

# Climate-related genetic variation in a threatened tree species, *Pinus albicaulis*<sup>1</sup>

Marcus V. Warwell<sup>2</sup> and Ruth G. Shaw<sup>3</sup>

**PREMISE OF THE STUDY:** With ongoing climate change, understanding of intraspecific adaptive variation is critical for conservation and restoration of plant species. Such information is especially scarce for threatened and endangered tree species, such as *Pinus albicaulis* Engelm. Therefore, our principal aims were to assess adaptive variation and characterize its relationship with climate of seed origin.

**METHODS:** We grew seedlings from 49 *P. albicaulis* populations representative of the interior northwestern United States in two common garden field experiments under warm-dry conditions that mimic climatic conditions predicted in the current century for areas within the species' range. Differences among populations were assessed for growth and survival. We then used regression to describe clines of apparent adaptive variation in relation to climate variation among the populations' origins.

**KEY RESULTS:** We detected genetic divergence for growth and survival among populations of *P. albicaulis*. These differences corresponded to distinct climatic clines. Populations originating from locations with lower spring precipitation exhibited greater survival in response to natural drought. Populations originating from increasingly milder climates exhibited greater height growth under relatively limited stress in early years and greater fitness after 12 yr.

**CONCLUSIONS:** The results suggest that *P. albicaulis* exhibits adaptive variation for drought tolerance and growth in response to selection pressures associated with variation in moisture availability and temperature, respectively. Even so, clinal variation was relatively gentle. Thus, apparent differences in local adaptation to climate among populations appears to be relatively low.

**KEY WORDS** adaptive variation; aster models; bioclimate models; biogeography; climate-change impacts; ecological genetics; genecology; Pinaceae; provenance test; seed transfer

Many plant species are composed of populations that are adapted to a portion of the ecological breadth occupied by their species as a whole. How variation in adaptation is structured within a species' distribution tends to be unique to each species and is presumed to result from differences in selection acting on hereditary variation within a historic context. Within this process, climate is a principal agent of selection. The influence of climate on adaptive patterns within plant species is supported by an abundance of common garden (genecology) studies, including the seminal works of Turesson (1925) and Clausen and Hiesey (1958). In general, these genecology studies have identified evidence of genetic variation in quantitative

traits that corresponds with climatic variation along geographic gradients (see Heslop-Harrison, 1964; Morgenstern, 1996).

Many past genecology studies of trees were conducted to inform reforestation practices for commercial reforestation. Consequently, only a few economically important tree species have been assessed in relatively productive environments and rarely under harsh climates where survival and growth could be substantially limited (Matyas and Yeatman, 1992). The threat of ongoing rapid climate change, however, necessitates the expansion of genecology to more plant species of ecological importance and the prediction of their genetically based survival and growth under predicted future conditions.

Whitebark pine (*Pinus albicaulis* Engelm.; Pinaceae) is a subalpine species that occupies the cool-wet climate extreme among forest ecosystems of western North America (Daubenmire, 1966; Rehfeldt et al., 2008). It is considered both a keystone (Tomback and Kendall, 2001) and foundational species (Ellison et al., 2005). Timberline populations of whitebark pine modulate snowmelt runoff (Farnes, 1990). In addition, the species' relatively large, wingless seeds, which are dispersed predominantly by Clark's nutcracker

<sup>1</sup> Manuscript received 10 April 2017; revision accepted 27 June 2017.

<sup>2</sup> Rocky Mountain Research Station, U.S. Department of Agriculture, Forest Service, 1221 S. Main Street, Moscow, Idaho 83843 USA; and

<sup>3</sup> Department of Ecology, Evolution, and Behavior, University of Minnesota, 1479 Gortner Avenue, St. Paul, Minnesota 55108 USA

<sup>4</sup> Author for correspondence (e-mail: mwarwell@fs.fed.us); ORCID id 0000-0002-8546-4837 <https://doi.org/10.3732/ajb.1700139>

(*Nucifraga columbiana*) (Tomback, 1978; Hutchins and Lanner, 1982), are a major food source for many species of mammals and birds (Mattson et al., 2001).

Whitebark pine populations have been in decline since the mid-20th century due to fire suppression, the emergence of white pine blister rust caused by an invasive pathogen *Cronartium ribicola*, and other disturbances (Tomback et al., 2001). In addition, rapid ongoing climate change in the North American Pacific Northwest is predicted to lead to warmer winters and drier summers through the century (Mote and Salathé, 2010). Under these conditions, the contemporary realized climate niche for U. S. populations of whitebark pine is projected to be nearly eliminated by the middle of the present century (Warwell et al., 2007). In consideration of these and other factors, whitebark pine was listed as a candidate species by the U. S. Fish and Wildlife Service (2011) under the Endangered Species Act and declared endangered by the Canadian federal government in accordance with the Species at Risk Act (COSEWIC, 2012).

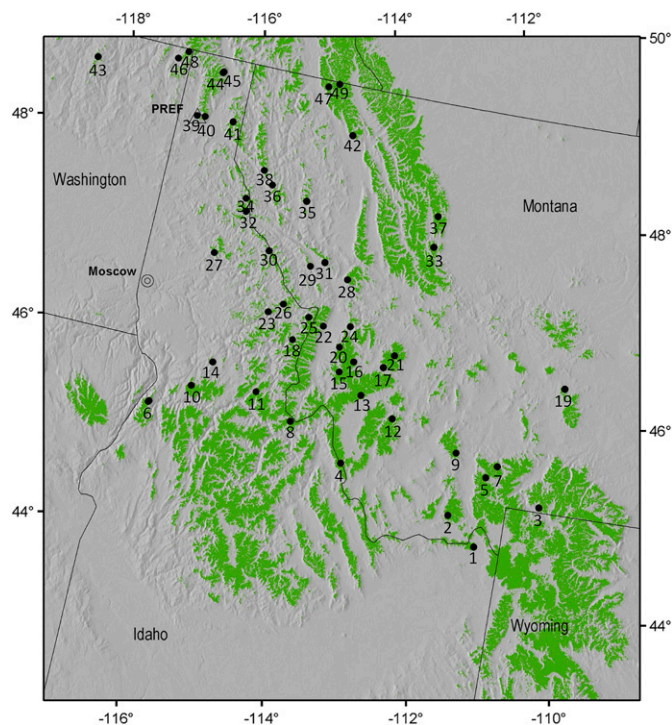
The extent of genetic variation in quantitative traits of whitebark pine and its relationship to geographic distribution have been previously assessed in a few short-term common garden studies conducted in nursery environments using potted containers or raised beds. These studies report genetic variation among populations for total height (Mahalovich et al., 2006; Hamlin et al., 2008; Bower and Aitken, 2008; Hamlin et al., 2011), root and shoot dry mass, date of needle flush (Bower and Aitken, 2008), cold hardiness (Bower and Aitken, 2006, 2008; Mahalovich et al., 2006), needle color (Hamlin et al., 2011), and rust resistance (Mahalovich et al., 2006). However, information on adaptive variation for growth and survival expressed in a warm-dry climate in the field has not been reported.

To expand understanding of adaptive variation among whitebark pine populations, we collected seeds from 49 representative whitebark pine populations from the interior northwestern United States and grew the resulting plants for 10 to 12 yr in two common garden field experiments. We examined genetic variation among populations for quantitative traits and related the observed variation to climate estimates at seed origin. We employed a novel analysis using aster modeling (Geyer et al., 2007; see Shaw et al., 2008) to analyze variation in height while explicitly accounting for variation in mortality.

The primary objectives of this study were to (1) assess genetic variation for growth and traits that approximate fitness among whitebark pine populations under climate where temperature and moisture availability approach expectations with changing climate; and (2) model this genetic divergence in relation to climate of seed origin. This study advances understanding of adaptive differences among populations of long-lived species in which wind-pollination and animal seed dispersal promote extensive gene flow (see Richardson et al., 2002). Moreover, the study advances understanding of the relationship between climate and fitness differences among populations, which is critical to decisions about gene conservation and reforestation.

## MATERIALS AND METHODS

**Plant materials**—The current study used seeds from wind-pollinated cones collected during 1991 to 1997 from 49 wild whitebark populations in the interior northwestern United States (Fig. 1, Table 1).



**FIGURE 1** Location of whitebark pine (*Pinus albicaulis*) populations (●) and study site (Δ near 39). Location labels correspond with Table 1. Green area indicates estimated contemporary distribution using the predicted realized climate niche of whitebark pine (Warwell et al., 2007).

Seeds were collected from 5 to 20 trees per population; however, eight populations were represented by bulk cone collections in which the total number of contributing maternal sources is unknown (Table 1). All populations were represented by cones collected in a single year with the exception of Heaven's Gate and Burke Summit, Idaho, which used collections from two consecutive years (1995 and 1996). Each population was spatially defined as trees occurring together on a mountain top ridge and/or in a basin within approximately 3.5 km in horizontal distance and 125 m in elevation.

Seeds were germinated in 164-mL Ray Leach Cone-tainer super cells (Stuewe and Sons, Corvallis, Oregon, USA) in a greenhouse in Lewiston, Idaho in 1998. Following germination, seedlings were maintained in a shelter house in Moscow, Idaho. Seedlings were allocated into two experiments. Seedlings in Experiment 1 were grown only in super cells; seedlings in Experiment 2 were transplanted into 656-mL Deepot containers (Stuewe and Sons) in between June and August 2000.

**Planting sites, design, and procedure**—Common garden field experiments of 46 (Experiment 1) and 42 (Experiment 2) populations, with 39 populations common to both experiments, were outplanted into two forest openings at Priest River Experimental Forest on 24–26 April 2000 and 2–5 October 2001, respectively (Fig. 1). At both sites, the surrounding forest was *Tsuga heterophylla*–*Clintonia uniflora* habitat type (Cooper et al., 1991). Both experiment sites were located at a relatively low elevation (671 m a.s.l.) where the climate was drier than at most seed origins and substantially warmer than all seed origins (Table 1).

Experiment 1 (Exp. 1) was established to assess variation in fitness at a climatically mild site. The Exp. 1 site (48.352°N, 116.848°W,

**TABLE 1.** Number of maternal families and trees per population, geographic location, inferred climate (Rehfeldt, 2006) for whitebark pine (*Pinus albicaulis*) seed origins, and observed climate (2001–2012) at study location at Priest River Experimental Forest (PREF).

| Pop. no.         | Seed source        | No. families | No. trees: Test 1 | No. trees: Test 2 | Lat. °N | Long. °W | Elev. (m a.s.l.) | PRATIO | D100 | SPRP (mm) | ADIMMINDO | MAP (mm) | MAT (°C) |
|------------------|--------------------|--------------|-------------------|-------------------|---------|----------|------------------|--------|------|-----------|-----------|----------|----------|
| 1                | Sawtel Peak        | 10           | 25                | 27                | 44.54   | 111.42   | 2545             | 0.481  | 175  | 118       | 119.3     | 734      | −0.8     |
| 2                | W.F. Cabin         | 8            | 23                | 34                | 44.82   | 111.87   | 2683             | 0.537  | 181  | 118       | 122.4     | 663      | −1       |
| 3                | Palmer Mtn.        | Bulk         | 26                | 16                | 45.05   | 110.58   | 2774             | 0.513  | 187  | 134       | 98.9      | 786      | −2.2     |
| 4                | Goldstone Pass     | 9            | 27                | 21                | 45.15   | 113.55   | 2561             | 0.604  | 176  | 93        | 186.6     | 429      | 0        |
| 5                | Lone Mtn.          | 10           | 25                | —                 | 45.27   | 111.42   | 2743             | 0.523  | 184  | 140       | 96.5      | 792      | −1.4     |
| 6                | Heaven's Gate      | 11           | 23                | 22                | 45.37   | 116.49   | 2438             | 0.352  | 183  | 155       | 61.3      | 1005     | 0.4      |
| 7                | Little Bear        | 8            | 28                | 16                | 45.4    | 111.28   | 2621             | 0.532  | 180  | 142       | 99.0      | 784      | −0.7     |
| 8                | Tin Cup            | 9            | 27                | 29                | 45.47   | 114.4    | 2396             | 0.471  | 176  | 109       | 125.5     | 613      | 0.2      |
| 9                | S. Baldy Mtn.      | 10           | 27                | 21                | 45.47   | 111.91   | 2743             | 0.556  | 183  | 138       | 103.4     | 710      | −1       |
| 10               | Gospel Peak        | 10           | 13                | 18                | 45.62   | 115.94   | 2499             | 0.366  | 185  | 150       | 65.0      | 982      | −0.3     |
| 11               | Burnt Knob         | 11           | 13                | 8                 | 45.7    | 114.98   | 2499             | 0.400  | 185  | 131       | 83.4      | 837      | −0.5     |
| 12               | Quartz Hill        | 9            | 15                | 21                | 45.7    | 112.93   | 2438             | 0.621  | 170  | 105       | 162.1     | 467      | 0.6      |
| 13               | Mudd Ridge         | 11           | 24                | 22                | 45.88   | 113.45   | 2408             | 0.571  | 174  | 107       | 148.0     | 506      | 0.2      |
| 14               | Pilot Knob         | 12           | 21                | 19                | 45.9    | 115.7    | 2252             | 0.374  | 180  | 143       | 70.7      | 941      | 0.4      |
| 15               | Coyote Mdws.       | 6            | —                 | 23                | 46.07   | 113.83   | 2451             | 0.506  | 181  | 121       | 113.2     | 629      | −0.2     |
| 16               | Mt. Emerine        | Bulk         | 18                | 26                | 46.2    | 113.65   | 2560             | 0.509  | 183  | 129       | 103.6     | 662      | −0.6     |
| 17               | Cable Mtn.         | Bulk         | 24                | 27                | 46.2    | 113.2    | 2439             | 0.563  | 176  | 123       | 123.0     | 577      | 0.2      |
| 18               | Diablo Mtn.        | 11           | 22                | 26                | 46.3    | 114.61   | 2256             | 0.407  | 177  | 129       | 82.4      | 826      | 0.4      |
| 19               | Forty Cr. Crazies  | Bulk         | 23                | 21                | 46.31   | 110.48   | 2438             | 0.559  | 169  | 166       | 86.7      | 791      | 0.8      |
| 20               | Willow L.O.        | 7            | 21                | 21                | 46.32   | 113.9    | 2499             | 0.478  | 183  | 133       | 94.1      | 719      | −0.4     |
| 21               | Powell Mine        | Bulk         | 26                | —                 | 46.34   | 113.07   | 2438             | 0.559  | 176  | 130       | 114.7     | 606      | 0.2      |
| 22               | St. Mary's         | 9            | 25                | 25                | 46.5    | 114.2    | 1972             | 0.448  | 160  | 118       | 101.4     | 687      | 2        |
| 23               | Indian Post Office | 10           | 28                | 23                | 46.53   | 115.05   | 2134             | 0.363  | 175  | 132       | 67.6      | 953      | 0.8      |
| 24               | Daisy Pass         | Bulk         | 28                | 26                | 46.55   | 113.8    | 2134             | 0.495  | 165  | 126       | 105.8     | 655      | 1.3      |
| 25               | Beaver Ridge       | 11           | 25                | —                 | 46.56   | 114.44   | 2225             | 0.410  | 175  | 129       | 80.6      | 822      | 0.6      |
| 26               | Blacklead Mtn.     | 16           | 26                | 24                | 46.64   | 114.85   | 2195             | 0.372  | 177  | 131       | 68.5      | 931      | 0.6      |
| 27               | Freeze Out         | 10           | 25                | —                 | 47.01   | 116.03   | 1804             | 0.319  | 161  | 130       | 50.4      | 1048     | 2.5      |
| 28               | Snow Bowl          | 10           | 24                | 13                | 47.02   | 113.98   | 2396             | 0.427  | 182  | 146       | 71.3      | 869      | −0.2     |
| 29               | Stark Mtn.         | 11           | 22                | 26                | 47.08   | 114.57   | 2145             | 0.377  | 173  | 129       | 67.9      | 906      | 0.8      |
| 30               | Little Joe         | 11           | 26                | 26                | 47.15   | 115.23   | 2150             | 0.328  | 177  | 121       | 55.2      | 1027     | 0.7      |
| 31               | Squaw Peak         | 10           | 25                | 28                | 47.15   | 114.37   | 2121             | 0.392  | 170  | 131       | 70.8      | 876      | 1        |
| 32               | Burke Summit       | 11           | 21                | —                 | 47.5    | 115.7    | 1877             | 0.294  | 163  | 99        | 49.8      | 1037     | 2.2      |
| 33               | Sheep Shed Mt      | 8            | 23                | 25                | 47.52   | 112.79   | 2317             | 0.533  | 176  | 160       | 84.3      | 749      | 0.4      |
| 34               | Beaver Creek       | 10           | 20                | 20                | 47.63   | 115.74   | 1722             | 0.301  | 158  | 104       | 50.1      | 1021     | 2.7      |
| 35               | Thomas Peak        | 11           | 20                | 30                | 47.73   | 114.83   | 1872             | 0.357  | 162  | 113       | 65.8      | 880      | 1.8      |
| 36               | 7 Point Mtn.       | 8            | 22                | —                 | 47.82   | 115.39   | 1747             | 0.322  | 159  | 104       | 58.8      | 937      | 2.2      |
| 37               | Our Lake           | 7            | 27                | 19                | 47.84   | 112.81   | 2286             | 0.538  | 174  | 156       | 83.5      | 744      | 0.6      |
| 38               | Baree Mtn.         | 11           | 28                | 26                | 47.95   | 115.56   | 1829             | 0.318  | 163  | 112       | 52.8      | 1011     | 1.8      |
| 39               | Gizborn Mtn.       | 11           | 23                | 25                | 48.35   | 116.75   | 1689             | 0.332  | 158  | 164       | 41.5      | 1210     | 2.3      |
| 40               | Schweitzer Area    | 9            | 25                | 23                | 48.36   | 116.63   | 1920             | 0.329  | 170  | 167       | 39.2      | 1269     | 1.1      |
| 41               | Lunch Peak         | 10           | 28                | —                 | 48.37   | 116.19   | 1941             | 0.326  | 171  | 151       | 42.1      | 1208     | 1        |
| 42               | Big Mtn.           | 20           | —                 | 23                | 48.49   | 114.34   | 1829             | 0.397  | 161  | 143       | 61.3      | 943      | 1.4      |
| 43               | Copper Butte       | Bulk         | 25                | 20                | 48.7    | 118.46   | 2165             | 0.413  | 182  | 128       | 61.0      | 795      | 0.1      |
| 44               | Farnham Ridge      | 7            | —                 | 16                | 48.84   | 116.51   | 2042             | 0.345  | 182  | 177       | 37.3      | 1338     | 0        |
| 45               | Farnham Peak       | 5            | 29                | 26                | 48.85   | 116.5    | 1768             | 0.348  | 164  | 169       | 40.9      | 1263     | 1.4      |
| 46               | Sullivan L.O.      | 9            | 27                | 23                | 48.88   | 117.24   | 2175             | 0.370  | 186  | 183       | 36.7      | 1288     | −0.6     |
| 47               | Glacier Nat. P.    | 6            | 27                | 25                | 48.93   | 114.855  | 1841             | 0.391  | 165  | 136       | 60.4      | 928      | 0.8      |
| 48               | Salmo L.O.         | 7            | 29                | 26                | 48.97   | 117.1    | 2092             | 0.364  | 184  | 193       | 34.6      | 1380     | −0.4     |
| 49               | Frozen Lake        | Bulk         | 20                | 28                | 48.98   | 114.7    | 1646             | 0.418  | 157  | 135       | 67.3      | 862      | 1.8      |
| <b>Total</b>     |                    | <b>400</b>   | <b>1099</b>       | <b>964</b>        |         |          |                  |        |      |           |           |          |          |
| Study site       |                    |              |                   |                   |         |          |                  |        |      |           |           |          |          |
| PREF (2001–2012) |                    |              |                   |                   | 48.35   | 116.83   | 671              | 0.454  | 138  | 132       | 45.1      | 825      | 6.9      |

Notes: Population (Pop.) no. correspond to those in Fig. 1. Lat. = latitude, Long. = longitude, Elev. = elevation (a.s.l.), D100 = Julian date the sum of degree-days >5°C reaches 100, SPRP = spring precipitation: (April + May), ADIMMINDO (cold-dryness index) =  $\sqrt{\text{annual sum of degree day} > 5^{\circ}\text{C}} / \text{mean annual precipitation} \times \text{degree days} < 0^{\circ}\text{C}$  using mean minimum temperature, PRATIO = ratio of summer precipitation to total precipitation.

elev. 671 m a.s.l.) was located in a field that had been used as a forest nursery for decades. Soil was characterized as a coarse, loamy, mixed frigid Andic Xerochrept soil (Soil Survey Staff, 1996). Air temperature was measured using DS1922 Thermochron temperature data loggers (Maxim Integrated, San Jose, California, USA) with a  $\pm 1^{\circ}\text{C}$  accuracy. The data loggers were located inside radiation shields (product #7714; Davis Instruments, Hayward,

California, USA), which were mounted on fence posts at a height of 1.3716 m (4.5 ft). At least two data loggers were used at each experiment site for the study duration. During the study period of 2001 to 2012, mean annual air temperature and annual precipitation at Exp. 1 site were  $6.9^{\circ}\text{C}$  and 825 mm, respectively.

Experiment 2 (Exp. 2) site ( $48.332^{\circ}\text{N}$ ,  $-116.8477^{\circ}\text{W}$ , 671 m a.s.l.) was established in a cold-air drainage approximately 2.2 km south



of the Exp. 1 site. Differences in growing conditions between sites appeared to be primarily associated with soil conditions. Soil at the Exp. 2 site was characterized as an ashy, glassy, frigid, Andic Fragiu-dalf, "Mission series" soil (formally: medial, frigid Ochreptic Fragixera) (Page-Dumroese, 1993). This soil type is characteristically poorly drained and shallow (~25.4 mm to ~50.8 mm) to a fragipan where moisture penetration and root growth are restricted. In addition, the soil at this planting site was embedded with many large (ca. 10–20 mm diameter) cobblestones. These rocky soil conditions were more representative of whitebark pine's native conditions than the deeper and better-drained soil at the Exp. 1 site (see Weaver, 2001).

Both experiments used a rectangular-shaped, randomized, complete block design with an initial planting of 30 trees per population. Populations were organized in five trees per row-plot within each of six blocks (30 total rows) in Exp. 1. In Exp. 2, populations were organized into 10 trees per row-plot with 3 columns per row across 15 rows within three blocks (9 columns total). Columns were perpendicular to rows in equivalence with row-plots. Individual trees in Experiments 1 and 2 were planted using a dibble tool at a spacing of 1 × 1 m and 35.56 × 33.02 cm (14 × 13 in), respectively. Spacing in Exp. 1 was greater because the planting was intended to be used as a small orchard after completion of the study. A border row of nonmeasured whitebark pine seedlings was planted in each site to equalize competitive effect on measured trees.

Substantial efforts were made to control extraneous environmental influences in both experiments. Fencing was used to exclude ungulates and burrowing mammals. Weeds were regularly hoed in Experiment 1 and removed by hand in both experiments through 2005. Supplemental irrigation was applied in late summer as needed in 2003 and 2004 on both sites. Thinning to prevent competitive interaction among trees was not necessary despite close planting in Exp. 2 (35.56 × 33.02 cm) due to mortality before crowding and the species' characteristic slow growth.

**Growth and survival data and climate estimates**—Calipers were used to measure shoot elongation over multiple growing seasons from 2001 to 2005. Survival was measured over multiple years in fall 2001–2005, 2011 and 2012, in Exp. 1, and 2003–2006, 2010–2012 in Exp. 2. Total aboveground height was measured on 14-yr-old trees in fall 2012 for both experiments.

To assess height growth under benign conditions (growth potential), we focused the current study on results from early apical shoot elongation, 2003–2005, when natural drought stress was likely low. Supplemental irrigation had been applied in 2003 and 2004 and growing season precipitation in 2005 was relatively high.

For each population's geographic origin, monthly precipitation and minimum and maximum and average temperatures at the seed origin were interpolated using the program ANUSPLINE version 4.3 as a function of latitude, longitude, and elevation (Rehfeldt, 2006 and available at <http://charcoal.cnre.vt.edu/climate/customData/>). These data were then used to calculate derived values for 24 climate variables of demonstrated importance in biology (see Tuhkanen, 1980; Rehfeldt et al., 2006; Larson and Kipfmüller, 2010) that represent the extent and seasonality of temperature and moisture and their interaction (Appendix S1, see Supplemental Data with this article). The point estimates of climate were calculated using data from weather stations in North America that were normalized for the period of 1961 to 1990 (Environment Canada, 1994; U. S. Department of Commerce, 1994; Rehfeldt, 2006).

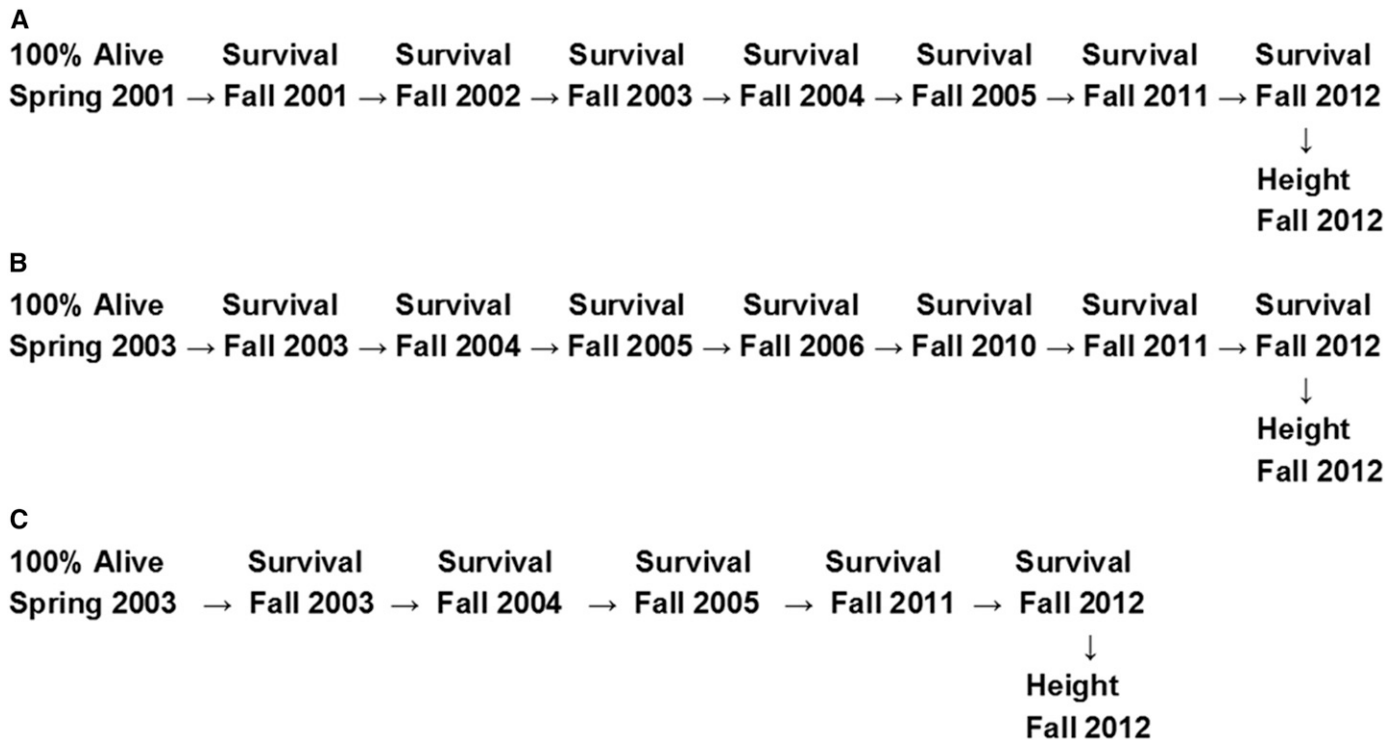
**Statistical analyses**—In assessments of population performance through studies of traits, it is common to focus on survivors alone and ignore mortality. Trait expression is, however, conditional on survival. For example, average height of individuals has been used as a proxy for fitness of tree populations, given that future fecundity is likely associated with height. However, the expression of individual height is dependent on survival, which is a key component of fitness. Therefore, comparison of fitness among populations using height as a proxy is appropriate when survival is similar but is likely to be misleading when survival differs. To account for both survival and height as components of overall fitness, we employed aster modeling (Geyer et al., 2007; Shaw et al., 2008) in novel analyses to estimate mean height of individuals while accounting for mortality from the initial cohort. We use the term unconditional expected height to refer to estimates of mean height that explicitly account for structural zeros due to mortality as our best proxy for individual fitness, given that future fecundity both depends on survival and is likely associated with height. All other estimates refer to conditional measures.

We implemented our aster analysis by means of the reaster (random effects aster) function (Geyer, 2013) in R (R Core Team, 2015). Survival and unconditional expected height were modeled to the year 2012 using survival beginning in 2001 for Exp. 1 and 2003 for Exp. 2 (Fig. 2). Experiments 1 and 2 were also analyzed jointly. Survival was modeled as a Bernoulli random variable, and mean height was modeled using the normal distribution. All analyses used a constant of 1 as the root node. Following the first stage (initial survival), each successor variable (succeeding year of survival or final height) was modeled as depending on the one preceding it in the graphical model (Fig. 2). Analysis of survival alone considered survival for the year of interest and survival for the year(s) before that year. The degree of differentiation among populations for survival and fitness (as the joint expression of survival and height) was then assessed using maximum likelihood.

The degree of differentiation among populations for mean apical shoot elongation in 2005 and mean height in 2012, conditional on survival, were assessed using generalized linear mixed-effects models (GLMMs) using the lmer function (Bates et al., 2013) in R (R Core Team, 2015). The GLMM form for analysis of mean apical shoot elongation in 2005 and mean height in 2012 was:

$$Y_{ijkl} = U + E_i + R(E)_{ij} + C(E)_{ik} + P_l + EP_{il} + e_{ijkl},$$

where  $Y_{ijkl}$  is the observed unit value of the  $l$ th population, in the  $j$ th row and  $k$ th column nested within the  $i$ th experiment;  $U$  is the overall mean;  $E_i$  is the experiment effect;  $R(E)_{ij}$  is the effect of row nested within experiment;  $C(E)_{ik}$  is the effect of column nested within experiment;  $P_l$  is the population effect;  $EP_{il}$  is the interaction of the  $i$ th experiment and the  $l$ th population; and  $e_{ijkl}$  is the random residual error. To better account for study plot effects, we used row and columns in place of blocks. For both aster and GLMM analysis of the degree of differentiation among populations for their respective response variables (unconditional expected height and survival; mean height, and mean annual apical shoot elongation of survivors), experiment was treated as categorical fixed effect. Columns and rows within experiment, population, and the interaction of population and experiment were treated as random effects. Statistical significance of the fixed effect was tested by comparing the likelihoods of nested models.



**FIGURE 2** Graphical models for full aster analysis unifying population survival and mean height data to assess fitness for (A) Experiment 1, (B) Experiment 2, and (C) Experiments 1 and 2 combined. Each node represents a component of life history; arrows represent the dependent association between predecessor and successor life-history components.

**Climate patterns of genetic variation**—To evaluate the relationships between fitness measures and climate of seed origin, we independently assessed each experiment using the statistical framework presented by Leites et al. (2012). The GLMM form for the analysis was:

$$Y_{ijkl} = U + E_i + R_j + C_k + P_l + e_{ijkl},$$

where  $Y_{ijkl}$  is the observed unit value of the  $l$ th population; in the  $i$ th experiment, in the  $j$ th row and  $k$ th column,  $U$  is the overall mean;  $E_i$  is the effect of environment (climate or geography) at seed origin;  $R_j$  is the effect of row;  $C_k$  is the effect of column;  $P_l$  is the population effect; and  $e_{ijkl}$  is the random residual error. Climate and geography of seed origin were treated as fixed effects. Effects of columns, rows, and population were treated as random effects. Here, climate or geography of seed origin ( $E_i$ ) and population ( $P_l$ ) jointly account for differences among populations. The inclusion of a population-level random effect accounted for population level effects not explained by climate or geography of seed origin. Including this random effect was necessary to account for within-group correlation.

The process used to select environmental variables and identify the best climate model for fitness related traits was conducted as follows. Forward stepwise selection was used to identify environmental variables that were significantly associated with each response variable using aster for unconditional expected height and survival and GLMM for mean height and mean apical shoot elongation. Twenty-four climate (Appendix S1) and three geographic variables (latitude, longitude, and elevation) were tested using maximum likelihood. Geographic variables were

tested separately from climate variables to determine how fitness variation among populations corresponded with other environmental factors independent of the climate variables tested. Significant ( $P < 0.05$ ) variables were retained. Those variables that were highly correlated (Pearson's correlation coefficient  $\geq 0.7$ ) with the climate variable in the best model were eliminated. The process was then repeated, adding a single variable from the remaining pool to the best model to test models using two variables. Correction for multiple comparisons was not made because of substantial collinearity among variables, the comparisons were hypothesis-driven, and an increased risk of type II error (see Rothman, 1990). All comparisons are presented in Appendix S1.

The procedure used to describe seed transfer distance for practical application followed the floating seed zone model approach described by Rehfeldt (1983). The estimation of mean within-population variance used residual error variance divided by the number of blocks for each experiment. The square root of the estimation of mean within-population variance provided a mean within-population standard deviation. Confidence intervals were calculated at the significance level 0.2 to reduce the probability of committing a type II error. For gene conservation applications, type II errors are as great if not a greater concern than type I errors (Brosi and Biber, 2009). Confidence intervals were used to identify the climatic distance per unit that reasonably distinguished two populations with respect to a particular trait. A population's performance for traits examined was considered to include the population's mean and its upper and lower confidence intervals. Two populations were considered to be significantly different when one population's mean was outside of the confidence

interval of the other. The formula used for confidence intervals was:

$$\begin{aligned}\text{Upper C.I.}_{0.2} &= T_{\Delta/2} * \text{sqrt}((\text{REV})/b) \text{ and } \text{Lower C.I.}_{0.2} \\ &= -(T_{\Delta/2} * \text{sqrt}((\text{REV})/b)),\end{aligned}$$

where  $\text{CI}_{0.2}$  is the 80% confidence interval;  $T_{\Delta/2}$  is the value of  $t$  at the desired significance level; REV (an estimate of the root within-population variance) is the residual error variance, and  $b$  is the number of blocks. Estimation of confidence intervals for survival used the standard score at the desired significance level multiplied by the standard error.

The study data set excluded plant response data from the first growing season following outplanting to allow time for establishment. Due to mortality during this establishment period, the number of trees for each population in each experiment varied (Table 1). In addition, the few plants that died apparently due to white pine blister rust and beetle larvae attack in Exp. 1 and deer browsing in Exp. 2 were omitted from the analysis. In total, 1099 trees and 964 trees were assessed in Exp. 1 and Exp. 2, respectively.

## RESULTS

After 12 and 10 yr of growth in the field in the warm-dry climate, mean heights of survivors for the 14-yr-old trees were 1479 mm and 1103 mm with 39% and 40% survival for Experiments 1 and 2, respectively (Table 2). Differences between the two experiments were statistically significant for mean height of survivors and mean apical shoot elongation in 2005 (Table 3) but not for survival or unconditional expected height (i.e., height, taking into account the null heights of those trees that died, Table 4). In both experiments, survival declined episodically in association with dry growing season in 2002 and 2006–2011 (Table 2). Accordingly, nearly all mortality appeared to be associated with drought.

**Population differentiation**—In Exp. 1, survival varied among populations from 8 to 75%, while apical shoot elongation in 2005 varied from 73.3 mm to 164.5 mm, and height among survivors in 2012 varied from 904 mm to 2144 mm. In contrast, populations in Exp. 2 ranged from 19 to 77% survival and 46.4 mm to 136.5 mm for apical shoot elongation in the 2005, and 188 mm to 1243 mm for height in 2012.

In the joint analysis of Experiments 1 and 2, populations differed between experiments for apical shoot elongation in 2005 (Table 3) and survivorship (Table 4), as revealed by a significant ( $P < 0.05$ ) interaction between experiment and population. Given these interactions, Experiments 1 and 2 were assessed independently in all subsequent analyses. Notably, however, populations with the lowest survival and apical shoot elongation in Exp. 2, also had the lowest survival and apical shoot elongation in 2005 in Exp. 1. In the

separate analysis of each experiment, survival and apical shoot elongation in 2005 differed significantly among populations. Inferences of unconditional height, which reflected variation in survival more so than variation in height (Table 5) and height among survivors, were only detectably different among populations in Exp. 1 (Table 4 and Table 3, respectively).

**Environmental clines**—Forward stepwise multiple regression analysis detected significant relationships between climate and geography of the seed origin for unconditional expected height in Exp. 1 and apical shoot elongation in 2005 and survival in Experiments 1 and 2 (Table 6). Model performance did not improve with additional predictors; hence, models with a single environmental predictor were chosen for all response variables.

In Exp. 1, apical shoot elongation in 2005 was negatively related to the annual ratio of growing season precipitation to mean annual precipitation (PRATIO). Higher values of PRATIO describe climate that exhibits increasingly higher proportion of annual precipitation during the growing season. In the study region (region of seed collection), increasing values of PRATIO were largely determined ( $r^2 = 0.86$ ) by decreasing winter precipitation (e.g., snow). PRATIO accounted for 5.4% of the variation in apical shoot elongation among populations (Fig. 3A). Survival and unconditional expected height were negatively related to winter cold weighted by the annual dryness index (ADIMMINDD0), which is a unitless index where increasing values describe climate that is increasingly dryer and colder. ADIMMINDD0 accounted for 5 and 7% variation in survival (Fig. 3B) and unconditional expected height (Fig. 3C) among populations, respectively. Notably, ADIMMINDD0 and PRATIO are highly correlated over the study region (Table 5). The general geographic pattern of genetic variation is a cline of increasing growth and survival among seed origins from a south-east to northwest direction and with decreasing elevation in correspondence with increasingly mild climate in the study region (Fig. 4A, B).

In Exp. 2, shoot elongation varied significantly in relation to the Julian date when the sum of degree-days  $>5^\circ\text{C}$  reached 100 (D100) at the seed origin. D100 is a measure of the timing of spring warming and is positively correlated with elevation over the study region. Height growth decreased with increasing D100 (later spring warming) at the seed origin. D100 accounted for 21.3% of variation among populations for apical shoot elongation in 2005 (Fig. 3D). Similar to height growth in Exp. 1, height growth generally increased with decreasing elevation and from a southeast to northwest direction in correspondence with milder climate among seed origins (Fig. 4C).

In Exp. 2, survival declined significantly in relation to increasing annual spring precipitation (SPRP) at the seed origin (Fig. 3E). SPRP accounted for 15.2% of variation in survival among populations. Notably, survival was not significantly related to SPRP when mortality following the drier than average growing season of 2006 was excluded from the analysis. The general geographic pattern

**TABLE 2.** Total survival (%) by year for whitebark pine (*Pinus albicaulis*) in common garden Experiments (Exp.) 1 and 2. Mortality in the first year after outplanting was excluded to avoid aberrant effects of transplanting. Therefore, for each experiment, survival is given as 100% at the start of the year following outplanting.

| Exp. | Spring 2001 | Fall 2001 | Fall 2002 | Spring 2003 | Fall 2003 | Fall 2004 | Fall 2005 | Fall 2006 | Fall 2010 | Fall 2011 | Fall 2012 |
|------|-------------|-----------|-----------|-------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| 1    | 100%        | 96%       | 68%       | —           | 64%       | 63%       | 63%       | —         | —         | 44%       | 39%       |
| 2    | —           | —         | —         | 100%        | 93%       | 87%       | 86%       | 49%       | 42%       | 41%       | 40%       |

**TABLE 3.** Summary of model comparison test for the effects of experiment (Exp.), climate and geographic origin of seed origin on mean apical shoot elongation in 2005 (Shoot elongation) and mean total height among survivors in 2012 (Total height).

| Response variable | Term             | Model df | Model $\chi^2$ | $\chi^2$ df | P value ( $>\chi^2$ ) | Random         | RLRT    | P value    |
|-------------------|------------------|----------|----------------|-------------|-----------------------|----------------|---------|------------|
|                   |                  | df       |                |             |                       | Effect         |         |            |
| Exp. 1 + 2        |                  |          |                |             |                       |                |         |            |
| Shoot elongation  | Null             | 6        |                | —           | —                     | Population     | 1.0646  | 0.1338     |
|                   | Experiment (Exp) | 7        | 11.408         | 1           | <0.0001***            | Exp:Population | 7.6396  | 0.0032**   |
|                   |                  |          |                |             |                       | Row            | 132.21  | <0.0001*** |
|                   |                  |          |                |             |                       | Column         | 150.23  | <0.0001*** |
| Total height      | Null             | 6        |                | —           | —                     | Population     | 1.8385  | 0.0784     |
|                   | Experiment (Exp) | 7        | 18.252         | 1           | <0.0001***            | Exp:Population | 2.4922  | 0.0513     |
|                   |                  |          |                |             |                       | Row            | 42.979  | <0.0001*** |
|                   |                  |          |                |             |                       | Column         | 43.422  | <0.0001*** |
| Only Exp. 1       |                  |          |                |             |                       |                |         |            |
| Shoot elongation  | Null             | 5        |                | —           | —                     | Population     | 25.079  | <0.0001*** |
|                   | PRATIO           | 6        | 6.5139         | 1           | 0.0171*               | Row            | 7.7837  | 0.002**    |
|                   | Elevation        | 6        | 8.3788         | 1           | 0.0038**              | Column         | 18.55   | <0.0001*** |
| Total height      | Null             | 5        |                | —           | —                     | Population     | 14.837  | 0.0001***  |
|                   | PRATIO           | 6        | 3.5474         | 1           | 0.0596                | Row            | 7.8404  | 0.0017**   |
|                   | Latitude         | 6        | 2.8747         | 1           | 0.0900                | Column         | 6.3519  | 0.0048**   |
| Only Exp. 2       |                  |          |                |             |                       |                |         |            |
| Shoot elongation  | Null             | 5        |                | —           | —                     | Population     | 24.151  | <0.0001*** |
|                   | D100             | 6        | 7.3933         | 1           | 0.0065**              | Row            | 0       | NA         |
|                   | Elevation        | 6        | 6.7091         | 1           | 0.0096**              | Column         | 5.7654  | 0.0054**   |
| Total height      | Null             | 5        |                | —           | —                     | Population     | 0.74038 | 0.1747     |
|                   |                  |          |                |             |                       | Row            | 0       | NA         |
|                   |                  |          |                |             |                       | Column         | 6.9104  | 0.0036**   |

Notes: Null models included only intercepts for life history components. For each response variable, only the most significant geographic and climate variable were included in the model. For each predictor variable, its effect was tested against the null model. Random effects show results from the null model. RLRT P value based on 10,000 simulated values. See Table 1 for explanation of climate variables. \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

of genetic variation observed is a cline of increasing survival in a generally northwest to southeast direction in the study region in correspondence with decreasing annual spring precipitation (Fig. 4D).

The amount of variation among populations for growth and survival explained by the geographic variables was similar to that of the associated climate variables. However, one exception was found in Exp. 2, where elevation at seed origin and D100 explained 21.4% and 6.6% of variation in height conditional on survival, respectively (Table 6).

## DISCUSSION

The identification of genetic divergence that corresponds to environmental variation represents strong evidence of adaptive clines. The current study detected evidence of genetic divergence of quantitative traits (growth and survival) among populations of whitebark pine that varied significantly with climate of seed origin (i.e., population origin). The rate of detectable change (slope or steepness of cline) among populations for differences in growth and survival in relation to climate was relatively gentle in comparison to many tree species (cf. Morgenstern, 1996; Rehfeldt et al., 2014). Thus, the extent of apparent local adaptation to climate among populations was found to be relatively low.

The current study was conducted at a relatively low elevation (671 m a.s.l.) where climate approaches predicted future climate for the present distribution of whitebark pine (see Mote and Salathé, 2010; see Table 1). In comparison to the warmest seed origin among study populations (Beaver Creek, Idaho), the study sites were warmer in mean annual temperature by  $\sim 4.2^\circ\text{C}$ . In addition, conditions for dry soil were observed during several growing seasons at

both experiment sites, while soils in whitebark pine's natural habitat are generally moist (Daubenmire, 1968) and thought to rarely be subject to drought (Weaver, 2001). Thus results of this study may not necessarily indicate growth and survival in the current native habitat. Nevertheless, in common garden studies, significant phenotypic variation among populations that is associated with climate at seed origin is indicative of genetic divergence that reflects response to natural selection mediated by conditions at the seed origin (Turesson, 1925).

**Survival**—Survival is a complex trait that can reflect performance in relation to the environment. Indeed, survival among populations varied between differing experimental environments in the current study (Table 4). In Exp. 1, survival slightly favored seed sources from increasingly warm-wet origins (decreasing ADIMMINDD0), while in Exp. 2 survival favored seed sources from increasingly drier locations (decreasing SPRP). This interaction may have resulted from differences in drought severity mediated by the stark contrast in soil composition between the closely located ( $\sim 3.5$  km) study sites. The soil in the Exp. 2 site was shallow and rocky, whereas soil in the Exp. 1 site was deep and well tilled; therefore, populations in Exp. 2 may have experienced more severe drought effects due to restricted root development and drier soil conditions during dry growing seasons.

The detection of differential mortality following a dry growing season that was negatively associated with precipitation (SPRP) among seed sources suggests that whitebark populations had adapted to variation in water availability. In a range-wide study comparing populations in common gardens, Bower and Aitken (2008) also identified variation in survival that was correlated with water availability at the seed source. In particular, they found that variation in survival was positively correlated with summer precipitation and

TABLE 4. Results from aster model comparisons testing for the effects of experiment (Exp.), climate and geographic origin of seed origin on survival, and unconditional expected height in 2012 in Experiments (Exp.) 1 and 2 and their combination.

| Response variable             | Term             | Model df | Model deviance | Test df | Test deviance | Test P  | Random effects: square roots of variance components |          |            |
|-------------------------------|------------------|----------|----------------|---------|---------------|---------|-----------------------------------------------------|----------|------------|
|                               |                  |          |                |         |               |         | Estimate                                            | SE       | P value    |
| Exp. 1 + 2<br>Survival        | Null             | 6        | 12,146,386     | —       | —             | —       | 0.163                                               | 0.2144   | 0.2236     |
|                               | Experiment (Exp) | 7        | 12,146,386     | 1       | 0.66039       | 0.4164  | 0.3202                                              | 0.1502   | 0.0165*    |
|                               |                  |          |                |         |               |         | 1.0199                                              | 0.1402   | <0.0001*** |
| Unconditional expected height | Null             | 6        | 3,207,830      | —       | —             | —       | 1.0565                                              | 0.212    | <0.0001*** |
|                               | Experiment (Exp) | 7        | 3,207,830      | 1       | 0.0076264     | 0.9304  | 0.001644                                            | 0.07470  | 0.4910     |
|                               |                  |          |                |         |               |         | 0.03899                                             | 0.00449  | <0.0001*** |
| Only Exp. 1<br>Survival       | Null             | 8        | 1224.2         | —       | —             | —       | 0.063643                                            | 0.00684  | <0.0001*** |
|                               | ADIMINDDO        | 9        | 1228.1         | 1       | 3.8812        | 0.0488* | 0.063076                                            | 0.01064  | <0.0001*** |
|                               | Latitude         | 9        | 1228           | 1       | 3.7142        | 0.0540  | 0.4475                                              | 0.1286   | 0.0003***  |
| Unconditional expected height | Null             | 8        | 1240.6         | —       | —             | —       | 1.3166                                              | 0.2009   | <0.0001*** |
|                               | ADIMINDDO        | 9        | 1246           | 1       | 5.4012        | 0.0201* | 1.6397                                              | 0.09624  | <0.0001*** |
|                               | Latitude         | 9        | 1245.7         | 1       | 4.722         | 0.0237* | 0.0004229                                           | 0.00008  | <0.0001*** |
| Only Exp. 2<br>Survival       | Null             | 8        | 367.18         | —       | —             | —       | 0.000792                                            | 0.00012  | 0.0001***  |
|                               | SPRP             | 9        | 373            | 1       | 5.1998        | 0.0158* | 0.00103                                             | 0.00029  | <0.0001*** |
|                               | Latitude         | 9        | 373.23         | 1       | 5.0491        | 0.0139* | 0.25127                                             | 0.11166  | 0.0122*    |
| Unconditional expected height | Null             | 8        | 367.83         | —       | —             | —       | 0                                                   | NA       | NA         |
|                               |                  |          |                |         |               |         | 0.23789                                             | 0.09624  | 0.0067**   |
|                               |                  |          |                |         |               |         | 1.64E-04                                            | 1.05E-04 | 0.0595     |
|                               |                  |          |                |         |               |         | 0                                                   | NA       | NA         |
|                               |                  |          |                |         |               |         | 2.11E-04                                            | 0.00008  | 0.0040***  |

Notes: Null models included only intercepts for life history components. For each response variable, only the most significant geographic and climate variable were included in the model. For each predictor variable, its effect was tested against the null model. Random effects show results from Null model. See Table 1 for explanation of climate variables. \*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001.



**TABLE 5.** Pearson correlation coefficients among population means for quantitative traits and geographic and climatic variables.

|            | S1      | S2     | UHT1    | UHT2    | HT1     | HT2    | SE1    | SE2    | Lat.     | Long.   | Elev.   | D100  | SPRP     | ADIMMINDDO |
|------------|---------|--------|---------|---------|---------|--------|--------|--------|----------|---------|---------|-------|----------|------------|
| S2         | 0.28    |        |         |         |         |        |        |        |          |         |         |       |          |            |
| UHT1       | 0.77*** | 0.11   |         |         |         |        |        |        |          |         |         |       |          |            |
| UHT2       | 0.17    | −0.06  | 0.10    |         |         |        |        |        |          |         |         |       |          |            |
| HT1        | 0.47*   | −0.08  | 0.64*** | 0.24    |         |        |        |        |          |         |         |       |          |            |
| HT2        | 0.30    | 0.05   | 0.19    | 0.65*** | 0.21    |        |        |        |          |         |         |       |          |            |
| SE1        | 0.33*   | −0.27  | 0.56**  | 0.19    | 0.72*** | 0.26   |        |        |          |         |         |       |          |            |
| SE2        | 0.18    | −0.05  | 0.12    | 0.31    | 0.23    | 0.25   | 0.46*  |        |          |         |         |       |          |            |
| Lat.       | −0.05   | −0.40* | 0.20    | 0.28    | 0.18    | 0.29   | 0.47*  | 0.37*  |          |         |         |       |          |            |
| Long.      | −0.05   | 0.19   | −0.29   | −0.08   | −0.03   | −0.16  | −0.24  | −0.07  | −0.66*** |         |         |       |          |            |
| Elev.      | 0.09    | 0.33*  | −0.16   | −0.35*  | −0.13   | −0.33* | −0.38* | −0.39* | −0.84*** | 0.70*** |         |       |          |            |
| D100       | 0.15    | 0.18   | 0.08    | −0.32   | 0.00    | −0.28  | −0.21  | −0.48* | −0.53**  | 0.30    | 0.83*** |       |          |            |
| SPRP       | −0.10   | −0.34* | 0.04    | −0.14   | 0.01    | −0.18  | 0.17   | −0.02  | 0.45*    | −0.36*  | −0.11   | 0.27  |          |            |
| ADIMMINDDO | −0.02   | 0.23   | −0.34*  | −0.12   | −0.28   | −0.13  | −0.37* | −0.14  | −0.72*** | 0.70*** | 0.65*** | 0.22  | −0.60*** |            |
| PRATIO     | −0.04   | 0.13   | −0.37*  | −0.14   | −0.25   | −0.18  | −0.32  | −0.09  | −0.61*** | 0.81*** | 0.72*** | 0.33* | −0.30    | 0.90***    |

Notes: S = survival, UHT = unconditional height, HT = height, SE = total apical shoot elongation (growth potential), 1 = Experiment 1, 2 = Experiment 2. Results represent only means from populations present in both experiments. See Table 1 for explanation of geographic climate variables. \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

negatively correlated with the summer aridity index among populations originating from the Cascade Range in Oregon and California. They did not, however, detect variation for survival among populations from the Northern Rockies as identified in the current study. The dissimilarity between study results for the Northern Rockies may be due to differences in experimental power or differences in drought stress between study environments.

The map projection of annual spring precipitation (SPRP) is representative of the geographic distribution of clinal variation for whitebark pine survival under warm-dry climate and natural drought. It reveals a trend of increasing survival in a generally northwest to southeast direction (Fig. 4D). Thus, seed origins from locations with low rainfall during whitebark pine's growing season, which are mostly located in relatively colder regions of southern Idaho and Wyoming, appear to represent populations better adapted for survival in response to drought. Clinal variations associated with drought resistance have also been reported in Douglas-fir where seed source from regions with relatively cold winters and arid summers were identified to be best adapted to drought (Kaya et al., 1994; Bansal et al., 2015). In addition, clinal variation for survival in association with variation in precipitation patterns (heat to moisture ratio) among seed origin has also been reported for the co-occurring species lodgepole pine (*Pinus contorta*, Rehfeldt et al., 1999).

**Growth potential**—Height growth measured during the juvenile stage when stress is limited (i.e., growth potential) can be predictive of mature height on favorable sites that are relatively stress-free.

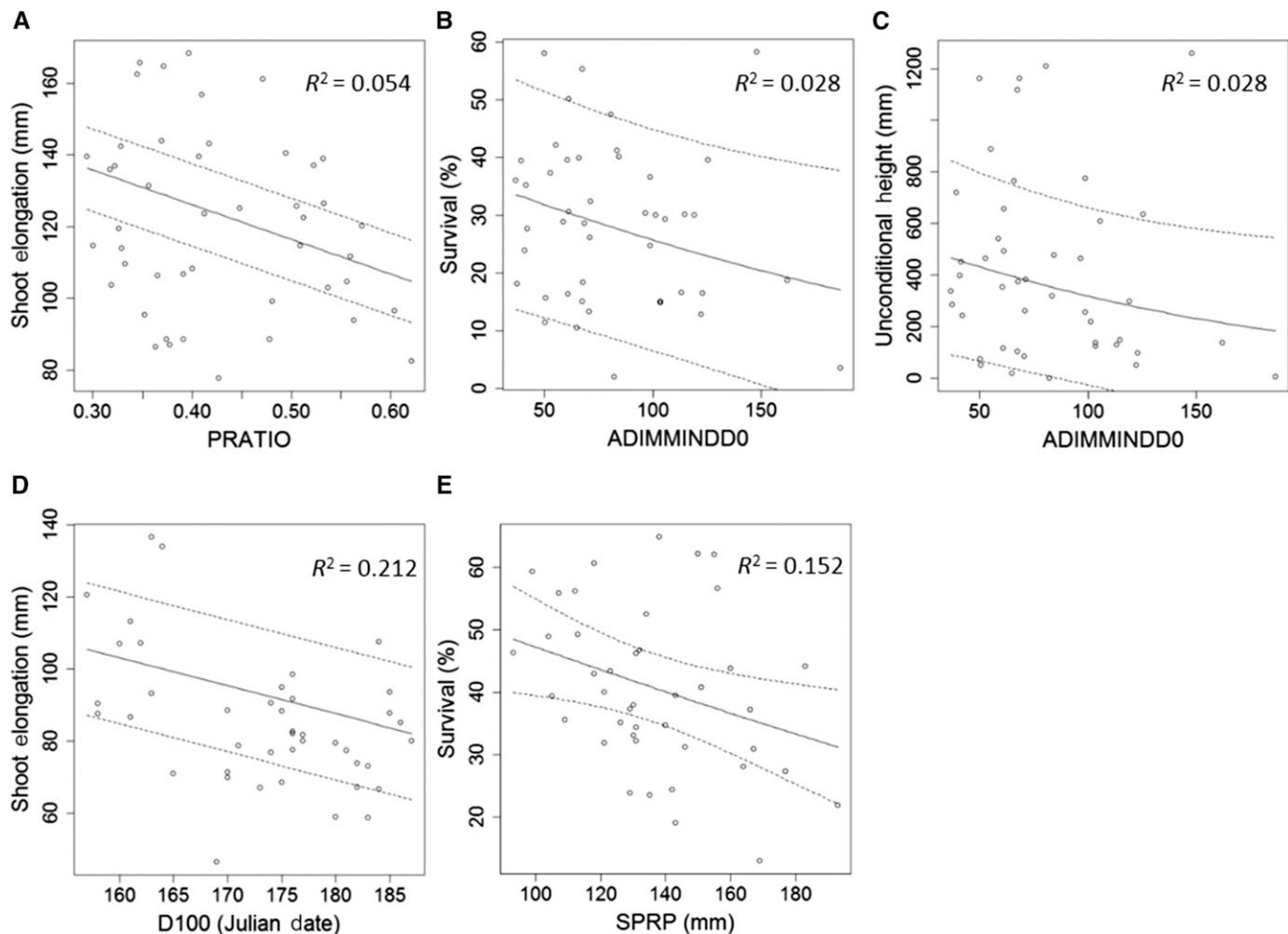
For example, height variation among seed sources of 2-yr-old Scots pine (*Pinus sylvestris*) grown under limited stress in a greenhouse, accounted for 80% of the variation in 13-yr height growth observed among the same seed sources located at 46 favorable field sites across Russia (Rehfeldt, 2004). In the current study, growth potential was assessed using total shoot elongation in 2005, following two consecutive growing seasons with limited moisture stress. By this measure, variation in growth potential accounted for at most 23.6% variation in height at age 14 yr. The relative weakness of this relationship can be interpreted as a general indication that the cumulative environmental stress over the full study period impaired the growth potential of individuals within most populations. Alternatively, this result could be explained by random environmental effects or differential adaptive responses at the test sites.

Growth potential differed significantly among populations (Table 3) and was positively related to mildness of climate at the source location, as indicated by timing of spring warming (D100) and the ratio of annual precipitation to growing season precipitation (PRATIO). These results are generally consistent with findings of Bower and Aitken (2008), who found increasing height growth with mean annual temperature (MAT) of the seed origin of 2-yr-old trees from populations in the Rocky Mountain region. In the current study, MAT was a nearly significant predictor of height growth (Appendix S1). The positive relationship between growth and mildness of climate at seed origin is well documented and common among temperate and boreal conifers as evidenced by similar findings among many species including western larch

**TABLE 6.** Results of multiple regression analyses that describe genetic variation in whitebark pine (*Pinus albicaulis*) in response to climate of seed origin.

| Term             | Independent climate variable | R <sup>2</sup> | Model     |           | Independent geographic variable | R <sup>2</sup> | Model     |         |
|------------------|------------------------------|----------------|-----------|-----------|---------------------------------|----------------|-----------|---------|
|                  |                              |                | Intercept | Slope     |                                 |                | Intercept | Slope   |
| Experiment 1     |                              |                |           |           |                                 |                |           |         |
| Survival         | ADIMMINDDO*                  | 0.05           | 0.37      | −0.001102 | Latitude*                       | 0.061          | 0.371     | −0.0011 |
| Shoot elongation | PRATIO*                      | 0.054          | 164.70    | −96.6     | Elevation **                    | 0.098          | 192.209   | −0.0311 |
| Unconditional    | ADIMMINDDO*                  | 0.074          | 525.57    | −1.722    | Latitude*                       | 0.092          | −2083.9   | 52.7    |
| Expected height  |                              |                |           |           |                                 |                |           |         |
| Experiment 2     |                              |                |           |           |                                 |                |           |         |
| Survival         | SPRP*                        | 0.152          | 0.66458   | −0.0019   | Latitude*                       | 0.177          | 2.133     | −0.0368 |
| Shoot elongation | D100**                       | 0.212          | 254.8241  | −0.9764   | Elevation**                     | 0.2            | 145.904   | −0.0273 |

Notes: See Table 1 for explanation of climate variables. \* $P < 0.05$ , \*\* $P < 0.01$ .



**FIGURE 3** Experiment 1, (A) predicted apical shoot elongation of whitebark pine (*Pinus albicaulis*) plotted in relation to PRATIO at seed origin and (B) predicted survival and (C) unconditional expected height plotted in relation to ADIMMINDD0 [(cold-dryness index) =  $\sqrt{\text{annual sum of degree day} > 5^{\circ}\text{C}} / \text{mean annual precipitation} \times \text{degree days} < 0^{\circ}\text{C}$  using mean minimum temperature at seed origin. Experiment 2, (D) predicted mean annual apical shoot elongation plotted in relation to D100 (Julian date the sum of degree-days  $> 5^{\circ}\text{C}$  reaches 100) at seed origin and (E) predicted percentage survival plotted in relation to SPRP (spring precipitation: April + May) at seed origin. Open circles represent observed population means. Dotted line represent 80% CI.

(*Larix occidentalis*, Rehfeldt, 1995), Engelmann spruce (*Picea engelmannii*, Rehfeldt, 2004), Douglas-fir (*Pseudotsuga menziesii*, St Clair et al., 2005; Rehfeldt et al., 2014), eastern white pine (*Pinus strobus*, Joyce and Rehfeldt, 2013), ponderosa pine (*Pinus ponderosa*, Rehfeldt et al., 2014) and Hartweg's pine (*Pinus hartwegii*, Loya-Rebollar et al., 2013).

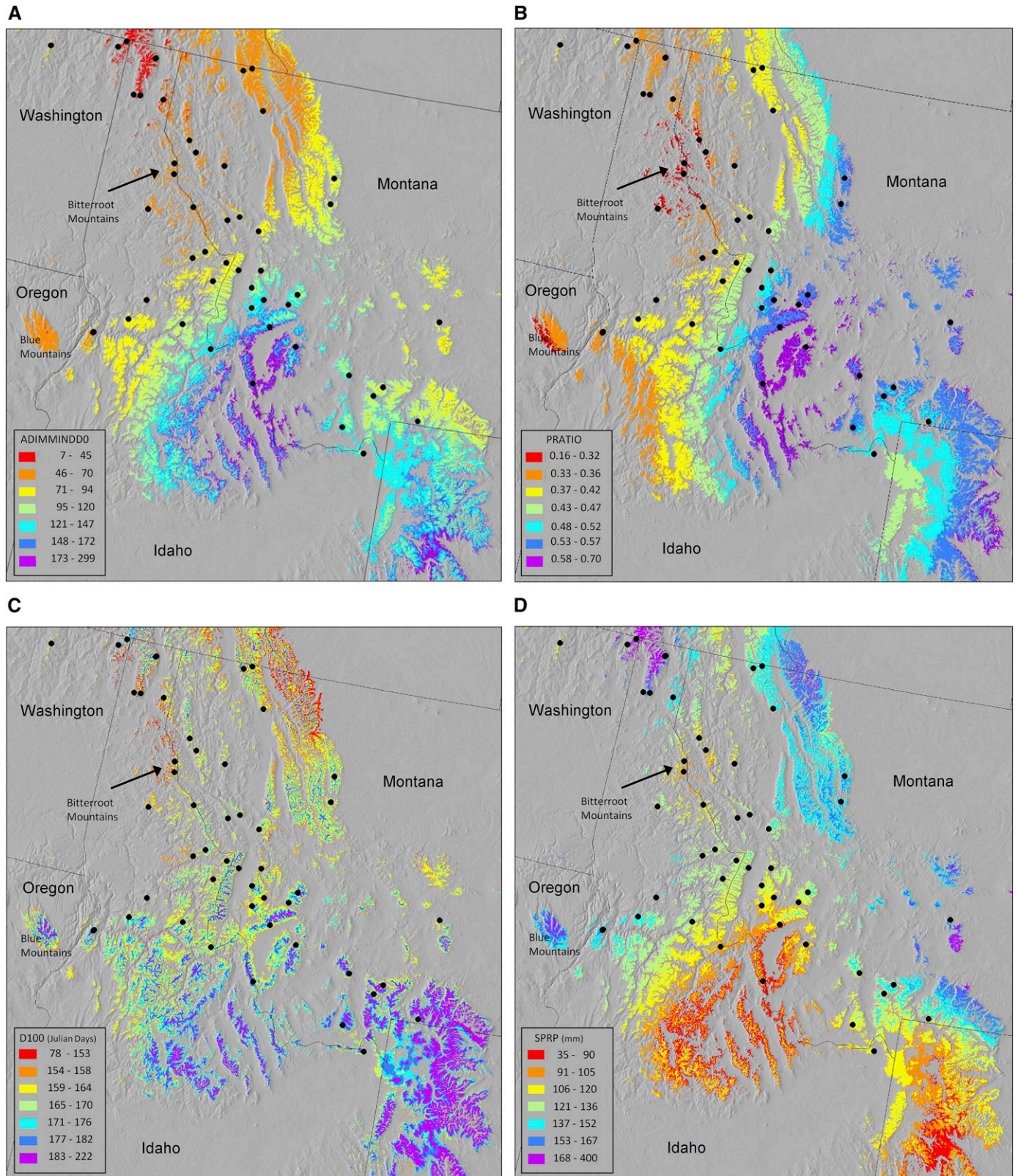
**Fitness**—A population's fitness or tendency to survive and reproduce in a given environment may be interpreted as a measure that predicts its persistence over time in the given environment. However, direct assessment of fitness for many tree species is difficult given their long life span and delayed, intermittent reproduction. For this reason, height, which is correlated with eventual reproductive output is commonly used as a proxy for fitness.

Greater height in conifers is positively associated with male fecundity (see Shea, 1987; Ne'eman et al., 2011; Arista and Talavera, 1994), reproductive surface (see McGraw and Wulff, 1983; Weaver and Forcella, 1986), and competitive ability for light (King, 1990),

which can contribute to fitness. However, height is dependent and thus conditional on survival through the life cycle. Therefore, assessing fitness among populations using inferences of height alone may provide misleading conclusions under conditions where survival varies substantially. Alternatively, use of survival alone to assess population fitness does not account for variation in dependent variables such as height, which may well represent reproductive fitness of survivors. Therefore, joint analyses of survival and height in addition to the independent analysis of each trait can provide a more complete and thus more informative assessment of fitness in comparison to analyses that only consider these fitness proxies independently.

Inferred values of unconditional height from the current study estimate the expected value of height 10 and 12 yr following out-planting taking into account mortality at earlier years. When there has been no mortality, unconditional height is equivalent to height conditional on survival (i.e., height of survivors); with increasing mortality, unconditional height decreases. For example, trees from





**FIGURE 4** (A) Geographic distribution for ADIMMINDD0 (B) PRATIO, (C) D100 (Julian date the sum of degree-days  $>5^{\circ}\text{C}$  reaches 100), and (D) SPRP (spring precipitation: April + May), projected over predicted contemporary climate niche of whitebark pine (*Pinus albicaulis*) in interior northwestern United States. Solid points (●) indicate origin of study populations.



seed that originated from Farnham Peak, Idaho, and Forty Cr. Crazies, Montana, had the same mean height among survivors (1254 mm) but differed in survival (54% and 13%, respectively) in Exp. 1. The inferred unconditional height for Farnham Peak was 658 mm and Forty Cr. Crazies was 188 mm. In this case, unconditional height conveys the fitness advantage of greater survival of the Farnham seed source. As a second example from the opposite extreme, trees from seed that originated from Daisy Pass, Montana and Salmo L.O., Washington had the same survival of 46%, but differed in mean height among survivors (1141 mm and 786 mm, respectively) in Exp. 2. The inferred unconditional height for Daisy Pass was 523 mm and 459 mm for Salmo L.O. In this case, unconditional height conveys the assumed fitness advantage of greater height of the Daisy Pass seed source.

In Exp. 1, the detection of differences among populations for unconditional height that corresponded with ADIMINDDO of seed origin suggests that populations originating from milder climates will exhibit increased fitness under warm-dry conditions where growth is not hindered by restrictive soil conditions. Therefore, where soils (or drought) are not restricting, seed source originating from milder climates appear to be best suited to exhibit higher fitness under predicted warmer climate. In contrast, differences among populations were not detected at the  $P < 0.05$  level, for unconditional height in Exp. 2, even though significant differences were detected for survival and growth potential when assessed independently (Table 4). This result likely reflects a degree of incongruence between survival and growth expressed under growing conditions at the Exp. 2 site. This incongruence did not, however, appear to support a trade-off between survival in response to drought and growth potential as evidenced by the low positive correlation between traits (Table 5). An absence of trade-offs between growth and drought tolerance was also reported for Douglas-fir (Darychuk et al., 2012). Taken together, results from the current study suggest that, to the extent that survival and height are representative of fitness and balanced in their contribution to fitness, populations are not expected to exhibit differences in fitness in response to drought.

Without question, assessing variation in fitness among long-lived trees based on 12 and 10 yr of field growth and survival is tentative and must be interpreted with caution. However, studies of relatively early growth and survival do capture variation expressed during the early life stages when forest trees are more susceptible to climate-related mortality (Namkoong et al., 1972; Namkoong and Conkle, 1976). Even so, in some cases where longer-term provenance experiments have been conducted, selection has been observed at intervals past 50 yr (see Bakker et al., 2006). Thus, provenance experiments of longer duration may yield different results.

**Environmental clines**—A comparison between the mapped projections of climate predictors for survival in response to natural drought and growth potential (Fig. 4D vs. A, B, and C) shows their geographic counterbalance of clinal variation over the study region where survival is expected to increase while growth potential decreases in a generally northwest to southeast direction. Even so, regions where growth and survival are not expected to be counterbalanced are also evident. For example, the climate habitat in the Bitterroot Mountains along the north-central border of Idaho and Montana was predicted to have populations that exhibit relatively high growth and high survival under warm-dry climate, while populations originating from the Blue Mountains in Oregon are

expected to exhibit relatively low survival with a broad range of growth potential under warm-dry climate.

**Management implications**—A fundamental objective of reforestation management is to plant trees that are adapted to the planting site. Results from genecology studies are directly applicable to and are used extensively toward meeting this objective in forest management (Mahalovich, 1995; Johnson et al., 2004; Ying and Yanchuk, 2006). Genecology research focused on assessing genetic variation in relation to climate has also been conducted to address grassland (e.g., St Clair et al., 2013) and rangeland (e.g., Richardson et al., 2014) restoration objectives.

Several analytical approaches (see Johnson et al., 2004) have been devised that use data from genecology studies to judge how far seed collected from a particular location can be moved while minimizing the risk of maladaptation. These approaches interpret clinal variation in terms of natural selection and are based on the breeder's equation ( $R = h^2S$ , see Falconer, 1989) for the response to selection (Morgenstern, 1996). In addition, these approaches assume that populations are best adapted to their local conditions and are less well adapted to conditions the farther from the home site they are grown. The most conservative results from the current study, which were estimated using a floating seed transfer approach (see Campbell, 1974; Rehfeldt, 1983), suggest that seed is reasonably adapted for survival under warm-dry climate if transferred within approximately  $\pm 23$  mm for the SPRP of the seed source climate. For height growth, seed transferred within approximately  $\pm 23.5$  Julian days for D100 (ca.  $\pm 228$  m elevation) of the cone collection site are expected to be reasonably adapted to the climate of the planting site. An examination of these transfer recommendations in relation to climate variation over the study region shows that the land area within the transfer distances is disjunct and spans the majority of the study region (Fig. 4). These results are similar in magnitude of transfer distance recommendations reported by Bower and Aitken (2008) who recommend seed transfer limits of 320 m in elevation in the Rocky Mountain region.

In comparison with other western forest species, our results suggest that the whitebark pine is intermediate between specialist and generalist mode of adaptation for growth potential (see Levins, 1968; Rehfeldt, 1994). Whitebark pine's intermediate mode of adaptation is similar to western larch (*Larix occidentalis*) where genetic differences for growth potential between any two populations are estimated as substantial at approximately  $\pm 225$  m in elevation (Rehfeldt, 1982) in the interior northern Rocky Mountains.

Ongoing climate change is expected to rapidly alter the association between climate and adaptive structure for many plant species in the western United States (Rehfeldt et al., 2006). For example, by the decade beginning in 2030, about 70% of the contemporary realized climate habitat for whitebark pine in the United States and southern Canada is projected to be eliminated due to climate change (Warwell et al., 2007). To the extent that future climate reflects the warm-dry conditions of the current study, results suggest that populations generally located more to the northwest are expected to exhibit greater mortality in comparison to more southeasterly populations in the region. To be sure, informed management decisions will require recommendations that explicitly consider the species' adaptive relationship across a broad range of climates in conjunction with models that consider multiple climatic predictions for specific geographic locations (see Rehfeldt and Jaquish, 2010; Joyce and Rehfeldt, 2013). Clinal variation



identified and described in the current study can be directly applied to inform such recommendations.

## ACKNOWLEDGEMENTS

The authors thank the USDA Rocky Mountain Research Station for funding. Many people provided assistance for this project including Donna Dekker-Robertson, Paul Leigh, Mose Harris IV, Amanda Link, Debra Eastman, and Drs. Charles Geyer, Nicholas Crookston, Gerald Rehfeldt, and Ned Klopfenstein. Thank you to Drs. Ned Klopfenstein, MeeSook Kim, Andrew David, Peter Tiffin, Jeannine Cavender-Bares, and three anonymous reviewers for their helpful comments on earlier drafts of this manuscript.

## LITERATURE CITED

- Arista, M., and S. Talavera. 1994. Pollen dispersal capacity and pollen viability of *Abies pinsapo* Boiss. *Silvae Genetica* 43: 155–158.
- Bakker, J. D., M. M. Moore, and W. W. Covington. 2006. Long-term vegetation studies in the Southwest. In L. C. Irland, A. E. Camp, J. C. Brissette, and Z. R. Donohew [eds.], Long-term silvicultural and ecological studies: Results for science and management, 187–195. GISF Research Paper 5. Global Institute for Sustainable Forestry, School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut, USA.
- Bansal, S., C. A. Harrington, P. J. Gould, and J. B. St Clair. 2015. Climate-related genetic variation in drought-resistance of Douglas-fir (*Pseudotsuga menziesii*). *Global Change Biology* 21: 947–958.
- Bates, D., M. Maechler, and B. Bolker. 2013. lme4: Linear mixed-effects models using S4 classes. Website <http://CRAN.R-project.org/package=lme4>.
- Bower, A. D., and S. N. Aitken. 2006. Geographic and seasonal variation in cold hardiness of whitebark pine. *Canadian Journal of Forest Research* 36: 1842–1850.
- Bower, A. D., and S. N. Aitken. 2008. Ecological genetics and seed transfer guidelines for *Pinus albicaulis* (Pinaceae). *American Journal of Botany* 95: 66–76.
- Brosi, B. J., and E. G. Biber. 2009. Statistical inference, Type II error, and decision making under the US Endangered Species Act. *Frontiers in Ecology and the Environment* 7: 487–494.
- Campbell, R. K. 1974. A provenance-transfer model for boreal regions. *Norsk Institutt for Skogforskning Rapport* 31: 544–566.
- Clausen, J., and W. M. Hiesey. 1958. Experimental studies on the nature of species. IV. Genetic structure of ecological races. Carnegie Institution of Washington Publication 615, Washington, D.C., USA.
- Cooper, S. T., K. E. Neiman, R. Steel, and D. W. Roberts. 1991. Forest habitat types of the northern Idaho: A second approximation. General Technical Report INT-GTR-236. U. S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- COSEWIC [Committee on the Status of Endangered Wildlife in Canada]. 2012. Part 1: Order Amending Schedule 1 to the Species at Risk Act. *Canada Gazette* 146(16): 1162–1208. Available at <http://www.gazette.gc.ca/rp-pr/p1/2012/2012-04-21/html/reg2-eng.html>
- Darychuk, N., B. J. Hawkins, and M. Stoehr. 2012. Trade-offs between growth and cold and drought hardiness in subarctic Douglas-fir. *Canadian Journal of Forest Research* 42: 1530–1541.
- Daubenmire, R. 1966. Vegetation: Identification of typical communities. *Science* 151: 291–298.
- Daubenmire, R. 1968. Soil moisture in relation to vegetation distribution in the mountains of northern Idaho. *Ecology* 49: 431–438.
- Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, et al. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3: 479–486.
- Environment Canada. 1994. Canadian monthly climate data and 1961–1990 normals. Prairie and Northern Region Commercial Weather Services Division, Edmonton, Alberta, Canada.
- Falconer, D. S. 1989. Introduction to quantitative genetics, 3rd ed. Longman, Burnt Mill, UK.
- Farnes, P. E. 1990. SNOTEL and snow course data: Describing the hydrology of whitebark pine ecosystems. Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource, Bozeman, Montana, USA, General Technical Report GTR-INT-270. U. S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- Geyer, C. J. 2013. aster: Aster models. Website <http://CRAN.R-project.org/package=aster>.
- Geyer, C. J., S. Wagenius, and R. G. Shaw. 2007. Aster models for life history analysis. *Biometrika* 94: 415–426.
- Hamlin, J., A. Kegley, and R. Snieszko. 2011. Genetic variation of whitebark pine (*Pinus albicaulis*) provenances and families from Oregon and Washington in juvenile height growth and needle color. The future of high-elevation, five-needle white pines in western North America. In R. E. Keane, D. F. Tomback, M. P. Murray, and C. M. Smith [eds.], Proceedings of the High Five Symposium, Missoula, Montana, USA. Proceedings RMRS-P-63. U. S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Hamlin, J. E., D. Doede, A. Kegley, and R. A. Snieszko. 2008. An assessment of genetic variation of *Pinus albicaulis* populations from Oregon and Washington in relation to height increment, phenology, and form. In N. David, W. Noh, J. King, and R. A. Snieszko [eds.], Breeding and genetic resources of five-needle pines, 104. Korea Forest Research Institute, Yangyang, Korea.
- Heslop-Harrison, J. 1964. Forty Years of Genecology. In J. B. Cragg [ed.], Advances in ecological research, vol. 2, 159–247. Academic Press, London, UK.
- Hutchins, H. E., and R. M. Lanner. 1982. The central role of Clark Nutcracker in the dispersal and establishment of whitebark pine. *Oecologia* 55: 192–201.
- Johnson, G., F. C. Sorensen, J. B. St Clair, and R. C. Cronn. 2004. Pacific Northwest forest tree seed zones: A template for native plants? *Native Plants Journal* 5(2): 131–140.
- Joyce, D. G., and G. E. Rehfeldt. 2013. Climatic niche, ecological genetics, and impact of climate change on eastern white pine (*Pinus strobus* L.): Guidelines for land managers. *Forest Ecology and Management* 295: 173–192.
- Kaya, Z., W. T. Adams, and R. K. Campbell. 1994. Adaptive significance of intermittent shoot growth in Douglas-Fir seedlings. *Tree Physiology* 14: 1277–1289.
- King, D. A. 1990. The adaptive significance of tree height. *American Naturalist* 135: 809–828.
- Larson, E. R., and K. F. Kipfmüller. 2010. Patterns in whitebark pine regeneration and their relationships to biophysical site characteristics in southwest Montana, central Idaho, and Oregon, USA. *Canadian Journal of Forest Research* 40: 476–487.
- Leites, L. P., A. P. Robinson, G. E. Rehfeldt, J. D. Marshall, and N. L. Crookston. 2012. Height-growth response to climatic changes differs among populations of Douglas-fir: A novel analysis of historic data. *Ecological Applications* 22: 154–165.
- Levins, R. 1968. Evolution in changing environments, 120. Princeton University Press, Princeton, New Jersey, USA.
- Loya-Rebollar, E., C. Sáenz-Romero, R. A. Lindig-Cisneros, P. Lobit, J. A. Villegas-Moreno, and N. M. Sánchez-Vargas. 2013. Clinal variation in *Pinus hartwegii* populations and its application for adaptation to climate change. *Silvae Genetica* 62: 86–95.
- Mahalovich, M. F. 1995. The role of genetics in improving forest health. In Forest health through silviculture: Proceedings of the 1995 National Silviculture Workshop: Forest Health Through Silviculture, Mescalero, New Mexico, USA, 200–207. General Technical Report RM-GTR-267. U. S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- Mahalovich, M. F., K. E. Burr, and D. L. Foushee. 2006. Whitebark pine germination, rust resistance, and cold hardiness among seed origins in the Inland Northwest: Planting strategies for restoration. In L. E. Riley, R. K. Dumroese, and T. D. Landis [tech. coords.], National Proceedings: Forest and Conservation Nursery Associations – 2005. Proceedings RMRS-P-43, 91–101. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

- Mattson, D., K. Kendall, and D. Reinhart. 2001. Whitebark pine, grizzly bears, and red squirrels. In D. Tomback, S. Arno, and R. Keane [eds.], *Whitebark pine communities, ecology and restoration*. 121–136. Island Press, Washington, D.C., USA.
- Matyas, C., and C. W. Yeatman. 1992. Effect of geographical transfer on growth and survival of jack pine (*Pinus banksiana* Lamb) populations. *Silvae Genetica* 41: 370–376.
- McGraw, J. B., and R. D. Wulff. 1983. The study of plant growth: A link between the physiological ecology and population biology of plants. *Journal of Theoretical Biology* 103: 21–28.
- Morgenstern, E. K. 1996. Geographic variation in forest trees: genetic basis and application of knowledge in silviculture. UBC Press, Vancouver.
- Mote, P. W., and E. P. Salathé. 2010. Future climate in the Pacific Northwest. *Climatic Change* 102: 29–50.
- Namkoong, G., and M. T. Conkle. 1976. Time trends in genetic control of height growth in ponderosa pine. *Forest Science* 22: 2–12.
- Namkoong, G., R. A. Usanis, and R. R. Silen. 1972. Age-related variation in genetic control of height growth in Douglas-fir. *Theoretical and Applied Genetics* 42: 151–159.
- Ne'eman, G., S. Goubitz, M. J. Werger, and A. Shmida. 2011. Relationships between tree size, crown shape, gender segregation and sex allocation in *Pinus halepensis*, a Mediterranean pine tree. *Annals of Botany* 108: 197–206.
- Page-Dumroese, D. S. 1993. Susceptibility of volcanic ash-influenced soil in northern Idaho to mechanical compaction. Research Note INT-RN-409. U. S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, Utah, USA. doi.org/10.2737/INT-RN-409.
- R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Website https://www.R-project.org/.
- Rehfeldt, G. E. 1982. Differentiation of *Larix occidentalis* populations from the Northern Rocky Mountains. *Silvae Genetica* 31: 13–19.
- Rehfeldt, G. E. 1983. Adaptation of *Pinus contorta* populations to heterogeneous environments in northern Idaho. *Canadian Journal of Forest Research* 13: 405–411.
- Rehfeldt, G. E. 1994. Genetic structure of western red cedar populations in the Interior West. *Canadian Journal of Forest Research* 24: 670–680.
- Rehfeldt, G. E. 1995. Genetic variation, climate models and the ecological genetics of *Larix occidentalis*. *Forest Ecology and Management* 78: 21–37.
- Rehfeldt, G. E. 2004. Interspecific and intraspecific variation in *Picea engelmannii* and its congeneric cohorts: Biosystematics, genecology, and climate change. General Technical Report GTR-134. U. S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Rehfeldt, G. E. 2006. A spline model of climate for the Western United States. General Technical Report GTR-165. U. S. Dept. of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Rehfeldt, G. E., N. L. Crookston, M. V. Warwell, and J. S. Evans. 2006. Empirical analyses of plant-climate relationships for the western United States. *International Journal of Plant Sciences* 167: 1123–1150.
- Rehfeldt, G. E., D. E. Ferguson, and N. L. Crookston. 2008. Quantifying the abundance of co-occurring conifers along Inland Northwest (USA) climate gradients. *Ecology* 89: 2127–2139.
- Rehfeldt, G. E., and B. C. Jaquish. 2010. Ecological impacts and management strategies for western larch in the face of climate-change. *Mitigation and Adaptation Strategies for Global Change* 15: 283–306.
- Rehfeldt, G. E., L. P. Leites, J. B. St Clair, B. C. Jaquish, C. Sáenz-Romero, J. López-Upton, and D. G. Joyce. 2014. Comparative genetic responses to climate in the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: Clines in growth potential. *Forest Ecology and Management* 324: 138–146.
- Rehfeldt, G. E., C. C. Ying, D. L. Spittlehouse, and D. A. Hamilton. 1999. Genetic responses to climate in *Pinus contorta*: Niche breadth, climate change, and reforestation. *Ecological Monographs* 69: 375–407.
- Richardson, B. A., S. J. Brunsfeld, and N. B. Klopfenstein. 2002. DNA from bird-dispersed seed and wind-disseminated pollen provides insights into postglacial colonization and population genetic structure of whitebark pine (*Pinus albicaulis*). *Molecular Ecology* 11: 215–227.
- Richardson, B. A., S. G. Kitchen, R. L. Pendleton, B. K. Pendleton, M. J. Germino, G. E. Rehfeldt, and S. E. Meyer. 2014. Adaptive responses reveal contemporary and future ecotypes in a desert shrub. *Ecological Applications* 24: 413–427.
- Rothman, K. J. 1990. No adjustments are needed for multiple comparisons. *Epidemiology* 1: 43–46.
- Shaw, R. G., C. J. Geyer, S. Wagenius, H. H. Hangelbroek, and J. R. Etterson. 2008. Unifying life-history analyses for inference of fitness and population growth. *American Naturalist* 172: E35–E47.
- Shea, K. L. 1987. Effects of population structure and cone production on out-crossing rates in Engelmann spruce and subalpine fir. *Evolution* 41: 124–136.
- St Clair, J. B., F. F. Kilkenny, R. C. Johnson, N. L. Shaw, and G. Weaver. 2013. Genetic variation in adaptive traits and seed transfer zones for *Pseudoroegneria spicata* (bluebunch wheatgrass) in the northwestern United States. *Evolutionary Applications* 6: 933–948.
- St Clair, J. B., N. L. Mandel, and K. W. Vance-Borland. 2005. Genecology of Douglas fir in western Oregon and Washington. *Annals of Botany* 96: 1199–1214.
- Soil Survey Staff. 1996. Keys to soil taxonomy, 7th ed. U. S. Department of Agriculture, Natural Resources Conservation Service, Washington, D.C., USA.
- Tomback, D. F. 1978. Foraging strategies of Clark's Nutcracker. *Living Bird* 16: 123–161.
- Tomback, D. F., S. F. Arno, and R. E. Keane. 2001. The compelling case for management intervention. In D. F. Tomback, S. F. Arno, and R. E. Keane [eds.], *Whitebark pine communities: Ecology and restoration*, 3–25. Island Press, Washington D.C., USA.
- Tomback, D. F., and K. C. Kendall. 2001. Biodiversity losses: The downward spiral. In D. F. Tomback, S. F. Arno, and R. E. Keane [eds.], *Whitebark pine communities: Ecology and restoration*, 3–25. Island Press, Washington D.C., USA.
- Tuhkanen, S. 1980. Climatic parameters and indices in plant geography. *Acta Phytogeogr Suecica* 67: 1–105.
- Turesson, G. 1925. The plant species in relation to habitat and climate. *Hereditas* 6: 147–236.
- U. S. Department of Commerce. 1994. U.S. divisional and station climatic data and normal, vol. 1. National Oceanic and Atmospheric Administration. National Climatic Data Center, Asheville, North Carolina, USA.
- U. S. Fish and Wildlife Service. 2011. Endangered and threatened wildlife and plants; 12-month finding on petition to list *Pinus albicaulis* as endangered or threatened with critical habitat. 50 CFR Part 17, docket no. FWS-R6-ES-2010-0047. *Federal Register* 76(138): 42631–42654. Available at https://www.gpo.gov/fdsys/pkg/FR-2011-07-19/pdf/2011-17943.pdf.
- Warwell, M. V., G. E. Rehfeldt, and N. L. Crookston. 2007. Modeling contemporary climate profiles of whitebark pine (*Pinus albicaulis*) and predicting responses to global warming. In E. M. Goheen and R. A. Snieszko [tech. coords.], *Proceedings of the conference whitebark pine: A Pacific Coast perspective*, 139–142, 2006, Ashland, Oregon, USA. R6-NR-FHP-2007-01. U. S. Department of Agriculture, Forest Service, Pacific Northwest Region, Portland, Oregon, USA. Available at https://www.fs.fed.us/rm/pubs\_other/rmrs\_2006\_warwell\_m001.pdf.
- Weaver, T. 2001. Whitebark pine and its environment. In D. F. Tomback, S. F. Arno, and R. E. Keane [eds.], *Whitebark pine communities: Ecology and restoration*, 41–73. Island Press, Washington, D.C., USA.
- Weaver, T., and F. Forcella. 1986. Cone production in *Pinus albicaulis* forests. In D. F. Tomback, S. F. Arno, and R. E. Keane [eds.], *Whitebark pine communities: Ecology and restoration*, 68–76. Island Press, Washington, D.C., USA.
- Ying, C. C., and A. D. Yanchuk. 2006. The development of British Columbia's tree seed transfer guidelines: Purpose, concept, methodology, and implementation. *Forest Ecology and Management* 227: 1–13.