	0.16	-0.02	-0.02	0.02	0.02	-0.07	-0.02	0.01	-0.02	-0.05	0.05	0.05	0.05
CMD	0.33	0.34	0.11	0.10	0.06	0.05	-0.06	-0.06	0.03	0.06	0.03	0.02	-0.04	-0.04	-0.04
MAR	-0.27	-0.26	-0.03	0.07	0.02	0.01	-0.09	0.03	0.10	0.05	-0.01	0.00	-0.11	-0.11	-0.11
RH	-0.32	-0.36	-0.21	0.14	0.09	0.03	0.05	0.11	0.07	0.06	0.04	0.06	0.03	0.03	0.03

Abbreviations: Climate variables are described in Table 2.1. Drought adaptation traits are described in Table 2.2.

Table 3.17. Correlations between family means for the Lost Creek plantation and parental geographic and climate variables. Variables were derived from ClimateNA (Wang et al. 2012). The shaded areas indicate where correlations are higher (e.g., $|r| \geq 0.20$) and statistically significant.

	Ht14	Ht15	Htinc	Flush	Flush_bin	SFlush	FD	FD_bin	SD	SD_bin	LD	LD_bin	Mort	Mort_F	Mort_S
MAT	0.44	0.43	0.11	0.07	0.06	0.32	0.01	0.07	0.13	0.12	0.05	0.04	0.01	0.00	0.01
MWMT	0.39	0.38	0.13	0.08	0.06	0.28	-0.03	0.02	0.10	0.10	0.02	0.00	-0.03	-0.04	-0.03
MCMT	0.28	0.26	0.03	0.22	0.17	0.23	0.04	0.08	0.07	0.05	0.08	0.09	0.04	0.03	0.04
TD	0.06	0.08	0.11	-0.22	-0.17	0.01	-0.09	-0.09	0.01	0.05	-0.09	-0.12	-0.10	-0.09	-0.09
MAP	0.04	0.04	0.00	-0.21	-0.17	0.13	-0.01	-0.03	0.07	0.10	0.03	0.03	-0.02	0.00	-0.02
MSP	0.09	0.08	0.02	-0.31	-0.25	0.08	-0.03	-0.04	0.06	0.09	-0.05	-0.04	-0.04	-0.02	-0.04
AHM	0.13	0.13	0.06	0.30	0.26	0.05	-0.01	0.05	-0.01	-0.05	0.01	0.01	0.00	-0.02	0.00
SHM	0.11	0.11	0.04	0.31	0.25	0.08	0.02	0.04	-0.02	-0.04	0.04	0.03	0.03	0.00	0.03
DD_0	-0.36	-0.34	-0.10	-0.15	-0.11	-0.30	-0.03	-0.07	-0.10	-0.06	-0.05	-0.05	-0.02	-0.02	-0.02
DD5	0.45	0.44	0.11	0.02	0.02	0.30	0.00	0.05	0.12	0.15	0.05	0.03	0.00	-0.01	0.00
DD_18	-0.44	-0.43	-0.11	-0.08	-0.06	-0.32	-0.01	-0.07	-0.13	-0.12	-0.05	-0.05	-0.01	0.00	-0.01
DD18	0.36	0.35	0.06	-0.01	0.00	0.22	0.00	0.05	0.08	0.12	0.02	0.01	0.02	0.00	0.02
NFFD	0.39	0.36	0.03	0.12	0.10	0.26	0.05	0.10	0.13	0.12	0.09	0.09	0.05	0.04	0.05
bFFP	-0.27	-0.24	0.01	0.08	0.09	-0.13	-0.08	-0.11	-0.10	-0.13	-0.09	-0.07	-0.09	-0.06	-0.08
eFFP	0.14	0.12	-0.03	0.30	0.26	0.14	0.02	0.04	0.07	0.02	0.11	0.12	0.03	0.01	0.03
FFP	0.26	0.23	-0.02	0.07	0.06	0.16	0.07	0.10	0.10	0.11	0.12	0.10	0.08	0.05	0.07
PAS	-0.35	-0.34	-0.09	-0.15	-0.12	-0.22	-0.02	-0.07	-0.09	-0.06	0.00	-0.01	-0.02	-0.02	-0.02
EMT	0.27	0.24	0.00	0.23	0.19	0.22	0.04	0.08	0.08	0.04	0.10	0.11	0.04	0.03	0.04
EXT	0.45	0.45	0.17	-0.01	0.00	0.32	-0.05	0.01	0.12	0.14	0.00	-0.01	-0.06	-0.06	-0.05
Eref	0.47	0.47	0.16	-0.03	-0.02	0.33	-0.01	0.04	0.12	0.14	0.00	0.00	-0.02	-0.02	-0.02
CMD	0.33	0.33	0.12	0.17	0.15	0.23	0.00	0.04	0.05	0.05	0.03	0.02	0.00	-0.01	0.00
MAR	-0.31	-0.30	-0.08	0.18	0.15	-0.18	-0.03	-0.08	-0.12	-0.10	-0.01	-0.02	-0.01	-0.03	-0.01
RH	-0.39	-0.41	-0.20	0.15	0.12	-0.26	0.06	0.01	-0.08	-0.12	0.05	0.06	0.06	0.05	0.06

Abbreviations: Climate variables are described in Table 2.1. Drought adaptation traits are described in Table 2.2.

Table 3.18. Correlations between family means across the Sprague and Lost Creek plantations and parental geographic and climate variables. Variables were derived from ClimateNA (Wang et al. 2012). The shaded areas indicate where correlations are higher (e.g., $|r| \geq 0.20$) and statistically significant.

	Ht14	Ht15	Htinc	Flush	Flush_bin	SFlush	FD	FD_bin	SD	SD_bin	LD	LD_bin	Mort	Mort_F	Mort_S
MAT	0.45	0.44	0.08	0.19	0.18	0.26	0.00	-0.10	0.04	0.04	-0.02	-0.04	0.03	0.04	0.03
MWMT	0.40	0.41	0.13	0.16	0.15	0.26	-0.04	-0.14	0.01	0.01	-0.03	-0.05	0.00	0.01	0.00
MCMT	0.29	0.26	-0.03	0.28	0.26	0.19	0.03	-0.02	0.08	0.09	0.03	0.02	0.05	0.07	0.05
TD	0.09	0.14	0.18	-0.17	-0.15	0.05	-0.08	-0.14	-0.09	-0.10	-0.07	-0.07	-0.06	-0.07	-0.06
MAP	0.02	0.03	0.03	-0.12	-0.11	0.08	0.05	-0.02	-0.02	-0.01	-0.11	-0.12	0.06	0.07	0.06
MSP	0.05	0.08	0.11	-0.23	-0.17	0.05	0.00	-0.06	-0.09	-0.10	-0.11	-0.13	0.02	0.02	0.02
AHM	0.16	0.15	0.03	0.21	0.22	0.09	-0.08	0.00	0.00	0.00	0.08	0.09	-0.09	-0.09	-0.09
SHM	0.15	0.13	-0.01	0.24	0.20	0.09	-0.04	0.01	0.05	0.07	0.06	0.07	-0.05	-0.04	-0.05
DD_0	-0.35	-0.33	-0.05	-0.22	-0.20	-0.25	-0.01	0.05	-0.04	-0.04	-0.02	-0.01	-0.03	-0.04	-0.03
DD5	0.47	0.46	0.10	0.14	0.14	0.25	-0.01	-0.12	0.02	0.03	-0.05	-0.07	0.03	0.04	0.03
DD_18	-0.45	-0.43	-0.08	-0.19	-0.18	-0.27	0.00	0.09	-0.04	-0.04	0.02	0.04	-0.03	-0.04	-0.03
DD18	0.41	0.40	0.07	0.10	0.09	0.18	0.01	-0.11	-0.01	0.01	-0.06	-0.07	0.05	0.05	0.05
NFFD	0.38	0.35	-0.02	0.23	0.22	0.23	0.07	-0.03	0.09	0.10	-0.02	-0.04	0.09	0.11	0.09
bFFP	-0.28	-0.25	0.02	-0.06	-0.09	-0.13	-0.11	-0.03	0.02	0.00	0.05	0.07	-0.12	-0.13	-0.12
eFFP	0.15	0.10	-0.13	0.32	0.28	0.13	0.10	0.02	0.12	0.14	0.02	0.02	0.12	0.12	0.12
FFP	0.26	0.22	-0.07	0.18	0.19	0.15	0.12	0.03	0.04	0.06	-0.02	-0.04	0.14	0.14	0.14
PAS	-0.36	-0.34	-0.05	-0.20	-0.20	-0.20	0.01	0.04	-0.03	-0.03	-0.03	-0.01	-0.01	-0.02	-0.01
EMT	0.26	0.22	-0.05	0.30	0.27	0.19	0.05	-0.01	0.12	0.13	0.00	-0.01	0.06	0.08	0.06
EXT	0.43	0.45	0.18	0.09	0.10	0.26	-0.08	-0.16	-0.01	-0.02	-0.04	-0.07	-0.05	-0.04	-0.05
Eref	0.46	0.47	0.18	0.08	0.09	0.25	-0.06	-0.13	-0.01	-0.02	-0.05	-0.08	-0.03	-0.02	-0.03
CMD	0.35	0.36	0.12	0.17	0.16	0.20	-0.10	-0.09	0.01	0.01	0.00	-0.01	-0.08	-0.07	-0.08
MAR	-0.30	-0.29	-0.05	0.01	-0.03	-0.16	-0.04	0.07	0.05	0.05	0.01	0.02	-0.06	-0.07	-0.06
RH	-0.36	-0.40	-0.23	0.06	0.02	-0.17	0.12	0.15	0.07	0.09	0.05	0.07	0.10	0.09	0.10

Abbreviations: Climate variables are described in Table 2.1. Drought adaptation traits are described in Table 2.2.

Table 3.19. Results of variable selection procedures for predicting Flush, SFlush, and Htinc from climate variables.

Site	Trait	Forward	Backward	Stepwise	Lasso
Sprague	Flush	MSP eFFP FFP	MWMT TD NFFD EXT CMD	MSP eFFP FFP	
	$adjR^2$	0.122	0.181	0.122	0.00
	SFlush	eFFP	MWMT NFFD EMT RH	eFFP	eFFP
	$adjR^2$	0.033	0.058	0.033	0.016
	Htinc	TD	MAT NFFD eFFP EXT	TD	
	$adjR^2$	0.041	0.091	0.041	0.00
Lost Creek	Flush	MSP bFFP eFFP	MAT MCMT TD DD_0 EXT CMD	MSP bFFP eFFP	
	$adjR^2$	0.188	0.257	0.188	0.00
	SFlush	DD_18	eFFP RH	DD_18	DD_18 Eref
	$adjR^2$	0.114	0.110	0.114	0.101
	Htinc	RH	RH	RH	
	$adjR^2$	0.028	0.028	0.028	0.00

Abbreviations: Climate variables are described in Table 2.1. Drought adaptation traits are described in Table 2.2.

Table 3.20. Lasso regressions coefficients and model performance statistics for predicting Flush, SFlush, and Htinc in terms of climate variables.

		Estimate				Model performance	
Site	**Trait**	**Intercept**	**eFFP**	**DD_18**	**Eref**	**SBC**	**Adj-R^2**
Sprague	Flush	0.007	-	-	-	-924.1	0.000
Sprague	SFlush	-0.243	0.001	-	-	-3069.6	0.016
Sprague	Htinc	-0.010	-	-	-	-324.0	0.000
Lost Creek	Flush	0.015	-	-	-	-445.3	0.000
Lost Creek	SFlush	39.092	-	-0.010	0.004	-1584.8	0.101
Lost Creek	Htinc	-0.021	-	-	-	-136.4	0.000

Abbreviations: eFFP= ending date of FFP; DD_18= degree-days below 18°C (DD < 8); Eref = reference atmospheric evaporative; SBC is Schwarz Bayesian information criterion (a.k.a., BIC). Low values are preferred; Adj-R^2 is the coefficient of determination. Higher values are preferred (i.e., values are closer to 1).

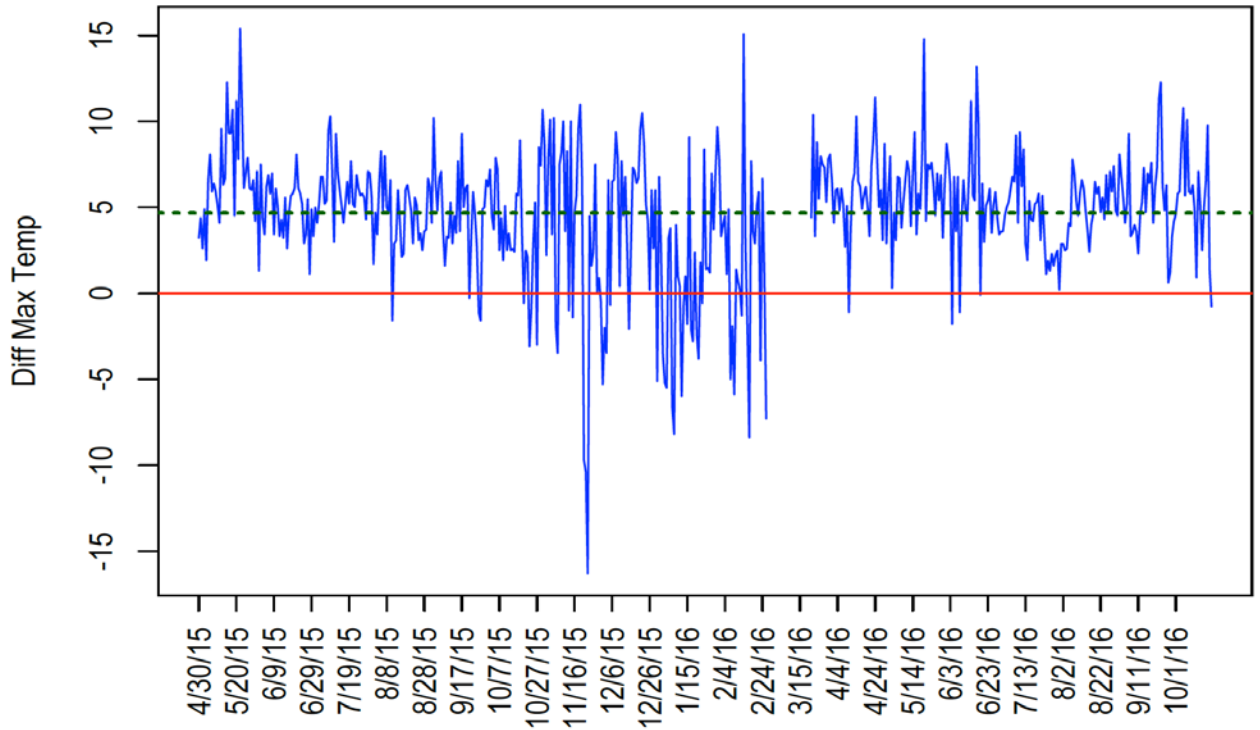


Figure 3.1. Difference between the maximum temperature at Sprague and Lost Creek from 4/30/2015 until 10/20/016.

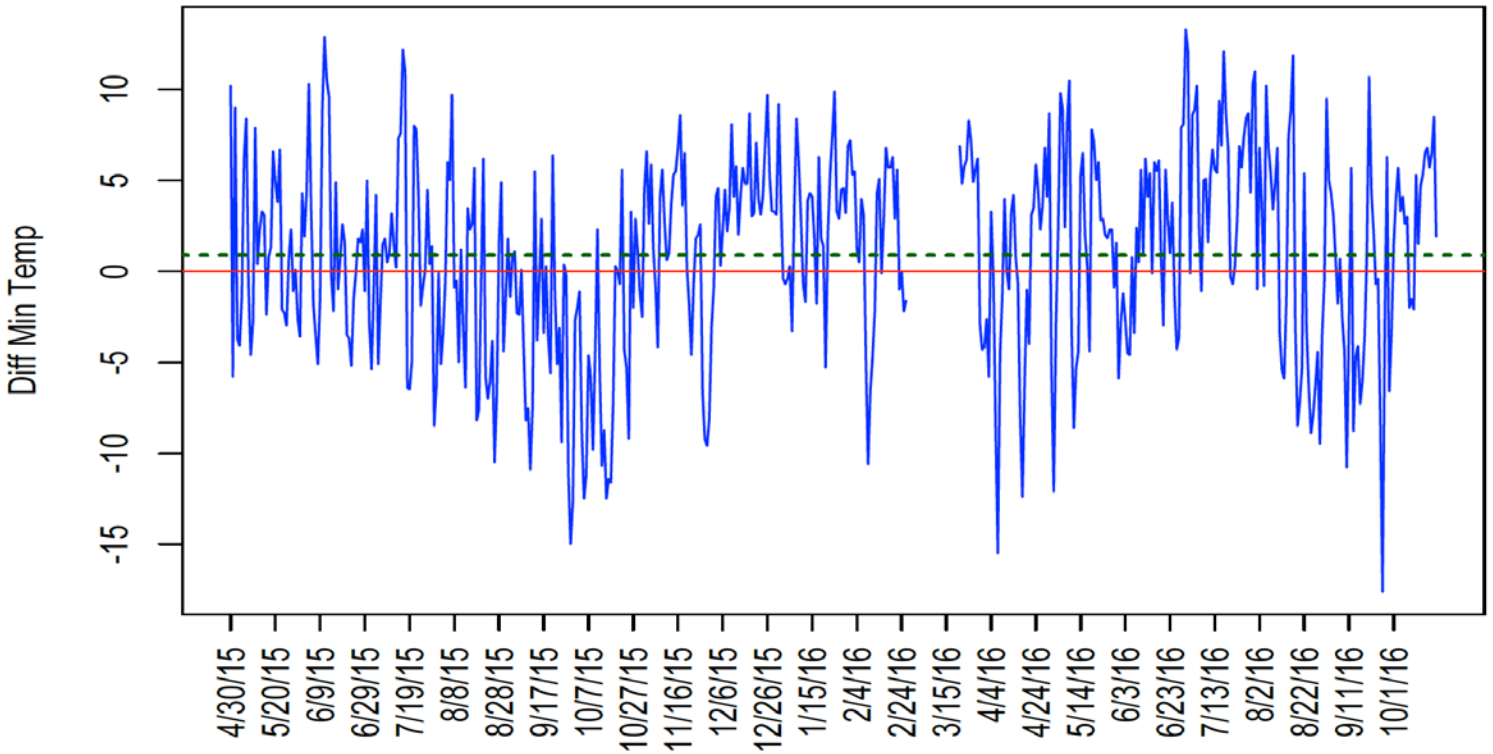


Figure 3.2. Difference between the minimum temperature at Sprague and Lost Creek from 4/30/2015 until 10/20/016.

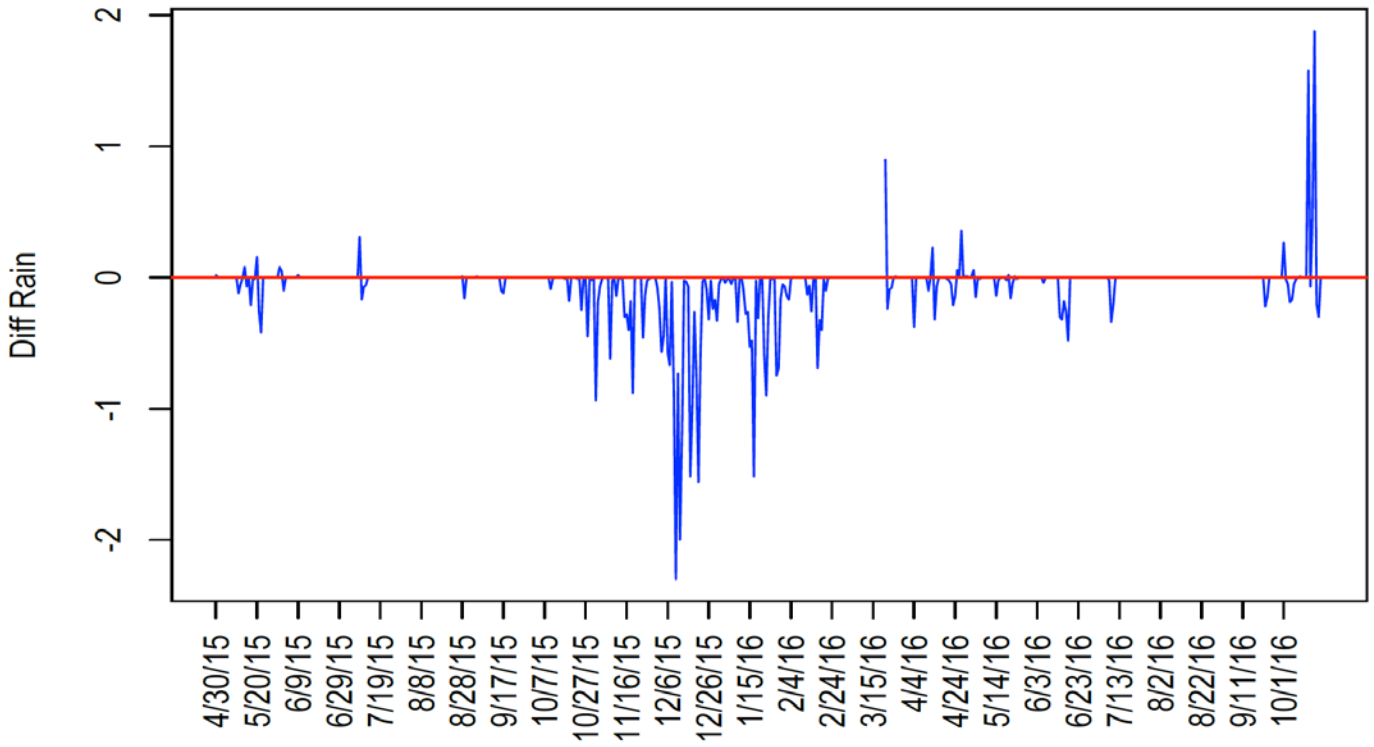


Figure 3.3. Difference between the amount rainfall at Sprague and Lost Creek from 4/30/2015 until 10/20/016.

4 Discussion

4.1 Obtain baseline measurements and climate data to help in the analysis and interpretation of future measurements in the Drought Hardiness Study

4.1.1 The Sprague site is typically hotter and drier than the Lost Creek site

The climate variables that were generated consisted of historical 30-year normals (1961-1990) from the ClimateNA software program (Wang et al. 2016). The ClimateNA software package can predict climate variables for a given location based on elevation and geographic coordinates (e.g., latitude and distance from the ocean). The ClimateNA data provide expectations for weather based on historical averages (e.g., at the planting sites), but not the actual weather when the seedlings were growing in the field. Historical climate data can be used to enhance understanding of the general patterns of plant adaptations in relation to their natural climates (Wang et al. 2016).

Whereas a climate refers to the long-term pattern of the average weather conditions in a place over a period of time (usually a period of 30 years or more), weather refers to the short-term conditions of the atmosphere over a period of hours or days (U.S. NOAA 2017). For short-term studies, weather station data can provide more useful and more reliable data for a location compared to climate data (e.g., ClimateNA). In this experiment, each site had a weather station that was installed for recording detailed weather data. These weather station data would be more relevant for understanding the

actual weather that the seedlings experienced during their first growing season. In the year of the study, weather station data show that the Sprague site was drier and slightly hotter compared to Lost Creek (Figures 3.1 and 3.2). Thus, the Sprague site was exposed to more droughty conditions. Based on the ClimateNA and weather station data collected in the year of the study (2015 to 2016), the Sprague site has been relatively hotter and drier than Lost Creek (890 m), probably due to the lower elevation of the Sprague site (325 m).

4.1.2 The trees at the Sprague site grew less, were more damaged, and had greater mortality than the trees at the Lost Creek site

Summer drought was a problem for Douglas-fir trees in southern Oregon in 2015 (U.S. Department of Agriculture 2016; Shaw 2015). The results obtained from ClimateNA models and weather station data indicate that Sprague should be a good screening site for drought adaptation because of the weather and climate conditions. Due to a relatively longer growing season with warmer temperatures, the stress conditions related to drought were present to greater extent at Sprague than at Lost Creek in the first growing season in the field. Thus, foliage damage and leader damage were greater and seedlings grew less at Sprague, where the conditions are hotter and drier compared to Lost Creek (Table 3.2).

Differences in climate and seedling growth at the two sites are clear looking at the summary statistics from the measures on individual trees. The mean height increment was slightly larger and second flushing was more frequent at Lost Creek compared to

Sprague, indicating that this experiment should be effective for screening families for drought adaptation (Htinc was 9.28 cm at Sprague versus 9.76 at Lost Creek).

I also found stem damage (sun scald) was greater at the Sprague site. However, I assume that most of this happened shortly after planting in the field because the trees had not experienced winter when sunscald damage was measured in the field. Furthermore, mortality probably occurred after seedling establishment due to the hotter and drier conditions at Sprague. Previous studies have shown that first year seedling mortality can be caused by "transplant shock" (Kellner and Swihart 2016). Differences in the growing conditions (i.e., from the greenhouse to the field) contribute to transplant shock (Vargas-Hernandez et al. 2002). In addition, first-year seedling mortality at Sprague might also have occurred from excessive pooling of water or poor weed control in localized spots.

4.1.3 Early height measurements will be helpful for the analysis and interpretation of later measurements

We saw large family differences in greenhouse growth (Ht14), but these do not reflect family differences in drought adaptation. That is, these differences do not reflect how these families will grow in the field, or respond to drought. These among-family differences could be diminished, maintained, or magnified in the field. Large family differences in Ht14 within the two sites probably resulted from a combination of genetic differences among families and large environmental differences in the greenhouse, including watering. In this study, Crawford (2015) argued the large family differences in

the greenhouse growth were primarily due to inconsistent watering in early spring. Large differences in height among families in the greenhouse may limit the ability to detect family growth differences in the field. However, the baseline measurements I took can be used for later analysis by future researchers.

Height in the field (Ht15) also largely reflects family differences in growth that occurred in the greenhouse. That is, the large family differences in greenhouse growth persisted in the field, leading to a high genetic correlation between Ht14 and Ht15 ($r = 0.97$). Thus, Ht15 cannot be used as a measure of how the seedlings are responding to field conditions. That is, the ability to detect family adaptation to drought may be limited in early seedling measurements. Thus, I focused on Htinc, the difference between height in the greenhouse and height in the field. Htinc is more relevant for understanding the genetics of field growth and drought adaptation. However, a positive genetic correlation between Ht14 and Htinc ($r = 0.23$) also indicates that Htinc partially reflects family differences that occurred in the greenhouse somewhat. That is, the large family differences in greenhouse growth may still obscure family performance in the field. For example, Clark (2009) found that distinguishing between greenhouse and field measurements was relevant to improve the accuracy of the measurements of first-year growth in oak species.

Some studies show that initial height is highly correlated with growth in conifers (Jacobs et al. 2005). Thus, either Ht14 or Ht15 can be used for later analysis by the future

researchers as an “initial height” to adjust later height measurements to understand drought adaptation in the field.

The strong relationships between Ht14, Ht15, and Htinc can be used to develop regression models that predict growth in the field. The values of greenhouse growth can also be used to obtain indirect measures of other potential variables of interest, such as diameter and stem weight, taking advantage of the correlations among these traits. Ht14 can also be used as a covariate for other traits that are phenotypically related to height growth to improve genetic analyses (Frank 2017b).

4.2 Characterize the quantitative genetics of drought adaptation traits

4.2.1 Heritability and genetic variance differed widely among traits

This objective will help answer the following question: In Douglas-fir, are drought adaptation traits heritable? I hypothesized that drought adaptation traits of Douglas-fir seedlings are partly determined by genetics, and this is supported by the results from this study. I estimated variance components and then calculated genetic, environmental, and phenotypic variances, as well as heritabilities. In the first growing season, the results show that the drought adaptation traits were genetically controlled, although estimated individual-tree heritabilities for drought adaptation traits were generally low at the two sites, and across both sites. Even though the individual-tree heritabilities for drought

adaptation traits were low, large variation among family means indicates that selection of families (or parents) for increased seedling drought adaptation would be possible. The evidence for genetic variation in drought adaptation traits suggests that genetic selection for drought adaptation traits measured in this study would be effective. For example, the individual tree heritabilities for Htinc were low, but were consistent with heritabilities for seedling growth from other experiments (Anekonda et al. 2002). Therefore, this trait would be amenable to genetic improvement.

The additive genetic coefficient of variation (AGCV) is a measure of additive genetic variation relative to the mean of a trait. The ratio of the additive genetic variation to the mean of a trait facilitates comparisons among traits in the magnitude of genetic variation. When assessing whether a trait is phenotypically variable, we standardize by its mean. Thus, AGCV seems to be a good measure for comparing genetic variability. The intent of any kind of standardization is to remove the effects of scale, but that does not always work completely. Thus, the effects of scale (e.g., units of measure) must be carefully evaluated and corrected for when comparing variation among traits (Houle 1992). Rohlf et al. (1983) also state that traits with small means are likely to be measured with less accuracy than traits with large means. This would cause a negative relationship between means and coefficients of variation based on phenotypes. In my study, values for the AGCV tend to be less than 23% for height. The AGCV of SD_bin was higher than for other drought adaptation traits. These results highlight that high individual-tree heritabilities are not necessarily associated with a high AGCV. For example, SD_bin,

which has a low heritability, has the highest AGCV. In contrast, Ht14 and Ht15, the traits with the highest individual tree heritabilities, tend to have a lower AGCV. However, the mean of LD_bin was very low (e.g., close to zero) for the Sprague and Lost Creek plantations. Therefore, the value of AGCV may not be very reliable, and the results should be carefully interpreted.

4.2.2 Estimated genetic gains were large for drought adaptation traits

Because of its high economic value, most tree improvement programs aim to increase growth rate. Even with low to moderate heritabilities for growth rate (h^2 = 0.10 to 0.30), large genetic gains can be achieved (White et al. 2007). In tree breeding programs, many different types of selection can be used to enhance the frequency of preferred alleles at loci influencing a given trait. Gain is achieved when the selected population has a higher frequency of favorable alleles than does the base population (White et al. 2007). A successful characterization of adaptive traits requires the use of cost effective and efficient techniques that allow for the screening of many trees in a reasonable amount of time (Aitken and Adam 1996).

Despite the low heritabilities for drought adaptation traits, such as SFlush, LD_bin, and Mort, estimated gains were large at both individual sites and across sites. Genetic gains from parental selection based on family means were obtained using two backward selection scenarios. To simplify the comparisons, family heritabilities were estimated assuming that for each family, the same number of trees was measured.

I found large genetic gains for Htinc, Flush, SFlush, LD_bin, and Mort for the selection of the best 25 of 200 parents (i.e., gain1) and for the selection of the best 25 of 1000 parents (i.e., gain 2). For example, for Flush, gain 1 was 65% and gain 2 was 93% across both plantations. These results indicate that Flush can be readily manipulated (e.g., can be easily changed) through artificial selection, and gains can be high when there are many parents (families) to choose from. In this experiment, the total number of families was 429. Therefore, Flush would be very responsive to selection. Intensive selection leads to greater predicted genetic gains. This means that selecting a smaller portion of the population allows for greater predicted gain (White et al 2007).

The genetic gain in drought adaptation traits would be very significant if the selection criteria precluded leader damage. Gain for LD_bin was very high compared to other drought adaptation traits. For example, gain 1 was 82% and gain 2 was 117% for LD_bin across the Sprague and Lost Creek plantations. Selection against leader damage would be very helpful. In addition, selection against SD_bin and mortality would also lead to genetic changes. For instance, for SD_bin, gain 1 was 70% and gain 2 was 100%. For Mort, gain 1 was 35% and gain2 was 50% across both plantations. Therefore, for selection purposes, Flush, LD_bin, SD_bin, and Mort are the recommended drought adaptation traits on which to focus.

Gain 1 was 25% and gain 2 was 36% for Htinc across Sprague and Lost Creek. However, the low genetic correlations between Htinc and other drought adaptation traits (i.e., across

both sites) implies that if selection were based on height growth alone, the selected trees will show moderate signs of drought adaptation. In addition, selection for height growth will not necessarily lead to genotypes (e.g., families) that grow well at later ages (Kaya 1993). Therefore, selection for height growth is not likely to have a significant effect on drought adaptation of seedlings.

SFlush is important among the drought adaptation traits, and can be used to understand variability in height growth in conifers. This knowledge may be helpful for achieving maximum gain in tree breeding programs (Kaya 1993). For instance, gain 1 was 29% and gain 2 was 42% for SFlush across the Sprague and Lost Creek plantations. Thus, in tree breeding programs, SFlush would be very responsive to selection. The ability to change the frequency of second flushing in tree breeding programs can increase height growth (Adams et al. 1994). Across the Sprague and Lost Creek plantations, low individual-tree heritabilities were obtained for SFlush (h_i^2 = 0.02), and the correlation between SFlush and Htinc was also low (r = 0.18). That is, selection for this trait is not expected to be very effective. However, it is unclear how well the traits are related to drought adaptation. This is because the study was conducted after one growing season in the field. Furthermore, it would be useful if the drought adaptation traits were well correlated with the climate variables (White et al 2007).

4.2.3 Genetic correlations among drought adaptation traits

Genetic correlations can be used to infer which traits are controlled by the same genes. Populations that are grown in different environments may have different genetic correlations among traits (St. Clair 1989). I calculated breeding values, which are estimates of the additive genetic values that are transmitted to offspring (i.e., by mating the individuals randomly to all other individuals in the population). Additive genetic values predicted by best linear unbiased prediction (BLUP) have the lowest error variance and highest correlation with the true (but unknown) breeding values of any possible linear functions of the data that produce unbiased predictions (White and Hodge, 1989). These breeding values can be used by breeding programs to select genetically improved breeding materials. Genetic correlations can be used to assess how selection will affect the relationships among traits. Tree breeders should take into account those traits that are strongly correlated. A large negative correlation (i.e., near -1) indicates a very strong tendency for a tree with high breeding value for one trait to have a low breeding value for a second trait (White et al. 2007).

Because of the low genetic correlations among traits, selection that aims to enhance drought adaptation would have only a modest effect on the other traits. For example, negative genetic correlations between FD_bin and Htinc were near zero at both sites. That is, low genetic correlations between these traits indicate that selection for greater height growth will have little impact on foliage damage, although trees that have more

foliage damage tend to grow slightly slower. Negative genetic correlations observed between Htinc and Mort suggest that selection for greater growth will also lead to less mortality. However, there was a strong genetic correlation between FD_bin and Mort at both sites, indicating that families with more foliage damage also had greater mortality. Foliage damage appears to be closely associated with mortality, perhaps as an early indicator or direct cause of tree death. In other words, these traits are probably functionally associated with each other. Foliage damage seems to be a good indicator of mortality. For this reason, foliage damage can be used as an indirect selection criterion for mortality.

Because of the economic importance of height growth, breeders aim to increase growth rate in most tree improvement programs. Therefore, based on my results, selection based on seedling growth alone would result in decreased mortality, and reduced foliage damage. Additional cost and efficiency criteria would also need to be considered.

In addition, moderately positive genetic correlations between Flush and LD_bin were found. This indicates that selection for earlier bud flush will tend to increase leader damage in young seedlings (i.e., high values for Flush indicate early bud flush).

There was a strong genetic correlation between Htinc and SFlush at Lost Creek, where the conditions were wetter and colder, and where more second flushing occurred. This indicates that selecting for greater second flushing would tend to increase height growth.

Thus, second flushing in seedlings could be used as an indirect selection criterion for height growth. Previous studies also found clear indications of genetic correlations between second flushing and height growth in the field (Adams and Bastien 1994). However, SFlush was very low at Sprague compared to Lost Creek (SFlush was 0.06 at Sprague versus 0.31 at Lost Creek). Thus, second flushing was not well expressed at Sprague compared to Lost Creek. These results show that the correlation between Htinc and SFlush was not consistent between the two sites. The heritability of SFlush was also very low at Sprague. Thus, it is not surprising that the results lead to different conclusions for the two sites. When there are large differences in expression of traits across sites, genotype-by-environment interaction of traits must be taken into account.

4.2.4 Low correlations between growth in the greenhouse and drought adaptation traits in the field

Genetic correlations between growth in the greenhouse and drought adaptation traits help to answer the following question: Is there an association between drought adaptation traits and seedling characteristics at the time of planting, as well as subsequent growth and survival? I examined the relationships between Ht14 versus drought adaptation traits in the field. I hypothesized that, because of high leaf areas, taller Douglas-fir seedlings (in the first year) are more prone to damage from drought. This is also because taller trees have a longer hydraulic pathway. This suggests that shorter trees with fewer leaves are more tolerant of drought. During the summer, because of low soil moisture, taller trees may also be subjected to greater hydraulic resistance, and may become gradually water

stressed (Woodruff and Meinzer 2011). On the other hand, it is possible that taller trees with more leaves might be unaffected by drought and survive well in the field.

A moderately negative genetic correlation was found between Ht14 and LD_bin at Sprague, indicating that taller trees in the greenhouse had less leader damage in the field ($r = -0.21$). In addition, a weakly positive genetic correlation between Ht14 and Mort was observed at Sprague, indicating that height growth in the greenhouse was weakly associated with greater mortality in the field. This may be because of the greater foliage (transpirational surface) of the taller trees. Nonetheless, this correlation was low.

4.2.5 Low genetic correlation between flushing versus height growth and mortality

Genetic correlations also help to answer the following question: Is early bud flush associated with other drought adaptation traits? Annual drought in the Pacific Northwest occurs from early summer until the rains begin in the fall (Woodruff and Meinzer 2011). At Lost Creek, where the conditions were wetter and colder, a fairly negative genetic correlation was observed between Ht14 and Flush, indicating that greater growth in the greenhouse was associated with later flushing in the field. However, I did not find any significant relationships between Flush versus Htinc and Mort. A strong negative correlation between Htinc and Mort suggests that trees that grow taller in the field have less mortality. It may take more time to get a better understanding of the seedling

responses to field conditions. In later measurements of the study, it will be interesting to see how seedlings respond to drought.

Regarding tree breeding programs, a positive genetic relationship between Flush and Htinc is preferred. One reason for this is that selection for bud flush may result in greater height growth. However, early flushing causes trees to be exposed to early spring frosts, which might adversely affect seedling growth and survivability. Thus, trees with earlier bud flush may have a greater risk of spring frost damage (Li and Adams 1993). Spring frost hardiness has a positive association with late spring bud flush (O'Neill et al. 2000). Trees that bud flush first are more vulnerable to spring cold damage (Aitken and Adams 1995; Schermann et al. 1997), which can reduce the influence of the leader. However, Howe et al. (2003) found that there is no conclusive association between height growth versus spring frost damage and bud flush. Both low to moderate positive genetic correlations (Kaya et al. 1989; Li and Adams 1993) and negative genetic correlations (Mangold 1987) have been found between bud flush and height in earlier studies of Douglas-fir.

Families from hotter and drier areas that flushed earlier tended to have damaged leaders. Because of the negative genetic correlation between Flush and Htinc at Sprague, early flushing trees were associated with reduced growth in the field ($r = - 0.31$). This suggests that trees that flushed earlier grew less. A negative relationship was observed between Flush and Mort, indicating that earlier flushing trees had reduced mortality ($r = -0.18$).

Nonetheless, these correlations were low. This may be consistent with the observation that there were frost pockets at Sprague site, which may have had a higher incidence of mortality. We may infer that trees that flush early may be able to avoid the more severe droughts that occur later in the growing season.

4.2.6 Genotype-by-environment interactions

Genotype by environment interactions can be used to study how the relative performance of families depends on the environment. Optimally, family rankings for drought adaptation would show negligible genotype-by-environment interaction when measured on different sites, and this is true for other adaptive traits. For example, O'Neill et al. (2000) measured the relative timing of bud flush of Douglas-fir and found that the timing of bud flush was consistent among sites and years. This was also demonstrated by strong genetic correlations between sites and ages. Likewise, genetic correlations were also high between sites and years for cold hardiness in Douglas-fir (Aitken and Adams 1996).
In my study, the families were exposed to contrasting temperature and moisture conditions at the two sites. Thus, genotype-by-environment interactions for drought adaptation traits may be expected. To quantify the genetic control of drought adaptation traits, I calculated the magnitude of family-by-site interaction in these traits by examining the family-by-site interaction variance component. I found that genotypes (e.g., families) responded somewhat differently across a range of environments. However, my results indicate that genotype-by-environment interactions should not present large difficulties

for obtaining adaptation to drought. However, genotype-by-environment interaction was high for mortality, and mortality was higher at Sprague than at Lost Creek. That indicates that different environmental conditions may be causing mortality at the two sites. For flushing, I found little genotype-by-environment interaction, indicating that regardless of the differences in environmental conditions between the two sites, the same families responded similarly across the sites.

Second flushing shows more genotype-by-environment interaction than does other adaptation traits. However, SFlush was very low at Sprague compared to Lost Creek. That means the trait was not expressed well at the Sprague site compared to Lost Creek, which may lead to different conclusions from the two sites. When there is a large difference in expression of a trait across sites, genotype-by-environment interaction of that trait may appear to be large due to differences in variation between the sites.

I also estimated the Type B genetic correlations (Burdon 1977), which can be used to assess G x E between two sites. When the site-to-site genetic correlation is close to 1, we can conclude that genotype-by-environment interaction is negligible and biologically unimportant. This means families perform nearly identically at both sites. Thus, we could infer that drought adaptation traits are controlled by the same genes.

Type B genetic correlations are typically used in breeding programs to measure interactions between families and sites (White et al. 2007). If the Douglas-fir families have the same performance relative to each other at Sprague and Lost Creek plantation ($r_g = 1$), then we could say that there is no genotype-by-environmental interaction and no variance due to the interaction ($V_{GE} = 0$). Conversely, if $r_g = 0$ or near zero, then the genotype-by-environment interaction variance is large. That is, the family rankings do not correlate well across sites. The Type B genetic correlations were higher for SD_bin and Flush compared to SFlush. The value for second flushing was particularly low and indicates that there is a significant amount of G x E for second flushing. That is, the Douglas-fir families did not rank consistently for second flushing across the Sprague and Lost Creek plantations. The lack of SFlush at Sprague may be the critical factor.

The Type B genetic correlations were lower for foliage damage compared to other drought adaptation traits. This suggests that G x E variance is large. This means that the Douglas-fir family rankings do not correlate well for foliage damage across the Sprague and Lost Creek plantations. This could imply that foliage damage is influenced by somewhat different sets of genes in the Sprague and Lost Creek plantation. The Type B genetic correlations were much higher for stem damage and bud flush. This indicates that family rankings are more similar at the two sites.

4.3 Determine whether drought adaptation traits are associated with the climatic origin of Douglas-fir seedlings

4.3.1 Relationships between drought adaptation traits and source climate

This discussion pertains to the correlations of family means and the correlations of family BLUPs with climate variables, which help to answer the following question: Are drought adaptation traits associated with the climatic origin of the Douglas-fir families? The seeds were collected from western Oregon and Washington and planted at two sites in southern Oregon to understand the capability of the Douglas-fir trees to tolerate drought stress. The origins of the female parents include a broad variety of environments where Douglas-fir trees are present. All of the seedling traits were significantly correlated with some parental climate variables. Given the variety of source environments, differences among drought adaptation traits were detected.

I hypothesized that natural selection for drought adaptation traits has been stronger in areas that are warmer and drier. The Sprague site was hotter and drier compared to Lost Creek, and these conditions adversely affected seedling growth, damage, and survival. This suggests that the Sprague site should be good for screening drought adaptation traits. In addition, looking at the heritabilities, drought adaptation traits are heritable. These results support the hypothesis that natural selection for drought adaptation traits has been stronger in areas that are warmer and drier.

Genetic correlations between breeding values and parental climate variables indicate that second flushing is associated with warmer climates with higher winter and summer temperatures. That is, parental genotypes from those areas are more likely to have second flushing.

A number of studies have shown that populations are adapted to their climatic and environmental conditions, suggesting local adaptation (St.Clair et al. 2015). In fact, adaptation to different sites has presumably led to population variation in drought adaptation traits. Genecological models can be used to study these relationships. We can also use these models to evaluate whether existing Douglas-fir populations will be able to cope with climate change. This information could help forest managers make decisions about which seedlings will be adapted to current and future climate conditions (St.Clair and Howe 2007; Hamann et al. 2011; Gould et al. 2012). These genecological models will be described in greater detail in the management and research implications section.

4.3.2 Source temperature was positively associated with growth in the greenhouse, but showed no relationship to growth in the field

Drought adaptation traits were studied in relation to source climate variables through correlation analysis. We found large and significant correlations between greenhouse growth and source climates. We can conclude that source climate is a good predictor of height growth in the greenhouse.

The correlation between Ht14 and climate variables showed that at least 16% of the variation was explained by MAT, DD5, DD_18, or EREF at Sprague. At Lost Creek, at least 16% of the variation was explained by MAT, DD5, NFFD, EXT, or EREF; and more than 19% of the variation was explained by DD_18. Across the Sprague and Lost Creek sites, at least 17% of the variation was explained by MAT, DD5, DD_18, or EREF. Climate variables, especially temperature variables, were found to be the variables that best correlated with growth in the greenhouse. This indicates that temperature variables tend to drive genetic variation, at least in traits that influence height growth in the greenhouse.

However, most climate variables do not seem to be associated with seedling growth in the field. This is probably because the seedlings were measured shortly after the seedlings were planted in the field (i.e., after one growing season). Likewise, the strength and direction of the correlations between Htinc and climate variables was about the same for both plantations. This agrees with the results across the Sprague and Lost Creek plantations (i.e., no associations between climate variables and height increment).

4.3.3 Moderate relationship between flushing and source climate

I hypothesized that early bud flush in Douglas-fir is a genetically controlled drought avoidance strategy. My results show that the initiation of height growth (i.e., date of bud flush) is associated with climate variables, especially MAP, MSP, AHM, SHM, eFFP,

and EMT. The correlation between Flush and climate variables suggests that the differences in climate conditions between the sites may have affected these correlations. For example, a negative correlation was found between Flush and MSP at both sites, whereas positive correlations were found between Flush versus eFFP, EMT, AHM, and SHM at Sprague, where the conditions are hotter and drier. These results indicate that trees from hotter and drier climates tend to flush earlier.

The timing of bud flush is an important trait that varies within species and is associated with the origin of the seed. For instance, trees from southwest Oregon that are adapted to droughty conditions flush sooner than more northern trees (Harrington et al. 2010). These authors also found that early bud flush continues to occur due to warmer winters observed with changing climate conditions. However, a substantial increase in winter temperatures may prevent chilling requirements from being met, resulting in later bud flush (or even no bud flush), limiting the growth of the trees. Recent studies have shown that the timing of bud flush was the most visible evidence of the effects of the climate change (Gould et al. 2012). In common garden trials, populations that come from xeric environments and higher elevations may flush early. This suggests that populations that flush earlier may be better adapted to current and future climates than previously believed (Gould et al. 2012).

Lomas (1999) also found that genotypes from dry areas have a slower growth rate and earlier bud set than those from humid environments, indicating that natural selection has

promoted tolerance to drought conditions. For instance, Douglas-fir seedlings from drier climates have earlier bud set, have shorter growing seasons, and less annual height growth. Also, compared to northern populations, southern populations have earlier bud set, fewer growth flushes (second flushing), and less height growth, which may enhance tolerance to drought (Howe et al. 2006). Under water-limited conditions, later bud flush might imply reduced annual growth; and trees that break bud sooner may be more vulnerable to frost damage and stunted growth (Harrington et al. 2010).

St. Clair et al. (2005) found that seedlings that burst bud early were associated with seed source locations with higher temperatures and lower precipitation in the summer. Early bud flush, as a selection mechanism to avoid drought, seems to act as a population differentiator (St Clair et al. 2005). Early bud flush seems to be a drought avoidance mechanism because trees start growing earlier and complete their annual growth before mid-summer droughts occur.

Early bud flush is also associated with cold weather conditions, and this is interpreted as consequence of either low chilling or low heat demands (Morgenstern, 1996; Howe et al. 2003). Some of the researches have also found similar relationships between bud flush and low precipitation, suggesting that early flushing helps trees avoid drought stress. From these studies, we can infer that early bud flush in Douglas-fir may be a genetically controlled drought avoidance strategy (Campbell and Sugano, 1979; White et al. 1979).

In my study, parental genotypes from areas with warmer and drier climates were more likely to flush early. This supports the hypothesis that early bud flush is a drought avoidance mechanism. We might also hypothesize that early bud flush is a strategy to ensure sufficient early growth by the time soil moisture becomes limited. Because of warmer winters, low soil moisture may reduce height growth of the seedlings after the initiation of bud flush. However, St. Clair et al. (2005) state that seedlings that flush earlier grew more and were most likely to survive and reproduce. This strategy means that early flushing is avoiding drought stress.

4.3.4 Across the Sprague and Lost Creek plantations, correlations between parental climates and seedling traits were low

Low correlations were detected between family means and climate variables across the Sprague and Lost Creek plantations. These results are consistent with the observed correlations between breeding values and parental climate at both individual sites and across sites.

4.3.5 Selection of climate variables

One of the purposes of genecological studies is to identify the climatic drivers of drought adaptation traits. In other words, to identify which climate variables explain genetic variation and, therefore, should be considered during seed transfer.

Based on data from the Sprague site, the beginning of the frost-free days (bFFP) seems to be one of the drivers of natural selection. At Lost Creek, degree-days below 18°C (DD_18) and reference atmospheric demand (Eref) seemed to be most important. I observed that higher values of DD_18 were associated with less second flushing. In contrast, higher values of Eref were associated with increased second flushing.

To obtain reasonable genecological models, it is important to assess (simultaneously) the contribution of the all possible variables, so that we can determine those that have a greater effect on the adaptation traits of interest. This is a difficult task because the climatic variables often show multicollinearity. For instance, the correlations between MAP versus MWMT, MCMT, DD_0, DD_5 and DD_18 were 0.926, 0.849, -0.920, 0.962, and -0.999, respectively. This has direct implications for the assessment of significance levels of the corresponding coefficients in the models. For example, when fitting a multiple linear regression model for Htinc at Sprague (using all 23 climate variables), none of them were statistically significant (results not shown). However, might not reflect a lack of association between the climatic drivers and the adaptation trait. Instead, it may be the result of the correlation structure among the independent variables, leading to high variance inflation factors. Thus, it is important to consider variable section alternatives that allow us to choose the most important variables. The adjusted R^2 values were generally low for the models under consideration, indicating a poor fit for the models relating climate variables to field performance. It is possible that the first year of height growth was too early to find strong associations between Htinc

and the climate variables. Another possibility is that there were other unaccounted factors (or interactions) that influenced adaptation to the sites, and masked the climatic signal.

One of the main problems with the selection of climatic drivers is the correlation among climate variables. One possible solution is to choose a subgroup of these variables that are not highly correlated (i.e., to avoid redundant information). For instance, a potential subgroup is MAT, TD, MAP, MSP, AHM, SHM, BFFP, eFFP, FFP, MAR, and RH. Of course, this alternative is only feasible if the total number of variables is relatively small. Variable selection procedures, such as those discussed in this study, also offer important alternatives, and could lead to models that are straightforward to interpret. If multicollinearity is a major concern, principal component analysis (PCA) could be used. Although the resulting models are harder to interpret, this technique is widely used.

5 Conclusions and Implications

5.1 Implications for future research on drought adaptation

Climate change will likely have an adverse effect on the growth and survival of Douglas-fir. Due to a rapidly changing climate, local seed sources may become genetically maladapted to local climates by the end of the century (Aitken and Whitlock 2013; Montwe et al. 2016). However, forest trees may be able to adjust to the changing climate by phenotypic plasticity (Aitken et al. 2008). Although phenotypic plasticity may be important in the short term, but it will probably be insufficient when species encounter novel future climates (see Morin et al. 2009).

Trees may adapt gradually through natural selection, but we do not know how fast natural populations can adapt to climate change. The worst-case scenario is that trees will become extinct in their local environments (Aitken et al. 2008). Because trees need time to disperse, propagate, and grow, they need several generations to adapt to projected climate change. Human aided movement (i.e., assisted migration) may help to mitigate the impact of climate change if we can predict which genotypes are suitable for future climates. That is why we need to understand how populations and genotypes of forest trees are adapted to climate.

I found evidence that natural selection for drought adaptation traits has occurred in areas that are warmer and drier. The hotter and drier conditions at the Sprague site were negatively associated with seedling growth, and positively associated with damage, and mortality.

I found large differences in height among families in the greenhouse. These large differences in Ht14 suggest that there are family differences in growth in the greenhouse. However, inherent family differences in greenhouse growth were probably accentuated because the trees were grown in unreplicated family blocks. Thus, for future research on drought hardiness, I recommend that randomization should be used in the greenhouse to reduce environmental sources of variability and better understand the genetic performance of the families in the field.

Given the high correlation between Ht14 and Ht15, either measurement can be used as an "initial height" (i.e., covariate) in later analyses of this experiment to better understand seedling responses to drought in the field. Initial height (Ht14) should be used as a covariate in analyses of growth, damage, and survival in the field (e.g., to remove the confounding effects of initial greenhouse height). Ht14 can also be used as a covariate for other traits that are phenotypically related to height growth (Frank 2017b).

I observed large and significant correlations between greenhouse growth and parental source climates. However, most climate variables do not seem to be associated with

seedling growth in the field. This is probably because the seedlings were measured shortly after the seedlings were planted in the field.

5.2 Implications for breeding

Quantitative genetic information can be used to guide breeding programs, and assisted migration can be implemented once seed transfer guidelines or seed zones are known. For example, population-level genetic information can be used to help guide deployment decisions and assisted migration (Ying et al 2006). To assess the potential effects of climate change, we need to understand: (1) population-level genetic variation in drought adaptation traits (Howe et al. 2003; Bansal et al. 2016); and (2) the climatic drivers of adaptive population differentiation.

There is potential for indirect (early) selection. Family heritabilities for drought adaptation traits were moderately high, suggesting that parental (backward) selection or family selection would be effective for genetically improving drought adaptation, and consequently improving seedling establishment. For example, across both plantations, drought adaptation traits had low individual-tree heritabilities, but moderate to strong heritabilities at the family level. The geometric mean number of Douglas-fir trees per family at Sprague and Lost Creek is 11. Therefore, 11 Douglas-fir trees per family per plantation are needed to obtain these levels of genetic gain. Thus, drought adaptation in Douglas-fir can be genetically improved by using early selection, and this may improve

the success of reforestation programs. However, we do not know yet how well the traits are related to drought adaptation because the study was conducted after one growing season in the field. Longer-term monitoring will be necessary to confirm these initial conclusions.

At Sprague and Lost Creek, MCMT, AHM, SHM, and EMT were positively correlated with the timing of spring bud flush (Flush). In addition, Flush was negatively correlated with MSP. At Lost Creek, MAT, MWMT, MCMT, DD5, DD18, NFFD, EMT, EXT, Eref, and CMD were positively correlated with second flushing. In addition, second flushing was negatively correlated with DD_0, DD_18, PAS, and RH.

Thus, these climate variables seem to be drivers of natural selection, leading to adaptation to the environment. Furthermore, Flush and SFlush seem to be good traits to use for assessing adaptive population differentiation. Assisted migration decisions should focus on these traits and climate variables, particularly in drought-prone areas such as Southwest Oregon. However, longer-term measurements are needed to validate the range of drought adaptation traits that are important for practicing assisted migration and making deployment decisions.

These adaptive traits should be included when evaluating the adaptability of Douglas-fir populations to future climates, predicting the risk of genetic maladaptation, and determining suitable seed transfer distances (i.e., how far populations can be moved to

new planting environments). For instance, we can build statistical models that relate bud flush or second flushing to climate variables, and then use these models to estimate optimal values of Flush and SFlush in future climate conditions. This approach can be extended to larger regions where climate information is available. This may help foresters make assisted migration decisions.

5.3 Implications for potentially adjusting to climate change

Given the wide variety of source environments represented in this experiment, all of the seedling traits were significantly correlated with some parental climate variables. Genecological approaches can be used to identify important climate variables affecting seedling performance (St.Clair et al. 2005). I developed genecological models using historical climate variables (1961-1990 normals) that could be used to refine current seed transfer guidelines and predict the potential effects of climate change on the performance of Douglas-fir seedlings. This information can be used to determine: (1) which populations and families are more adaptable to future climate conditions; and (2) the most important environmental variables in the Pacific Northwest.

5.4 Future analysis

Independently evaluating many adaptive traits may hinder the analysis and interpretation of results. Principal component analysis can be used as a dimension reduction technique

that permits variation in the variable of interest to be explained using a smaller number of explanatory variables (Howe et al. 2006; St.Clair et al. 2013). Linear mixed-effect models can be used to understand environmental adaptation and population differentiation. They can also be used to estimate variance components and obtain population and family-within-population effects (BLUPs for populations and families-within-population). Correlations and simple linear regression can be used to determine which traits of interest are related to environmental characteristics. Multivariate genecological models can be generated by linear regression to understand the relationships between population effects and climate variables.

Future analyses also include the development of genecological models that can accurately estimate the effect of climate change conditions on the performance of Douglas-fir trees. Genecological models can be developed using historical climate data (e.g., 1901-1990 normals), and can successfully identify the most significant environmental variables affecting drought adaptation. However, robust conclusions will require the collection of data at later stages of growth.

Seedling performance can be evaluated to infer appropriate climate transfer distances. The transfer distance is the difference between the climate at the planting site and the climate of the geographic origin of a population. In addition, the relationships between drought adaptation and source environments can be evaluated by using the Random Forest model. Relative risks of maladaptation to future climates can be estimated based

on additive genetic variance. The results can be compared to benchmarks such as the average risk using seed transfer guidelines. Spatial variation can be measured using principal component analysis. These results may help us to select populations of healthy trees for future climates (Frank 2017a).

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