

Adaptive Variation Among Whitebark Pine (*Pinus albicaulis*) Populations from the Interior Northwestern United States in Relation to Climate

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Abstract—Provenance tests of 49 populations of whitebark pine (*Pinus albicaulis*) revealed moderate genetic differentiation for growth potential (growth under conditions approaching physiological optimum). Moderate genetic differentiation was also detected for survival after more than 10 years under warm-dry climate in the field but not for unconditional expected height, which was considered the best available predictor of fitness. Height was considered unconditional because survival over multiple years was explicitly included in the analysis. Genetic divergence for growth potential and survival was found to correspond with climatic clines. Population differentiation for growth potential was estimated to require a separation of about ± 7.4 Julian days for timing of spring warming (D100) between climate of seed sources ($\approx \pm 210$ m elevation). Differentiation for survival was estimated to require about ± 2.66 cm annual spring precipitation between climate of population origin. These results inform seed transfer and may provide insight into the genetic response of populations under a warming climate, particularly during early growth.

INTRODUCTION

Many forest tree species are composed of populations that are genetically adapted to only a portion of environmental variation that the species occupies as a whole. Knowledge from genecology studies on intra-specific patterns of genetic variation in relation to the environment is fundamental to gene conservation and reforestation (Morgenstern 1996). In particular, knowledge of how genetic variation is related to climate may be critical to identify threatened populations and match genotypes with suitable climate under rapid ongoing climate change (Joyce and Rehfeldt 2013; Rehfeldt and Jaquish 2010; Rehfeldt et al. 2014).

Whitebark pine (*Pinus albicaulis*) is a keystone and foundational species in western U.S. subalpine ecosystems that is threatened by population decline due to anthropogenic disturbance (Tomback et al. 2001). In recent years, several regional (Hamlin et al. 2008,

2011; Mahalovich et al. 2006) and rangewide (Bower and Aitken 2006, 2008) studies have advanced knowledge of the genecology of whitebark pine genecology. Nonetheless, information on genetic variation among populations for growth and survival in the field and in relation to climate of population origin remains limited. Thus, the objectives of the present study were to (1) assess genetic variation in growth and survival among populations from the interior northwestern United States in the field and (2) model this genetic variation in relation to climate at population origin. This paper reports only preliminary results.

METHODS

This study used seeds from wind-pollinated cones, collected during 1991–1997 from 49 wild whitebark populations in the interior northwestern United States (fig. 1). Collections were made from 5 to 20

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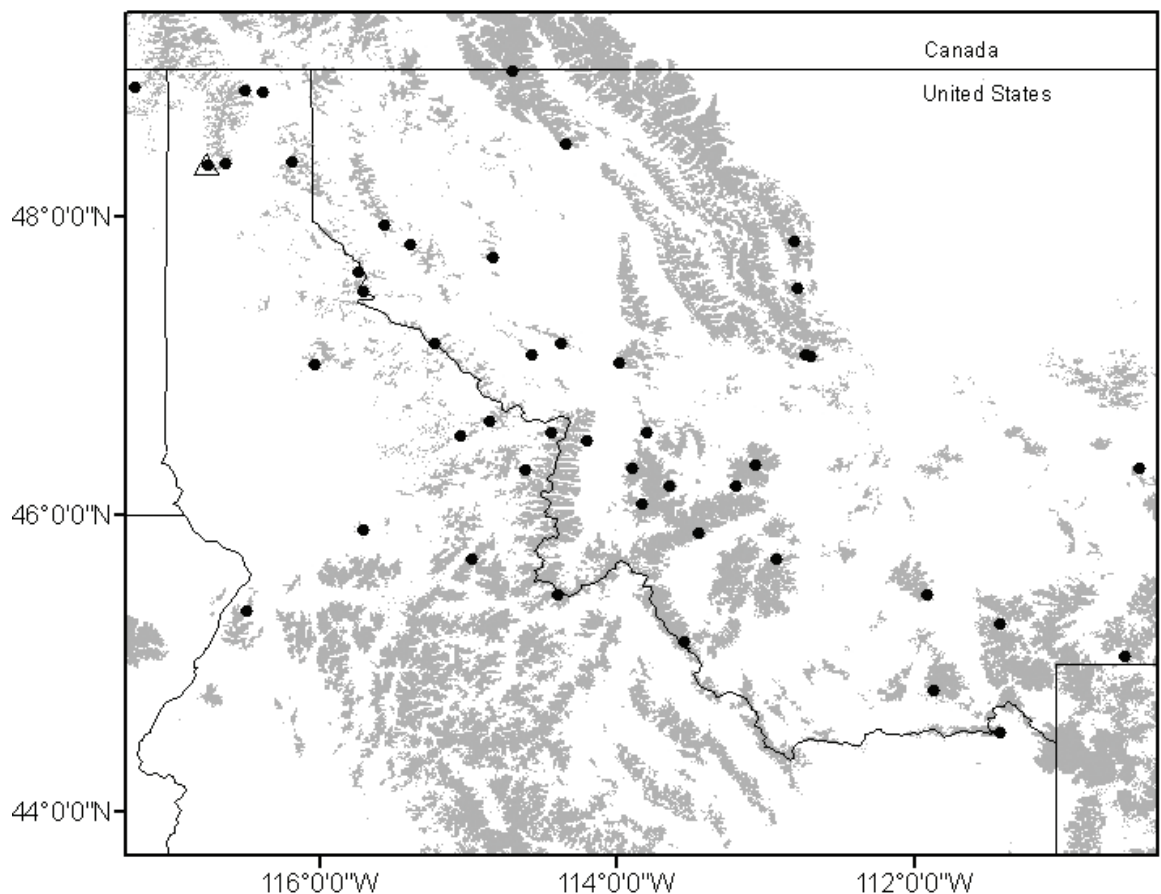


Figure 1—Location of whitebark pine (*Pinus albicaulis*) provenances (●) and study site at Priest River Experimental Forest (Δ). Shaded area indicates predicted contemporary realized climate niche for whitebark pine (Warwell et al. 2007).

trees per population. Seeds were sown in 1998, and outplanted into two provenance tests in forest openings at Priest River Experimental Forest (lat. 48.3°N, long. –116.8°W) in northern Idaho (USA) (fig. 1). Test 1 was outplanted in April 24–26, 2000 with 2-year-old trees representing 46 populations. Test 2 was outplanted 2.2 km south of test 1 in October 2–5, 2001 with 4-year-old trees representing 42 populations (fig. 2). Thirty-nine populations were common to both tests. Soil at the test 2 site was rocky and shallow to a hard pan (Page-Dumroese 1993) and appeared to be harsher than the test 1 site, where soil was tilled at planting, unobstructed, and well drained. Both tests were located at a relatively low elevation (671 m) where temperatures were warmer (+4.4 to 9.1 °C mean annual temperature) and growing seasons were longer (+5 to 99 frost-free days) than found among native elevations (1,646 m to 2,774 m) of the study populations.

A randomized complete block design was used in both tests. Each seed source was represented by 30 seedlings. Test 1 used five-tree row-plots per population within each of six blocks. Test 2 used 10-tree row-plots within each of 3 blocks. Individual trees were planted at a spacing of 1 m × 1 m at test 1 and 35.56 cm × 33.02 cm at test 2. Thinning to prevent competitive interaction among trees was not necessary despite close planting in test 2 due to high mortality and the species' characteristic slow growth. Total aboveground height measurements on 14-year-old trees were tallied in fall 2012 for both tests. Survival and shoot elongation were tallied in fall 2001–2005, 2011, and 2012 in test 1, and 2003–2006 and 2010–2012 in test 2.

The degree of differentiation among populations for survival and unconditional expected height was assessed with aster analysis (Geyer et al. 2007; see Shaw



Figure 2—Test 2 site in 2005, 3 years after outplanting. Trees are ~7 years old. Ten-tree row-plots are arranged from the foreground to the background edge.

et al. 2008) using the reaster function (Geyer 2013) in R (R Core Team 2012). Aster analysis permits unified analysis of multiple life history stages with appropriate statistical distributions. Thus, to assess unconditional height, where survival over multiple years was explicitly included in the analysis of height, survival was modeled using Bernoulli and height was modeled using normal distributions. For this procedure, unconditional expected height was assessed using seed source row-tree plot sums for height and mean survival to 2012. Differences in growth potential were assessed using general linear mixed model analysis using the lmer function (Bates et al. 2013) in R (R Core Team 2012). For this procedure, growth potential was assessed using seed source row-tree plot means for total shoot elongation in 2005.

To model genetic variation with climate, predictions for 26 climate variables (Rehfeldt 2006) representing the timing of moisture or temperature, or a combination, and their interaction at seed origins were tested by comparing the likelihoods of nested models following the statistical framework presented by Leites et al. (2012) and using a forward stepwise selection approach. Finally, regression analysis was used to describe climate based seed transfer guidelines following methods described by Rehfeldt (1983).

RESULTS AND DISCUSSION

After 12 and 11 years of growth in the field, mean height for the 14-year-old trees was 155 and 110 cm with 39- and 41-percent survival for tests 1 and 2,

respectively. Differences between the two test sites were statistically significant ($P < 0.05$) for mean height but not survival. In test 1, survival among populations varied from 8 to 75 percent; mean apical shoot elongation in 2005 varied from 7.3 to 16.5 cm and mean height in 2012 varied from 90.4 to 214.4 cm. In contrast, populations in test 2 ranged from 19- to 77-percent survival and 4.6 to 13.7 cm for mean apical shoot elongation in 2005, and 18.8 to 124.3 cm for mean height in 2012.

In both tests, no statistically significant ($P > 0.05$) differences among seed sources were detected for unconditional expected height, the best available approximation of fitness. In test 2, however, a negative trend was apparent for fitness in relation to annual spring precipitation (SPRP) at seed source. Survival was statistically significantly ($P < 0.05$) in test 2 but not test 1. In test 2, survival was negatively related to SPRP at seed source. SPRP accounted for 13.2 percent of variation in survival among populations. Variation in growth potential was statistically significant ($P < 0.05$) and negatively related to annual dryness and winter coldness at the seed source (ADIMINDD0) in test 1 and positively related to timing of spring warming (D100) at the seed source in test 2. In test 1, ADIMINDD0 accounted for 9.8 percent of population variation in growth potential. In test 2, D100 accounted for 21.3 percent of population variation in growth potential. Clinal variation for growth potential and height generally decreased in a northwest to southeast direction and with decreasing elevation in the study region. Conversely, survival and fitness generally increased in a northwest to southeast direction.

Results from the present study indicate that reasonable confidence in population differentiation for growth potential requires a separation of about ± 7.4 Julian days for D100 between climates of seed sources. This climate range corresponds to an elevation range of about ± 210 m. These results are in general agreement with findings reported by Bower and Aitken (2008). In comparison with other western forest species, these results suggest that whitebark pine is an intermediate between specialist and generalist modes for growth potential (Rehfeldt 1994).

Reasonable confidence in population differentiation for survival under warm-dry climate requires a separation of about ± 2.66 cm SPRP between seed sources. Differentiation of survival was assessed using young trees grown in a warm-dry climate for more than 10 years. The warm-dry climate conditions were similar to predicted future climate for the contemporary distribution of whitebark pine. Thus, results may provide insight into the genetic response of populations under a warming climate, particularly during early growth. To be sure, populations were tested outside of whitebark pine's native distribution; thus, results may not necessarily indicate performance in whitebark pine's native habitat.

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