

Phenotypic Selection on Growth Rhythm in Whitebark Pine (*Pinus albicaulis*) in Low Elevation Common Gardens

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Abstract—Growth rhythm represents the timing of annual plant growth and development in relation to the environment. Growth rhythm that is well synchronized with the local climate is understood to confer adaptation in plant species. Rapid ongoing climate change threatens to desynchronize growth rhythm for many plant populations, yet knowledge of how plant populations undergo selection on growth rhythm and how they will respond is limited. Therefore, to evaluate phenotypic selection on growth rhythm, seedlings from 49 populations of whitebark pine (*Pinus albicaulis*), representative of the interior northwestern United States, were grown in two common-garden field tests over a 12-year period under climate (+4.4 to 9.1 °C mean annual temperature) approximating projected climate change in the present century for the sampled species range. In addition, variation in growth rhythm among populations and its relation to the climate of the seed source were evaluated to clarify how growth rhythm varies over the study region. Height at the end of the study was used as the best available measure of fitness. Survival and the unconditional expected value for height were dependent on timing of apical shoot elongation rates within and among growing seasons. Comparison of models using survival versus unconditional expected height as the proxy for fitness showed that survival strongly influenced selection on elongation rates. The form and magnitude of selection on timing and rate of shoot elongation varied between test sites and over time. Analysis of the timing of selection detected directional and stabilizing selection on shoot elongation rates in the earliest years whereas only directional selection was detected for selection on elongation rate in later years. Differences among populations for growth rhythm were mild and were explained to a moderate extent ($r^2 = 0.08\text{--}0.28$) by climatic clines. Taken together, these findings suggest that growth rhythm in whitebark pine has been mildly selected for in relation to past climate and will undergo phenotypic selection in response to ongoing climate change. .

INTRODUCTION

Growth rhythm represents the timing of annual plant growth and development in relation to the environment. Growth rhythm that is well synchronized with the local climate is understood to confer adaptation in woody plant species (Dietrichson 1964; Howe et al. 2003; Rehfeldt 1992). Rapid ongoing climate change threatens to desynchronize growth rhythm for many tree populations in the western United States (see, for example, Rehfeldt 2004), resulting in maladaptation. Over the long term, the persistence of natural

populations is determined by the process of evolutionary adaptation. Indeed, evolutionary adaptation is expected when the traits under selection vary within a given population and are heritable (Darwin 1859; Endler 1973; Falconer and Mackay 1996). In keeping with this understanding, evolutionary trajectory may be estimated when information about selection on the phenotype and trait inheritance is available. However, selection on phenotype is not well understood for many tree species under predicted rapid climate change.

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Whitebark pine (*Pinus albicaulis*) is of particular interest given its status as a keystone (Tomback and Kendall 2001) and foundational (Ellison et al. 2005) species in subalpine forest ecosystems of western North America. In addition, due to rapid ongoing climate change, whitebark pine's contemporary (1961–1990) realized climate niche is projected to be eliminated by mid-century for almost all of its distribution in the United States (Warwell et al. 2007). Therefore, the primary objectives of the present study were to (1) assess variation in growth rhythm among populations under warmer and drier climate than the climate of seed origin and (2) estimate the direction and magnitude of selection on variation in growth rhythm. This paper reports only preliminary results.

METHODS

The present study used whitebark pine provenance tests of 46 (test 1) and 42 (test 2) populations, with 39 populations common to both tests. The provenance tests were outplanted in forest openings at Priest River Experimental Forest (Idaho, USA) in April 2000 using 2-year-old trees in test 1 and October 2001 using 4-year-old trees in test 2. These trees were grown over a 12-year period under nonnative climate (+4.4 to 9.1 °C mean annual temperature) that approximated projected climate change in the present century for whitebark pine's contemporary distribution. Growing conditions were mild at the test 1 site, which was characterized by deep, well-drained soil that was tilled prior to planting. In contrast, growing conditions were harsh at the test 2 site. At that site, air temperature was 0.25 °C colder over a 17-month period while soil was shallow, poorly drained, and rocky. Both provenance tests used a randomized complete block design with populations planted in 5-tree row-plots in each of 6 blocks in test 1 and 10-tree row-plots in each of 3 blocks in test 2. Each provenance was represented by 30 seedlings. Measurements of annual incremental apical shoot elongation growth were recorded approximately weekly to biweekly from late March through July in 2001–2005 in test 1 and in 2003–2006 in test 2. Because sequential events of annual development tend to be intercorrelated (Dietrichson 1964), the timing and magnitude of apical shoot elongation were used as proxies for growth rhythm.

To evaluate selection on growth rhythm, the relationship between fitness and timing of intra-annual rate, cessation, initiation, and duration of apical shoot elongation was assessed with aster models (Geyer and Shaw 2008; Geyer et al. 2007) following a general multivariate selection approach (Lande and Arnold 1983). Aster, using the “reaster” function (Geyer 2013) in R (R Core Team 2012) was used to model unconditional expected height, which is an inference of population height that explicitly considers population survival. Normal distributions were used to model final height in 2012 conditional on survival to that year, and Bernoulli was used to model survival through each of multiple intervals concluding in 2012. Unconditional estimates of final height were used as the best available proxy for fitness because they provide a more complete measure of population fitness than either survival or height measures separately. Survival alone was also used as a proxy for fitness. Results from selection analyses using unconditional height and survival alone were compared to distinguish the influence of height from survival on inferred selection.

RESULTS AND DISCUSSION

Elongation rates at the test 1 site were greater than at the test 2 site throughout the study period. Total aboveground mean height of survivors in 2012 differed significantly ($P < 0.05$) between test sites, with 61.4 cm at the test 1 site and 45.3 cm at the test 2 site. Survival to 2012 was 39 and 41 percent in tests 1 and 2, respectively. Survival declined substantially in single episodes in the fall following relatively dry growing seasons in 2002 at the test 1 site and 2006 at the test 2 site.

Timing of initiation, timing of cessation, and duration of elongation were highly correlated. Higher elongation rates were correlated with earlier initiation, later cessation, and longer growth duration overall. Variation in the timing of initiation of shoot elongation spanned 2 weeks; timing of cessation of shoot elongation varied by as much as 3 weeks. Finally, total duration of shoot elongation for most individuals ranged from about 7 to 10 weeks.

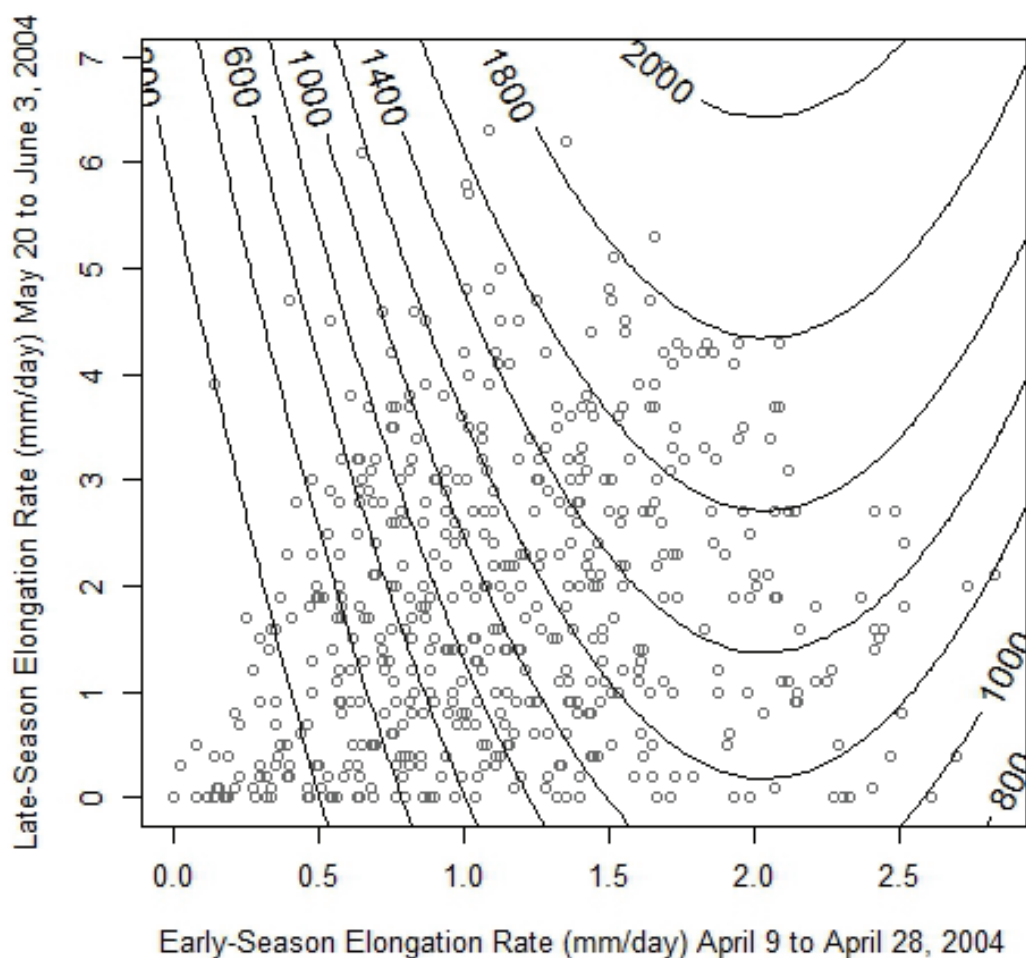


Figure 1—Fitness surfaces showing observed (open circles) apical shoot elongation rates (mm/day) early (Julian dates 108-127) and late (Julian dates 141-155) in the 2004 growing season in relation to modeled unconditional expected height (mm) in 2012 at test 1 site.

Survival and the unconditional expected value for height were dependent on timing of apical shoot elongation rates within and among growing seasons. A comparison of models using survival versus unconditional expected height as the proxy for fitness showed that survival strongly influenced selection on shoot elongation rates. The form and magnitude of selection on timing and rate of shoot elongation varied between test sites and over time. More complex selection was observed in test 1, which had more favorable growing conditions than test 2. Analysis of the timing of the form of selection detected directional and stabilizing selection in the earliest years, whereas only directional selection was detected for selection on elongation rate in later years (fig. 1).

A substantial range of variation in timing and rate of apical shoot elongation was observed within all populations. Differences among populations for growth rhythm were mild and were explained to a moderate extent ($r^2 = 0.08\text{--}0.28$) by climatic clines. Faster and longer growing populations originate from locations where winters were milder and precipitation was more balanced over the year. This climate tends to occur in an increasing southeast to northwest direction in the interior northwestern United States.

Taken together, study findings suggest that growth rhythm in whitebark pine has been mildly selected for in relation to past climate and is likely to undergo further selection in response to ongoing climate

change. In addition, this study is an initial step toward assessing how growth rhythm in pine populations may evolve in response to ongoing climate change. Continuing research is needed to assess phenotypic selection of growth rhythm and other key adaptive traits of forest tree species during seed emergence, early establishment, and sexual maturity and under novel and contemporary climate.

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