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Phenotypic selection on growth rhythm in whitebark pine under climatic conditions warmer than seed origins

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Abstract

Growth rhythm that is well synchronized with seasonal changes in local climatic conditions is understood to enhance fitness; however, rapid ongoing climate change threatens to disrupt this synchrony. To evaluate phenotypic selection on growth rhythm under expected warmer and drier future climate, seedlings from 49 populations of whitebark pine (*Pinus albicaulis* Engelm.) were grown and measured over more than 10 years in two common garden field experiments on sites that approximate the projected future climate of the seed origins. Selection on growth rhythm was assessed by relating individual plant fitness to timing and rate of shoot elongation. Differential survival clearly evidenced selection on growth rhythm. We detected directional and stabilizing selection that varied in magnitude between experimental sites and among years. The observed phenotypic selection supports the interpretation of clinal variation among populations within tree species as reflecting adaptive variation in response to past natural selection mediated by climate. To the extent that growth rhythm is heritable, results of the present study suggest evolution of whitebark pine toward a more distinct timing of shoot elongation and generally more rapid elongation in the immediate next generation under ongoing climate change in environments similar to the study sites.

Introduction

Differences in growth rhythm among populations within many woody plant species have long been observed and interpreted as a key intraspecific adaptation to climate (e.g. Dietrichson, 1964; Rehfeldt, 1993; Howe *et al.*, 2003). Growth rhythm is a phenological trait that refers to the timing and duration of sequential developmental events that organisms express annually in a particular environment. For many forest trees in temperate and boreal climates, the expression of growth rhythm begins with the timing of deacclimation (i.e. seasonal loss of freezing tolerance) in the spring and includes the timing and rates of root elongation, shoot elongation, leaf expansion, bud development, diameter growth, lignification, pollen development and cone/flower development and concludes with cold acclimation (see Rehfeldt, 1993). Trees in temperate and boreal forest regions that are well adapted to their climate conditions generally complete growth and development (excluding deacclimation and acclimation) within the growing season between springtime temperature increases and the onset of seasonal drought or extreme cold in the late summer or fall (see Dietrichson, 1964; Rehfeldt, 1993).

Prior studies have established the role of growth rhythm in adaptation to climate. Variation in growth rhythm among populations within many species corresponds to the local climate of origin even when plants are growing under novel climate as with many common garden studies. For example, in provenance tests, early cessation of apical shoot elongation or bud set has been observed in populations originating from locations characterized by distinct late-summer drought (e.g. Bouvarel, 1961; Joly *et al.*, 1989) or early fall frost (Howe *et al.*, 2003; Savolainen *et al.*, 2007). Populations with growth

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rhythms that were poorly synchronized with annual timing of the local climate suffered reduced vigour, increased injury and/or increased mortality (e.g. Rehfeldt, 1983; White, 1987; Skrøppa & Kohmann, 1997).

This study investigates phenotypic selection on growth rhythm in whitebark pine (*Pinus albicaulis* Engelm.). Whitebark pine is of particular interest given its status as a keystone (Tomback & Kendall, 2001) and foundational (Ellison *et al.*, 2005) species in subalpine forest ecosystems of western North America. This species has been in decline since the mid-twentieth century (Tomback *et al.*, 2001) and has consequently been placed on the United States Endangered Species Act Candidate List (U.S. Fish and Wildlife Service, 2011) and declared endangered by the Canadian federal government in accordance with the Canadian Species at Risk Act (COSEWIC, 2012).

Whitebark pine has historically occupied the cool-wet climatic extreme among forest ecosystems in western North America. However, this region's climate has recently become warmer with drier summers than the previous century (Kunkel *et al.*, 2013), and this trend is predicted to continue through the twenty-first century (Mote & Salathé, 2010; IPCC, 2013). Consequently, over almost all of its current distribution in the USA, whitebark pine's contemporary (1961–1990) realized climate niche is projected to be eliminated by midcentury (Warwell *et al.*, 2007).

Ongoing climate change is predicted to substantially alter climates throughout the twenty-first century (IPCC, 2013). In particular, the accelerating rate of climate change threatens to disrupt the synchrony of growth rhythm of woody plant populations with local climate. Populations subject to climate that compromises their physiological plasticity and fitness may genetically adapt and shift their ranges through seed dissemination into areas with suitable climate, or they may undergo extirpation (Lynch & Lande, 1993; Davis & Shaw, 2001; Rehfeldt *et al.*, 2001; Davis *et al.*, 2005). Genetic adaptation depends on heritable variation in the traits under selection (Darwin, 1859; Endler, 1973; Falconer & Mackay, 1996). Therefore, improved understanding of how populations may adapt genetically under changing climate requires information on trait heritability and selection. Moderate-to-high heritability of measures of growth rhythm has been found for whitebark pine populations (Bower & Aitken, 2006), as well as those of numerous other tree species (see Howe *et al.*, 2003). However, climate-related selection on growth rhythm of tree species is poorly understood. In particular, little is known about selection on growth rhythm of trees at early ages, a period when trees are more susceptible to climate-related stress in comparison with later years (e.g. Haig *et al.*, 1941; Leck *et al.*, 2008).

Therefore, the objective of this study was to quantify, over multiple growing seasons, the form and magnitude of selection on growth rhythm during the vulnerable juvenile stage under a climatic regime that approximates predicted climate late in the present century (see Mote & Salathé, 2010). Because the longer growing season of the study site would likely allow growth and development over longer periods than under most native climates (Table 1), we hypothesized that directional selection would increasingly favour phenotypes that annually began shoot elongation earliest, concluded shoot elongation latest and maintained the highest elongation rates.

Table 1 Geographic description and observed mean weather for study sites at Priest River Experimental Forest from 2001 to 2012 and minimum and maximum geographic range and predicted mean climate from spline climate model (Rehfeldt *et al.*, 2006, and available at http://charcoal.cnre.vt.edu/climate/species/) for seed origins used in study.

Geographic/Climate Variables	Abbreviation	Study Sites	Seed origins
Geographic			
Elevation (m)	ELEV	671	1646 to 2774
Latitude	LAT	48.35	44.5 to 49
Longitude	LONG	116.8	110.5 to 118.5
Temperature			
Mean annual temperature (° C)	MAT	6.9	−2.2 to 2.7
Mean temperature in the warmest month (° C)	MTWM	18.9	10.2 to 14.3
Mean temperature in the coldest month (° C)	MTCM	-4.1	−12.6 to −7
Degree-days < 0° C (based on mean minimum monthly temperature)	MMINDD0	942	1657 to 3776
Timing of Seasonal Temperature			
Julian date the sum of degree-days > 5° C reaches 100	D100	138	157 to 186
Length of the frost-free period	FFP	97	17 to 100
Precipitation			
Mean annual precipitation (mm)	MAP	825	429 to 1380
Spring precipitation: (April and May) (mm)	SPRP	132	93 to 193
Ratio of growing season precipitatioin (April to Sept.) to total precipitation	PRATIO	0.45	0.29 to 0.62

Materials and methods

Seed collection and common garden experiments 1 and 2

Wind-pollinated cones were collected from natural populations of whitebark pine in the interior northwestern USA from 1991 to 1997 (Fig. 1). Seeds were sampled from approximately 10 trees per population. Seeds were germinated in glasshouse in Lewiston, Idaho. Resulting seedlings were maintained in shelter houses in Moscow, Idaho, and outplanted in two common garden field experiments at Priest River Experimental Forest, Idaho. Experiment 1 was planted in spring 2000 with 2-year-old seedlings from 46 provenances in a well-drained site (lat. 48.352°N, long. −116.848°W, elev. 671M; soil: Andic Xerochrept; Staff, 1996) that was tilled prior to planting. Experiment 2 was planted in fall 2001 with 3-year-old seedlings from 42 provenances of which 39 provenances were shared in common with Exp. 1. Experiment 2 was located 2.2 km from Exp. 1 (lat. 48.332°N, long. −116.8477°W, elev. 671 m) in a cold air drainage with rocky soil that was shallow and poorly drained ('Mission series'; Page-Dumroese, 1993). The site for Exp. 2 was selected to assess seedling growth and survival under growing conditions that contrasted with Exp. 1 site and more closely resembled whitebark pine's high elevation habitat. However, within the study period (2002–2012), air temperature (Table S1) and precipitation did not differ detectably between the sites. Thus, differences between sites appear to have been chiefly related to soil factors.

For each seed origin, climate estimates from the period of 1961 to 1990 were calculated using a spline climate model (Rehfeldt, 2006; see http://charcoal.cnre.vt.edu/climate/species/). In comparison with these climate estimates for seed origins, the observed weather during the study period at the Exp. 1 and Exp. 2 sites exhibited substantially warmer air temperature, earlier spring warming and intermediate precipitation (Table 1). In addition, soil moisture of the study sites was likely drier than most seed origins because of evaporation over generally longer growing season at lower elevations (Weaver, 2001).

Study design and procedure

A randomized complete block design with provenances represented in five-tree row-plots in each of six blocks

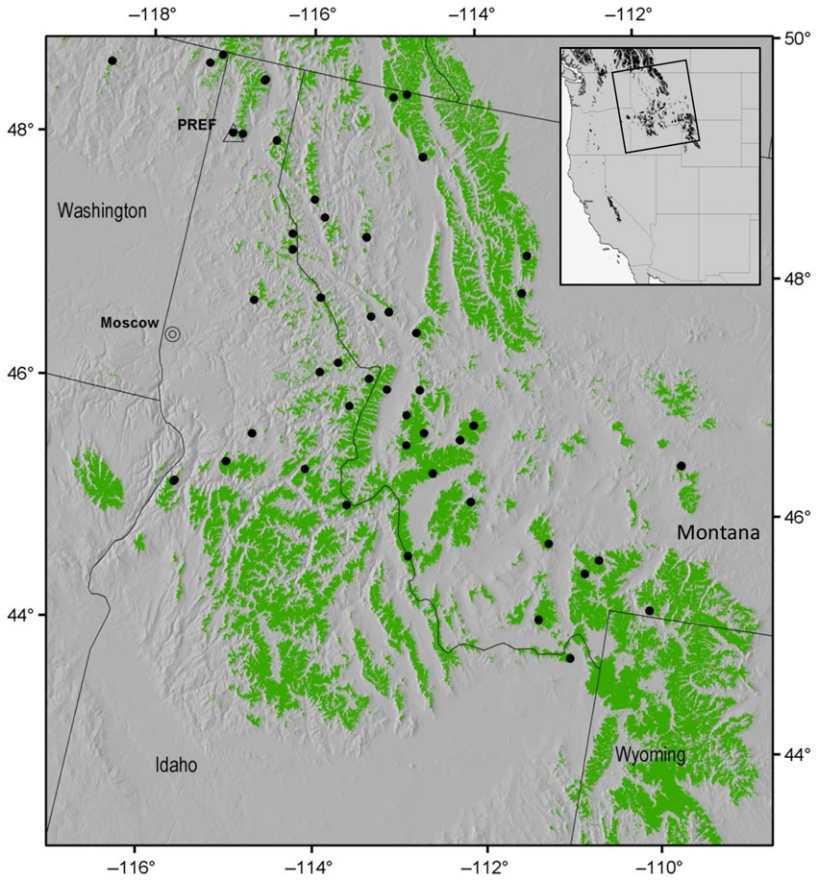

Fig. 1 Location of sampled whitebark pine (*Pinus albicaulis*) provenances (●) and study sites (Δ). Shaded or green area indicates estimated distribution of predicted realized climate niche for whitebark pine for the study region (Warwell *et al.*, 2007). Inset shows whitebark pines rangewide distribution indicated by black regions. The area represented in the larger image is indicated by the black rectangle.

was used in Exp. 1 and 10-tree row-plots in each of three blocks was used in Exp. 2. In Exp. 1 and Exp. 2, individual trees were planted using dibble tools at a spacing of 1 m × 1 m and 35.56 cm × 33.02 cm, respectively. A border row was planted in each site to equalize competitive effects on measured trees. High mortality prior to crowding and characteristic slow growth minimized competitive interactions.

We focused on trait expression after effects of transplanting had dissipated by omitting consideration of measures of plants during the first growing season. Survival was recorded in fall 2002–2005, 2011 and 2012 in Exp. 1 and in fall 2003–2006 and 2010–2012 in Exp. 2. Very little mortality was attributed to white pine blister rust in Exp. 1 in 2011 and 2012; these cases were retained in the analysis for simplicity. Mortality that was clearly due to deer browsing was excluded from analysis. Thus, analysis of selection in Exp. 1 and Exp. 2 used a total of 1103 and 906 live trees, respectively. Measurements of annual incremental apical shoot elongation were recorded approximately weekly to biweekly beginning in late March before bud flush and extending past bud set through July in 2002–2005 in Exp. 1 and in 2003–2006 in Exp. 2. Total height was measured in 2012 in both experiments (see Table S2 for data).

The timing and rate of apical shoot elongation were used as proxies that reflect growth rhythm. Rates of apical shoot elongation for each tree were calculated by dividing the difference in shoot height between consecutive measurement dates within a growing season by the duration of the respective interval. This procedure produced a data set that represented apical shoot elongation of individual trees over each growing season as a series of shoot elongation rates corresponding to intervals of time. The number of intervals varied by year from four to eight (Table 2). Intervals within a growing season were categorized as early vs. late in the growing season. These terms are used as relative descriptors although elongation in late-season exclusively included maximum shoot elongation and the tapering off phases of shoot elongation. Observations to calculate timing of apical shoot elongation were only available for 2005 and 2006. The interval where elongation was first detected between incremental height measurements was used to approximate the timing of initiation of apical shoot elongation. Timing of cessation of apical shoot elongation was determined to be the interval when no further elongation of the shoot was detected. Duration of elongation was calculated by subtracting the timing of cessation from the timing of initiation.

Maternal effects can contribute to phenotypes of offspring and obscure genetic differences. Maternal effects are generally found to be most pronounced in early stages of a plant's life with effect declining over time (Roach & Wulff, 1987; Reich *et al.*, 1994). They have been shown to influence growth within the first two years following germination in several conifers (ex. Johnsen *et al.*, 2005; Zas *et al.*, 2013; Borgman *et al.*, 2014). To minimize maternal effects, measurements began when trees were ages 4 (Exp. 1) and 5 (Exp. 2) years.

Statistical analysis: selection

Previous joint analysis identified significant differences between experiments for total annual shoot elongation and interactions between experiment and provenance for growth and survival (Warwell & Shaw, 2017). Therefore, we assessed selection on growth rhythm in each experiment independently.

Aster models (Geyer *et al.*, 2007; Geyer & Shaw, 2008) permit statistically rigorous, unified analysis of multiple life-history stages. The relationship between fitness and timing of annual rate, cessation, initiation and duration of apical shoot elongation was assessed with aster models using the reaster function (Geyer, 2013) in R (R Development Core Team, 2015) by regressing fitness on trait values, according to the general approach of Lande & Arnold (1983, see Shaw & Geyer, 2010). For individuals present at the outset

Table 2 Intervals for timing of apical shoot elongation rates in Julian dates for each year used in aster model comparisons testing for Experiments 1 (Exp. 1) and Experiment 2 (Exp. 2).

Year	Early-season				Late-season						
	Exp.1										
2002	108–127				127–142	142–149	149–225				
2003	104–111	111–122			122–142	142–149	149–155	155–161	161–189		
2004	100–119	119–125			125–141	141–155	155–191				
2005	67–96	96–112	112–119		119–131	131–147	147–153	153–167	167–230		
	Exp.2										
2003	105–120	120–129	129–135		135–148	148–155	155–170				
2004	106–114	114–119	119–126		126–141	141–156	156–195				
2005	96–108	108–118	118–125		125–132	132–145	145–152	152–165	165–215		
2006	95–101	101–109	109–115	115–122	122–129	129–136	136–143	143–150	150–157	157–164	164–232

(spring 2002 in Exp. 1; spring 2003 in Exp. 2), their final height was used as a proxy for fitness. This measure explicitly included survival through multiple years. In contrast, conventional estimates of height alone ignore prior mortality and are therefore conditional on survival. All analyses used a constant of 1 (for each individual tree) as the root node (i.e. initial stage; alive in spring of first year). Following the root node, each successor variable (subsequent year of survival or final height) was modelled as depending on the preceding variable (graphical models for fitness shown in Fig. 2). Probability models chosen for the nodes of the graphical model were Bernoulli for survival through each interval and normal for final height in 2012 (ex. Fig. 2c). We also assessed differences in survival to 2012 alone with models beginning with seedlings present in 2002 (ex. Fig. 2a) and 2003 in Exp. 2. R script is provided in supporting information (S1 and S2).

Identifying the direction and magnitude of selection on a given trait requires a measure of the trait of interest prior to selection. In the present analysis, elongation rates were treated as unique to the growing season in which they were expressed. Thus, for example, we based inferences of selection on elongation rates expressed in 2005 on survival and unconditional expected height in 2012 of seedlings present in spring 2005.

Selection gradients (partial regression coefficients) were estimated to characterize the relationship between fitness and timing of apical shoot elongation for each experiment using the following procedure. First, Spearman's rank correlation coefficients between pairs of elongation rates expressed in each interval within a growing season were evaluated. Only one of any group of highly correlated ($r \geq 0.85$) intervals for elongation rates was retained to avoid serious multicollinearity (see Mitchell-Olds & Shaw, 1987). Following this step, in each experiment, at least four intervals were available in each growing season for the analysis (see Table 2).

Next, backward stepwise regression was used to identify which intervals in each growing season were significant predictors of survival to 2012 and also of unconditional expected height in 2012. For each test, linear selection gradients (β_i) and quadratic selection gradients (γ_{ii}) for intervals were estimated, with block and provenance treated as random effects. Statistical significance of the selection gradients was tested by

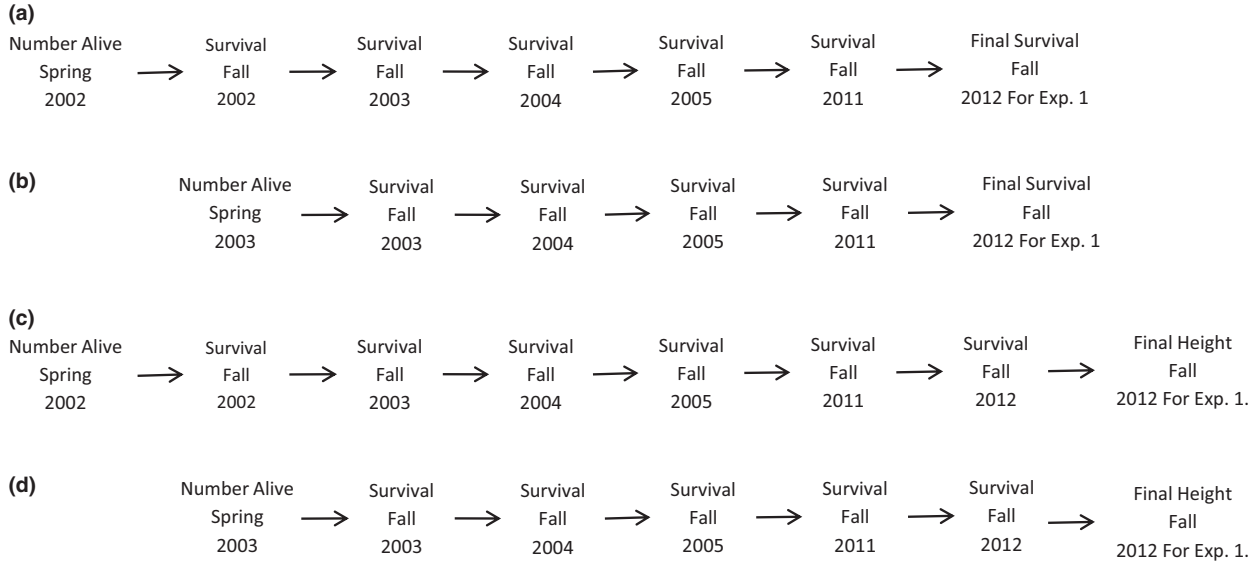

Fig. 2 Examples from Experiment 1 of graphical models used in aster analysis unifying survival over time and total height data and survival over time to assess fitness. Each node represents a component of life history, while arrows represent the dependent association between predecessor and successor life-history components. Survival was modelled as a Bernoulli random variable and total height as normal random variable. Graph (a) shows the model used to predict survival in fall 2012 that included survival from spring 2002 to fall 2012. This model was used in the regression analysis that corresponds with results shown in Fig. 3a. Graph (b) shows the model used to predict survival in fall 2012 that included survival from spring 2003 to fall 2012. This model was used in the regression analysis that corresponds with results shown in Fig. 3b. Graph (c) shows the model used to predict unconditional expected height in fall 2012 that included survival from spring 2002 to fall 2012. This model was used in the regression analysis that corresponds with results shown in Fig. 3c. Graph (d) shows the model used to predict unconditional expected height in fall 2012 that included survival from spring 2003 to fall 2012. This model was used in the regression analysis that corresponds with results shown in Fig. 3d.

comparing the likelihoods of nested models using maximum likelihood. Significant ($P < 0.05$) variables were retained. The detection of quadratic terms indicated curvature in the fitness surface. When more than one quadratic term was significant, the cross-product pairs of traits were included in the model. Cross-product terms (γ_{ij}) represent correlational selection gradients, which indicate selection on one trait depends on the second trait (Phillips & Arnold, 1989; Brodie *et al.*, 1995; Blows & Brooks, 2003). Therefore, correlational selection gradients indicate nonlinear selection along axes that are not parallel to the axes of either trait.

Fitness functions were visualized as univariate if selection on growth during a single interval within a growing season was detected or as bivariate if selection on growth during two intervals was detected. For each selection surface, fitness, whether as survival or unconditional expected height, was represented using contours, while the rates of apical shoot elongation for different growing season intervals were represented on the x and y axes. For a given trait combination, the steepness of the gradient, that is the magnitude of selection, is reflected by the relative closeness of contour lines on the fitness surface. Observed phenotypes were superimposed to make clear the range of the data in relation to the estimated surfaces. Higher dimensional surfaces were not plotted due to increased complexity of visualizing shapes in more than three dimensions.

The influence of mortality in a particular year on the form and magnitude of selection on timing of apical shoot elongation expressed in a particular year was assessed by modelling selection that included and excluded mortality in specific years from among multiple years concluding with 2012 and comparing differences in their corresponding fitness surfaces. For example, the influence of mortality in 2002 on form and direction of selection on timing of shoot elongation rates in 2002 used estimates of fitness that included (Fig. 2a and c) and excluded (Fig. 2b and d) mortality in 2002 in Exp. 1. The corresponding fitness surfaces were then compared to assess differences in selection.

Results

Phenotypic variability of survival, height and shoot elongation

Survival declined substantially in single episodes in the fall following relatively dry growing seasons in 2002 in Exp. 1 and 2006 in Exp. 2 (Table S3). Overall, survival to 2012 was 42 and 44%, while mean height in 2012 among survivors was 1556 mm and 1108 mm for Exp. 1 and 2, respectively. The influence of variation in initial tree height on measures of fitness appeared to be weak. Initial height in 2001 was not a significant predictor for either survival ($P = 0.1333$) or unconditional expected height ($P = 0.7269$) in 2012 in Exp. 1. This result suggests that material effects associated with growth and survival at the start of the study were not a strong influence on variation in the fitness measures assessed over the measurement period from 2002 to 2012. Initial heights were not available in Exp. 2.

The magnitudes of apical shoot elongation rates and their timing ranged broadly among individual trees over five consecutive growing seasons in each experiment. Within a growing season, variation in the timing of initiation of shoot elongation among individuals spanned 2 weeks, while timing of cessation of shoot elongation varied by as much as 3 weeks. Total duration of shoot elongation for the majority of individuals ranged from approximately 7 to 10 weeks. Even so, most shoot elongation occurred during a 2- to 3-week period in late May (Julian dates 127–152) of each year. The elongation rates during this period were the strongest predictors among measures of growth rhythm for total height at the end of the study in 2012 ($r^2 = 0.05$ to 0.24). In addition, trees that exhibited increasingly higher apical shoot elongation rates tended to cease elongation later in 2005 and 2006 growing seasons (Table 3). The timing of elongation rates between growing seasons was generally consistent among years (Table 3). Elongation rates in Exp. 1 were greater than Exp. 2 throughout the study period (Table S3). As a whole, apical shoot elongation rates tended to increase with increasing age.

Selection on timing and rate of apical shoot elongation

Survival and unconditional expected height of seedlings in 2012 were dependent on both the magnitude and timing of apical shoot elongation. In Exp. 1, the linear, nonlinear and bivariate nonlinear terms for the rate of apical shoot elongation in 2002 exhibited early and late in the growing season were significant predictors of survival and unconditional expected height in 2012 (Table 4a and h). The shape of the fitness surfaces based both on survival to 2012 alone (Fig. 3a) and on unconditional expected height in 2012 (Fig. 3c) in relation to elongation rates in 2002 was defined by a saddle separating two peaks and two valleys suggesting disruptive selection. One fitness optimum corresponded to low early-season and high late-season elongation rates, while the other corresponded to high early-season and low late-season elongation rates.

Observed elongation rates from 2002 plotted on the fitness surface based on survival alone show elongation rates well represented from 0 mm day^{-1} to a broad saddle spanning intermediate elongation rates early and late in the growing season (Fig. 3a). In addition, early-season elongation rates are reasonably represented spanning the gradient across the upper left of the graph. Thus, selection favouring low early-

Table 3 Spearman's rank correlations for intervals of apical shoot elongation rates (a) in Experiment 1 from 2002 and 2005, and (b) in Experiment 2 from 2003 and 2006. Approximate timing of apical shoot initiation, cessation and duration Intervals are coded by last digit of their respective year followed by last Julian day of the interval, while the first interval of each year code the first and last Julian date of the interval. Shoot elongation intervals (see Table 2) that were highly correlated ($R \geq 0.85$) periods significant ($P < 0.05$) are not shown.

	2/108–127	2/142–149	3/104–111	3/142–149	4/119–125	4/141–155	5/131–147	5/147–153	5/INIT	5/CES
(a)										
2/108–127										
2/142–149	0.62***									
3/104–111	0.49***	0.49***								
3/142–149	0.41***	0.65***	0.57***							
4/119–125	0.54***	0.50***	0.57***	0.52***						
4/141–155	0.19***	0.46***	0.32***	0.71***	0.24***					
5/131–147	0.28***	0.51***	0.36***	0.62***	0.50***	0.68***				
5/147–153	0.30***	0.45***	0.35***	0.60***	0.39***	0.65***	0.71***			
5/INIT	−0.02	−0.02	0.02	−0.07	−0.08	−0.19***	−0.19***	−0.16***		
5/CES	0.30***	0.40***	0.35***	0.50***	0.38***	0.53***	0.63***	0.87***	−0.10*	
5/DUR	0.28***	0.38***	0.32***	0.49***	0.38***	0.55***	0.64***	0.86***	−0.33***	0.96***

	3/135–148	4/119–126	4/126–141	5/108–118	5/132–145	6/109–115	6/143–150	5/Init	5/Ces	5/Dur	6/Init	6/Ces
(b)												
3/135–148												
4/119–126	0.52***											
4/126–141	0.69***	0.84***										
5/108–118	0.42***	0.62***	0.63***									
5/132–145	0.61***	0.56***	0.78***	0.67***								
6/109–115	0.22***	0.42***	0.35***	0.56***	0.34***							
6/143–150	0.41***	0.19**	0.46***	0.30***	0.65***	0.23***						
5/Init	0.30***	0.31***	0.42***	0.35***	0.52***	0.30***	0.33***					
5/Ces	0.01	0.08	0.07	0.15*	0.04	0.11	0.00	0.03				
5/Dur	0.02	0.10	0.09	0.25***	0.09	0.11*	0.04	0.05	0.66***			
6/Init	−0.02	−0.06	−0.05	−0.17**	−0.05	−0.13*	−0.04	−0.03	−0.79***	−0.54***		
6/Ces	0.04	0.01	0.14*	0.11	0.16**	0.07	0.36***	0.12*	−0.02	0.08	−0.02	
6/Dur	0.04	0.05	0.14*	0.19***	0.15**	0.14*	0.29***	0.11	0.50***	0.41***	−0.67***	0.76***

Init, initiation; Ces, cessation; Dur, duration. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

season and high late-season elongation rates was observed. However, few observations coincide with the second estimated fitness optimum corresponding with high early-season and low late-season elongation rates. Thus, the overall apparent disruptive selection represented by the estimated surface was weakly supported.

Observed elongation rates from 2002 plotted on the fitness surface for unconditional expected height (Fig. 3c) occurred over a range of the fitness surface that was similar to the distribution of observations for the fitness surface using survival described above. However, few observations were available to support directional selection against high early- and late-season elongation rates. Thus, when total height was considered along with survival (i.e. unconditional expected height), directional selection favouring low early-season elongation rates with high late-season elongation rate was observed, while directional selection against phenotypes with high early-season and high late-season elongation rates was not well supported.

In Exp. 1, beyond 2002, estimates of linear selection gradients for rates of apical shoot elongation expressed in 2003, 2004 and 2005 were positive and statistically significant in analyses of phenotypic selection based on survival (Table 4c, d and e, respectively) and on unconditional expected height (Table 4j, k and l, respectively) in 2012. Nonlinear coefficients were statistically significant for shoot elongation rates in 2003 and 2004 for survival (Table 4c and d, respectively), and 2003, 2004 and 2005 for unconditional expected height (Table 4j, k, and l, respectively) in 2012. When measures of elongation rate were superimposed on the fitness surfaces estimated based on survival as the proxy for fitness, directional selection favouring high early-season and low late-season elongation rates in 2003 (Fig. 4a) and 2004 (Fig. 4b) was apparent. However, fitness surfaces estimated based on unconditional expected height as the proxy for fitness gave evidence of selection favouring intermediate early-season elongation rates (stabilizing selection) and high late-season elongation rates (directional selection) in 2003 (Fig. 4d). In contrast, in

Table 4 Experiment 1, aster model comparison test results for the effects of timing of measures of growth rhythm within a given year on survival through 2012 beginning in the respective year and unconditional expected height in 2012 that included survival to 2012 beginning in the respective year.

Response	Table Subsection (Associated Figure)	Mortality Period	Year of Shoot Elongation	Shoot Elongation Interval (Julian Date)		Selection Gradient	Standard Error	Model d.f.	Model Deviance	Test d.f.	Test *P*-value
Survival	Table 4a	2002–2012	2002	Full Model				12	1399	–	–
	(see Fig. 3a)			108–127	β	4.61E+00	1.13E+00	9	1359.1	3	< 0.0001***
				142–149	β	1.00E+00	2.33E-01	9	1354.5	3	< 0.0001***
				$(108–127)^2$	γ_{ii}	1.52E-01	1.25E+00	10	1378.8	2	< 0.0001***
				$(142–149)^2$	γ_{ii}	1.17E-02	5.47E-02	10	1379.3	2	< 0.0001***
				108–127 * 142–149	γ_{ij}	−1.23E+00	3.83E-01	9	1359.8	3	< 0.0001***
	Table 4b	2003–2012	2002	Full Model				8	2356.7	–	–
	(see Fig. 3b)			108–127	β	1.18E+00	4.52E-01	7	2349.4	1	0.0067**
				142–149	β	3.26E-01	8.15E-02	7	2339.8	1	< 0.0001***
	Table 4c	2003–2012	2003	Full Model				11	2336	–	–
	(see Fig. 4a)			104–111	β	1.95E+00	5.09E-01	8	2305.8	3	< 0.0001***
				142–149	β	3.95E-01	1.30E-01	8	2324.5	3	0.0010**
				$(104–111)^2$	γ_{ii}	−2.06E-01	2.11E-01	9	2326.3	2	0.0078**
				$(142–149)^2$	γ_{ii}	−1.06E-02	1.59E-02	9	2326.8	2	0.0100*
				104–111 * 142–149	γ_{ij}	−1.57E-01	9.28E-02	10	2332.8	1	0.0728*
	Table 4d	2004–2012	2004	Full Model				11	2790	–	–
	(see Fig. 4b)			119–125	β	1.13E+00	2.45E-01	8	2707.4	3	< 0.0001***
				141–155	β	8.49E-01	2.75E-01	8	2771	3	0.0002***
				$(119–125)^2$	γ_{ii}	−5.93E-02	2.92E-02	9	2769.6	2	< 0.0001***
				$(141–155)^2$	γ_{ii}	−4.92E-03	4.42E-02	9	2777.2	2	0.0017**
				119–125 *141–155	γ_{ij}	−1.70E-01	5.09E-02	10	2777.4	1	0.0004***
	Table 4e	2005–2012	2005	Full Model				7	2538.8	–	–
	(see Fig. 4c)			131–147	β	7.20E-02	1.55E-02	5	2515.3	2	< 0.0001***
	Table 4f	2005–2012	2005	Full Model[a]				9	2586.7	–	–
	(see Fig. S2A)			96–112	β	6.99E-01	3.65E-01	6	2582.6	3	0.0434*
				131–147	β	3.50E-01	7.77E-02	6	2549.7	3	< 0.0001***
				Shoot initiation	β	−2.67E-02	4.24E-03	7	2538.8	2	< 0.0001***
				$(131–147)^2$	γ_{ii}	−1.27E-02	3.88E-03	6	2575.0	2	< 0.0006***
	Table 4g	2005–2012	2005	Full Model[b]				9	2589.7	–	–
	(see Fig. S2B)			131–147	β	1.64E+00	5.01E-01	6	2531.8	3	< 0.0001***
				Shoot cessation	β	−6.46E-01	1.47E-01	6	2538.8	3	< 0.0001 ***
				$(131–147)^2$	γ_{ii}	−8.45E-03	4.73E-03	6	2566.7	2	< 0.0001***
				(Shoot cessation)^2	γii	2.40E-03	5.85E-04	7	2563.9	2	< 0.0001***
				131–147 * Shoot cessation	γ_{ij}	−8.84E-03	3.54E-03	8	2583.0	1	0.0096**

later years, only directional selection on shoot elongation was apparent, whether via survival in 2005 (Fig. 4c) or unconditional expected height in 2004 and 2005 (Fig. 4e and f). In addition, selection resulting from mortality favoured phenotypes that started elongation earlier (Fig. S2A) and either ceased elongation later or exhibited generally higher late-season shoot elongation rates (Fig. S2B).

In Exp. 2, the linear and nonlinear coefficients for the rate of apical shoot elongation exhibited late in the 2003 growing season were statistically significant in analyses of phenotypic selection via variation in both survival alone and in unconditional expected height in 2012 (Table 5). The plotted relationship showed that as late-season elongation rates increased, the expected per cent survival (Fig. 5a) and unconditional expected height (Fig. 5c) increased to an intermediate optimum with an approximately symmetric decline thereafter. The corresponding 95% confidence interval for expected per cent survival and unconditional expected height widened with increasing elongation rates. Thus, selection favouring increasing elongation rate up to an intermediate optimum was well supported, while evidence of stabilizing selection or selection against the increasingly higher late-season elongation rates was weaker.

In Exp. 2, as detected in Exp. 1, the direction and magnitude of selection on elongation rates differed among growing seasons (2003–2006). The analysis evidenced selection that favoured increasing early-season and intermediate late-season shoot elongation rates in 2004 (Table S5A; Fig. S3A). In contrast, results

Table 4 (*Continued*)

Response	Table Subsection (Associated Figure)	Mortality Period	Year of Shoot Elongation	Shoot Elongation Interval (Julian Date)		Selection Gradient	Standard Error	Model d.f.	Model Deviance	Test d.f.	Test *P*-value
Unconditional	Table 4h	2002–2012	2002	Full Model				12	1506.1	–	–
Expected	(see Fig. 3c)			108–127	β	2.94E-03	7.24E-04	9	1487.3	3	< 0.0001***
Height				142–149	β	7.61E-04	1.46E-04	9	1420.9	3	< 0.0001 ***
				$(108–127)^2$	γ_{ii}	−2.86E-04	6.61E-04	10	1487.3	2	< 0.0001***
				$(142–149)^2$	γ_{ii}	−2.55E-06	2.92E-05	10	1488.5	2	0.0001***
				108–127 * 142–149	γ_{ij}	−6.31E-04	1.86E-04	9	1469.1	3	< 0.0001***
	Table 4i	2003–2012	2002	Full Model				8	2473.1	–	–
	(see Fig. 3d)			108–127	β	6.34E-04	2.67E-04	7	2467.2	1	0.0156*
				142–149	β	3.68E-04	4.93E-05	7	2410.7	1	< 0.0001***
	Table 4j	2003–2012	2003	Full Model				8	2445.7	–	–
	(see Fig. 4d)			104–111	β	1.43E-03	3.04E-04	6	2401.9	2	< 0.0001***
				142–149	β	1.35E-04	2.66E-05	7	2417.2	1	< 0.0001 ***
				$(104-111)^2$	γ_{ii}	−2.88E-04	9.52E-05	7	2436.1	1	0.0019**
	Table 4k	2004–2012	2004	Full Model				8	2925.1	–	–
	(see Fig. 4e)			119–125	β	0.00072	0.0001497	6	2796.2	2	< 0.0001***
				141–155	β	2.95E-04	4.72E-05	7	2881.6	1	< 0.0001***
				$(119–125)^2$	γ_{ii}	−4.13E-05	1.66E-05	7	2925.1	1	< 0.0094**
	Table 4l	2005–2012	2005	Full Model[a]				8	2623.3	–	–
	(see Fig. 4f)			131–147	β	0.00049	0.00004324	6	2586.6	2	< 0.0001***
				143–153	β	1.58E-04	2.91E-05	7	2607.8	1	< 0.0001***
				$(131–147)^2$	γ_{ii}	−1.75E-05	2.19E-06	7	2617.9	1	0.0202*

β = linear selection gradient, γ_{ii} = quadratic effects, γ_{ij} = cross-products, full models = use variables listed for each year, and the effect of each predictor variable was tested against the full model for each predictor variable, *a* = timing of shoot initiation, or *b* = timing of cessation included in fitness regression. **P* < 0.05, ***P* < 0.01, ****P* < 0.001.

evidenced that selection on shoot elongation expressed in 2005 and 2006 favoured increasing early- and late-season elongation (Table S5B, C, E and F; Fig. S3B, C, E and F). Selection on timing of initiation, cessation or duration was not detected in Exp. 2 when elongation rates were included in the models.

Interannual variation of selection on shoot elongation expressed in a single year

The direction of selection on measures of growth rhythm differed in both experiments as evidenced by the variation among years in the detection of highly significant quadratic terms (Tables 4 and 5) and corresponding differences among years in the comparison of model fit in relation to observed data (Figs 3 and 5). For example in Exp. 1, nonlinear predictors of elongation rates in 2002 were highly significant for regression of survival or unconditional expected height that included mortality from 2002 through 2012. However, when selection on elongation rate in 2002 was based on only plants surviving through 2002 (i.e. only subsequent mortality was used in modelling either survival to 2012 or unconditional expected height in 2012), nonlinear predictors were no longer detected as significant (compare Table 4a vs. b and corresponding Fig. 3a vs. b for survival; Table 4h vs. i and corresponding Fig. 3c vs. d for unconditional expected height). Likewise in Exp. 2, when selection on elongation rates in 2003 was based on plants surviving through 2005, nonlinearity was no longer detected (compare Table 5a vs. c and corresponding Fig. 5a vs. b for survival; Table 5d vs. e and corresponding Fig. 5c vs. d for unconditional expected height). These results imply that curvature in the form of selection on elongation rates in the earliest years resulted from a tendency towards higher mortality among individuals with the greatest elongation rates in earlier years.

Discussion

The present study demonstrated phenotypic selection on shoot elongation rates expressed at different times within the growing season in whitebark pine (*Pinus albicaulis*) through 10 and 11 years in the field under a climate warmer than the climates of seed origin. We detected directional and stabilizing selection, with estimates that varied in magnitude between experimental sites and among years. The direction of selection on shoot elongation rates expressed at different times in the growing season differed inversely between the earliest and later years resulting in stabilizing selection. Consequently, phenotypes with the highest elongation rates did not exhibit the highest fitness over the period of observation. Nonetheless,

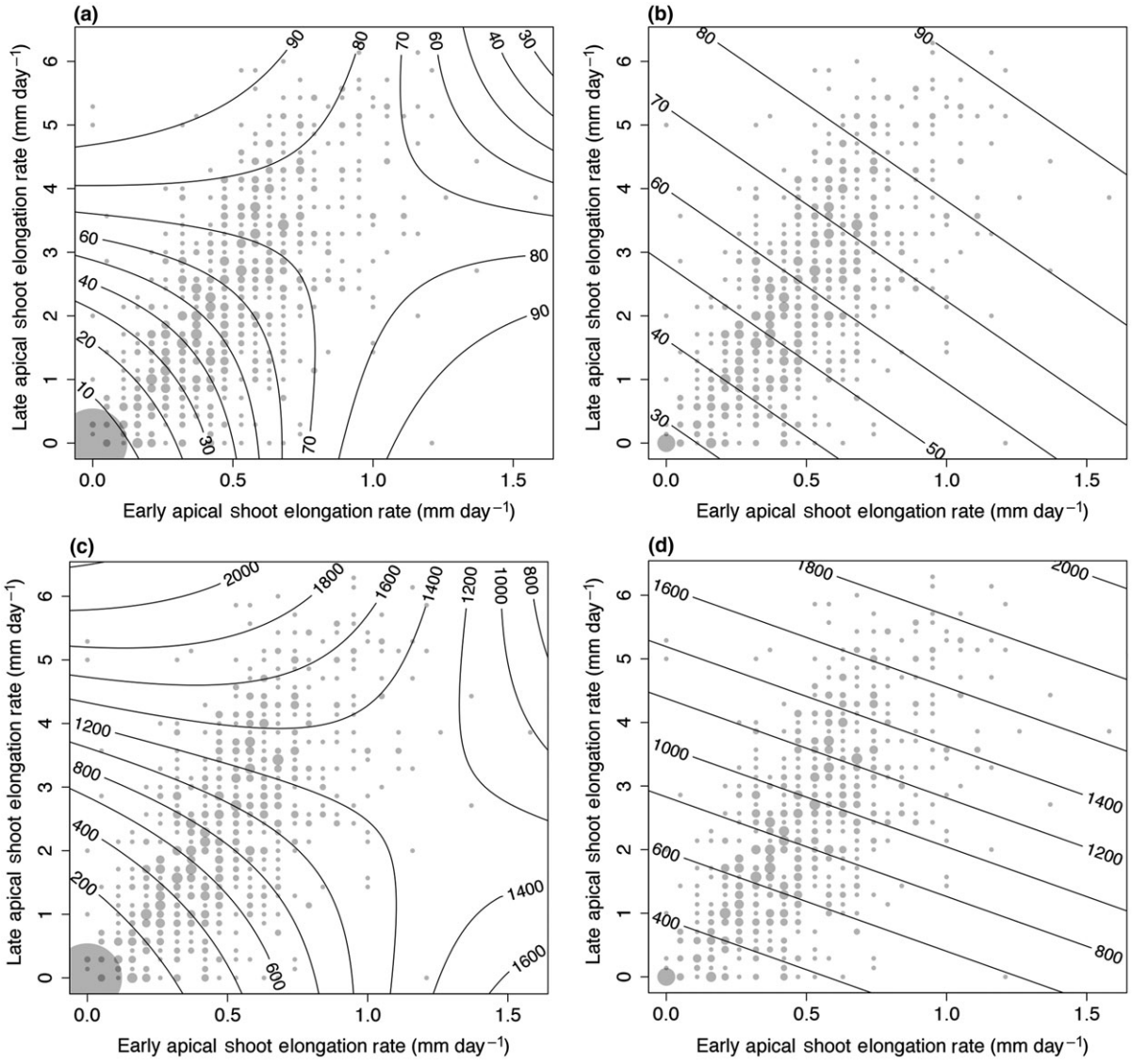

Fig. 3 Experiment 1, fitness surface showing observed (circles) apical shoot elongation rates (mm day^{-1}) early (Julian dates 108–127) and late (Julian dates 142–149) in the 2002 growing season in relation to modelled (contour lines) per cent survival to 2012 that includes (a) or excludes (b) mortality prior to 2003 and unconditional expected height (mm) in 2012 that includes (c) or excludes (d) mortality prior to 2003. Increasing circle size indicates increasing overlap of data points (i.e. phenotypes with higher frequency of occurrence).

the general pattern of selection on growth rhythm in the relatively warm study sites favoured higher growth rates. These results are consistent with clinal variation that shows evidence of adaptive variation among populations for greater height growth in association with increasing warmth of source climate in whitebark pine (Bower & Aitken, 2008; Warwell & Shaw, 2017) and other *Pinus* species (e.g. *Pinus ponderosa,* Rehfeldt 1999, M. Warwell and R. Shaw, unpublished data). Moreover, these results support the interpretation that clinal variation in growth rhythm among long-lived trees reflects genetic divergence in response to past natural selection mediated by climate (see Morgenstern, 1996).

Assessing selection using survival vs. unconditional expected height as measures of fitness

Fitness is difficult to measure directly, particularly in long-lived trees, which generally first produce offspring several decades following germination. As proxies for fitness, we used unconditional expected height in addition to survival alone. Survival to reproduction is

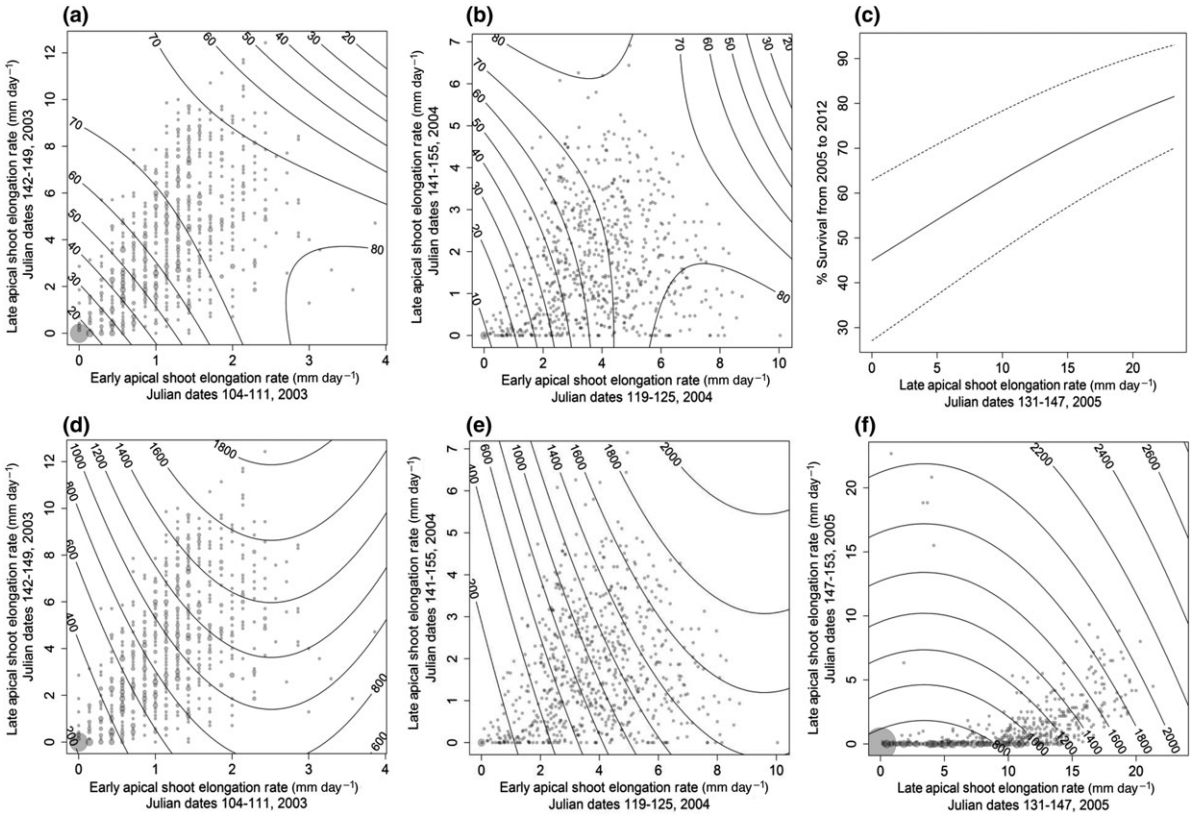

Fig. 4 Experiment 1, fitness surfaces showing observed (circles) apical shoot elongation rates (mm day^{-1}) in 2003 (a and d), 2004 (b and e) and 2005 (f) in relation to survival (contour) from (a) 2003–2012 and (b) 2004–2012 and unconditional expected height (contour) in 2012 that includes survival from (d) 2003–2012, (e) 2004–2012 and (f) 2005–2012. Increasing circle size indicates increasing overlap of data points (i.e. phenotypes with higher frequency of occurrence). Plot (c) shows fitness relation for only late apical shoot elongation in 2005 because no other interval was statistically significant ($P < 0.05$) in relation to survival. Dotted lines represent 95% confidence intervals.

fundamental to fitness, while greater height confers a fitness advantage in forest trees, for example through increased access to light (King, 1990) and enhanced reproductive output through male (see Shea, 1987; Arista & Talavera, 1994; Ne'eman *et al.*, 2011) and female function (see Mcgraw & Wulff, 1983). Prior studies have used a combination of height and survival to assess fitness (e.g. Savolainen *et al.*, 2007; Rousi *et al.*, 2018). We use unconditional expected height as a novel fitness measure that explicitly accounts for structural zeros due to mortality. Accordingly, in a population with no mortality, unconditional expected height is equivalent to average height, but as mortality increases, unconditional expected height decreases. Therefore, assessing both survival alone and unconditional expected height provided a more complete and informative assessment of fitness than an analysis that used only height or survival alone.

In the present study, estimates of fitness using unconditional expected height in relation to growth rhythm were compared between models using survival alone versus unconditional expected height. We found similarity between the estimated fitness surfaces, suggesting that survival to 2012 was the fitness component of primary importance for the inferred relationship between fitness and growth rhythm. Nonetheless, differences were apparent among the models. In particular, selection favouring phenotypes with high elongation rates in early years was more evident in models that used unconditional expected height in comparison with survival alone (Fig. 3a vs. c, Fig. 4a vs. d, and Fig. 5a vs. c). This finding suggests that, despite greater risk of mortality for individuals with high elongation rates, those that survived attained higher total height due, in part, to high elongation rates.

Variation in selection over time and between sites

Variation in temporal dynamics of selection within several natural populations has been reported (Siepielski *et al.*, 2009; but see Morrissey & Hadfield, 2012). Because the form of selection may vary substantially

Table 5 Experiment 2, aster model comparison test results for the effects of timing of measures of growth rhythm within 2003 on survival through 2012 beginning in the respective year and unconditional expected height in 2012 that included survival to 2012 beginning in the respective year.

Response	Table Subsection (Associated Figure)	Mortality Period	Year of Shoot Elongation	Shoot Elongation Interval (Julian Date)		Selection Gradient	Standard Error	Model d.f.	Model Deviance	Test d.f.	Test *P*-value
Survival	Table 5a	2003–2012	2003	Full Model				10	361.45	–	–
	(see Fig. 5a)			135–148	β	1.1939368	0.2063	8	298.77	2	< 0.0001***
				$(135–148)^2$	γ_{ii}	−0.19843	0.0498	9	344.89	1	< 0.0001***
	Table 5b	2004–2012	2003	Full Model				9	844.90	–	–
				135–148	β	0.9113294	0.2148	7	811.02	2	< 0.0001***
				$(135–148)^2$	γ_{ii}	−0.147923	0.0510	8	836.26	1	0.0033**
	Table 5c	2005–2012	2003	Full Model				8	1255	–	–
	(see Fig. 5b)			135–148	β	0.2901847	0.0695	6	1235.4	2	< 0.0001***
				$(135–148)^2$				7	1253.5	1	0.2179
Unconditional Expected Height	Table 5d	2003–2012	2003	Full Model				10	392.94	–	–
	(see Fig. 5c)			135–148	β	0.001075	0.0002	8	298.17	2	< 0.0001***
				$(135–148)^2$	γ_{ii}	−0.000154	4E-05	9	377.94	1	0.0001***
		2004–2012	2003	Full Model				9	873.05	–	–
				135–148	β	8.75E-04	0.0002	7	809.22	2	< 0.0001***
				$(135–148)^2$	γ_{ii}	−1.18E-04	0.00004	8	864.70	1	0.0039**
	Table 5e	2005–2012	2003	Full Model				8	1281.8	–	–
	(see Fig. 5d)			135–148	β	3.78E-04	0.00006	6	1232.4	2	< 0.0001***
				$(135–148)^2$				7	1280.2	1	0.2010

β = linear selection gradient, γ_{ii} = quadratic effects, full models = use variables listed for each year, and the effect of each predictor variable was tested against the full model for each predictor variable. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

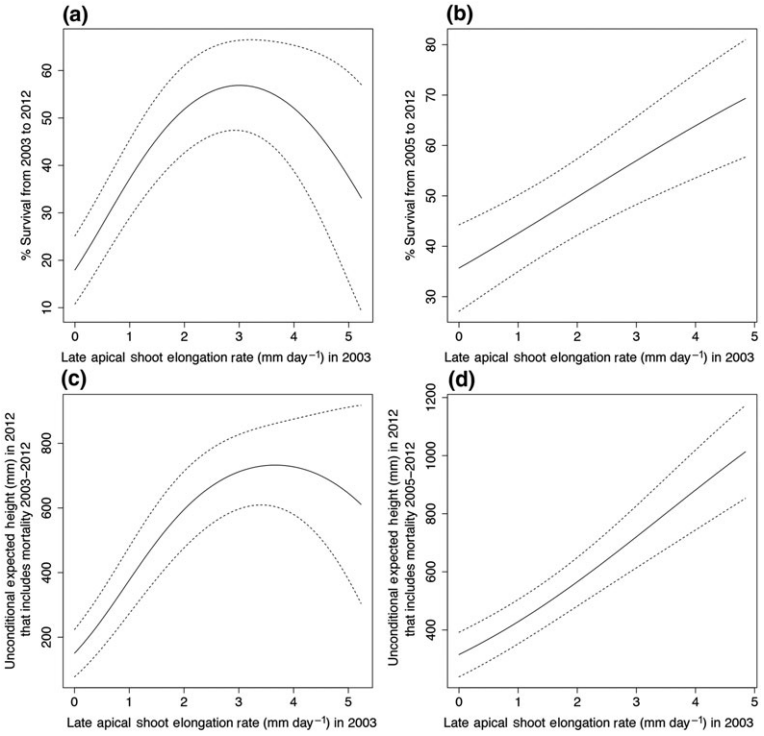

Fig. 5 Experiment 2, modelled relationship between apical shoot elongation rates (mm day^{-1}) in 2003 (Julian dates 135–148) in relation to per cent survival to 2012 that includes (a) or excludes (b) mortality prior to 2005 and unconditional expected height (mm) in 2012 site that includes (c) or excludes (d) mortality prior to 2005. Dotted lines represent 95% confidence intervals.

over time, accounting for temporal dynamics in selection is important. Indeed, for the present study, we detected shifts in the magnitude and direction of selection on shoot elongation expressed in a single year that differed in relation to yearly mortality over the 10- and 11-year study periods (Figs 3 and 5).

Selection against fast early- and late-season shoot elongation was detected for shoot elongation expressed in 2003 (Fig. 3a) and 2004 (Fig. 4a) when mortality in the respective year that the trait was expressed was included in the selection analysis. In contrast, selection favoured fast early- and late-season shoot elongation when mortality in the year of trait expression was excluded from the selection analysis (Fig. 3b). This pattern suggests that selection against the highest early- and late-season shoot elongation rates in Exp. 1 occurred predominantly in the year of trait expression. Conversely, selection against the highest shoot elongation rates in Exp. 2 was detected in the year of trait expression (i.e. 2003) and the year following trait expression (i.e. 2004). Nonetheless, contrasting direction of selection between mortality in the year of trait expressions and later years was only detected in the earliest years in both studies. Therefore, the overall pattern of stabilizing selection on timing of shoot elongation rates appears to have occurred between earlier and later years. Taken together, these results demonstrate the influence of early mortality on the direction of phenotypic selection within plant populations and underscore the importance of assessing selection in long-lived plant species over multiple years.

Stabilizing selection is generally expected in nature (Crow & Kimura, 1970); however, its detection has been relatively scarce among empirical studies (Kingsolver *et al.*, 2001). Shaw & Geyer (2010) suggest that in addition to methodological problems outlined by Travis (1989), statistical bias among some applications of Lande & Arnold's (1983) ordinary least squares (OLS) methods to quantify natural selection may also hinder detection of stabilizing selection. In particular, attempted adherence to assumptions of normality for the distribution of fitness in OLS analysis generally limited such analyses to consider only components of fitness over single episodes of selection. Even under these simplified conditions, estimates of selection gradients using best quadratic approximation in OLS methods can be misleading when the population's trait mean differs substantially from the trait value that confers highest or lowest fitness (Shaw & Geyer, 2010). Therefore, it is noteworthy that we detected stabilizing selection using aster analysis to explicitly include selection over multiple episodes of selection that together span critical stages of early tree growth and development in single, unified analyses.

The direction of selection in experiments 1 and 2 were similar. These similarities may reflect the similarity in selective environments having warm-dry climate with late-summer drought. Even so, the form of selection on growth rhythm was generally less complex in Exp. 2 than Exp. 1. This difference may represent relaxed selection (see Lewontin, 1957; Bradshaw, 1965; Schlichting, 1986; West-Eberhard, 1989; Scheiner, 1993) where more restrictive soils in Exp. 2 limited the expression of phenotypic variation for selection to act on. However, the present study cannot confirm this apparent relationship. Greater confidence in understanding the relationship between environmental stress (e.g. restrictive soils) and selection on plant traits requires study designs that assess selection under experimental manipulation using replicated variation in environmental stress (e.g. Stanton *et al.*, 2000).

Mechanism of selection

While we detected and describe selection on growth rhythm in the present study, the results do not confirm whether selection acted directly on the timing of apical shoot elongation rates or indirectly through direct selection on an unobserved and phenotypically correlated trait(s) (see Lande & Arnold, 1983). Moreover, our results do not definitively indicate mechanisms of selection. However, results do suggest that the likely mechanisms of selection on growth rhythm were predominately related to the inability of overall (early- and late-season) slower growing phenotypes to withstand environmental stress associated, to some extent, with the non-native warm environment (e.g. water limiting conditions). Selection against slower phenotypes did not appear to be related to competition. Interspecific competition was intensively controlled, while overall slow growth and spacing limited overtopping or crown closure that could result in intraspecific competition. Furthermore, most mortality occurred in the earliest years when open space among individuals was greatest. Selection against slower growth under water-limiting conditions has also been noted in studies examining intraspecific variation among functional trait syndromes (see Arntz & Delph, 2001; Bontemps *et al.*, 2017).

The detection of opposing directions of selection between the earliest and later years for the timing of shoot elongation suggests that growth rhythms that were desynchronized with the local growing season were selected against in the earliest years. Alternatively or in addition, selection against the highest growth rates in only the earliest years may reflect increased sensitivity of these phenotypes to environmental stress during early development that declined as the trees become more established (e.g. increase root development over time). Greater resolution of mechanisms underlying selection on growth rhythm would require further studies that manipulate either the environment or the phenotype.

Conclusion

Our results further support the hypothesis that climate-related selection during early juvenile stage is a key element underlying clinal variation in growth observed among populations of long-lived tree species. Given that the observed patterns of selection occurred under climate that approximated whitebark pine's predicted future climate (+4.4 °C to +9.1 °C, see Mote & Salathé, 2010; Friggens *et al.*, 2012) and that moderate heritability has been reported for measures of growth rhythm in whitebark pine (Bower & Aitken, 2006), results of the present study are likely indicative of the direction of evolutionary response of contemporary populations of whitebark pine in the immediate next generation under ongoing climate change. Moreover, climate-related selection likely continues to influence variation in growth rhythm within populations through mature stages (see Bakker *et al.*, 2006), although this was not addressed in this analysis. In addition, results do not account for potential influences of additional interactions in whitebark pine's native habitat under climate change. For example, the impacts of climate change on deleterious biotic interactions, such as with mountain pine beetle (*Dendroctonus ponderosae*) and the fungus that causes whitebark pine blister rust, *Cronartium ribicola,* are uncertain. Thus, broad interpretations of results using the present study should be made with careful consideration.

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Conflict of interests

The authors declare that they have no conflict of interests.

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Supporting information

Additional Supporting Information may be found online in the supporting information section at the end of the article:

Table S1 Monthly mean air temperature (°C) using measurements over a continuous 24-h period and 8-h, night-time period Experiment 1 and Experiment 2 sites in Priest River Experimental Forest.

Table S2 Experiment 1 Data (submitted as separate csv. File).

Table S3 Apical shoot mean elongation rate, standard deviation (σ), maximum elongation rate, mean apical shoot elongation, survival by experiment (Exp.), and year and observed yearly weather for Priest River Experimental Station at latitude 48.35°N, longitude 116.83°W and elevation, 971 m.a.s.l from National Climate Data Center (NCDC), the National Weather Service (NWS), and USDA Forest Service, Priest River Experimental Forest records.

Table S4 Experiment 1, aster model comparison test results for the effects of the timing of shoot elongation rates expressed in 2002 on estimates of survival and unconditional expected height among years.

Table S5 Experiment 2, aster model comparison test results for the effects of timing of measures of growth rhythm expressed in a given year on survival and unconditional expected height through to 2012.

Figure S1 Boxplot distribution of early (A) and late (B) (Julian Dates 108–127 and 142–149, respectively) shoot elongation rates in 2002 by provenance.

Figure S2 Experiment 1, fitness surfaces showing observed (circles) measures of apical shoot elongation rates (mm day^{-1}) and initiation (A) or cessation (B) of apical shoot elongation of individual seedlings in relation to survival from 2005 to 2012 (contour lines). Increasing circle size indicates increasing overlap of data points (i.e. phenotypes with higher frequency of occurrence).

Figure S3 Experiment 2, fitness surfaces showing observed (circles) apical shoot elongation rates (mm day^{-1}) in 2004 (A), 2005 (B and E) and 2006 (C and F) in relation to survival (contour) from (A) 2004-2012, (B) 2005-2012, and (C) 2006-2012 and unconditional expected height (contour) in 2012 that includes survival from (E) 2005-2012, and (F) 2006-2012. Increasing circle size indicates increasing overlap of data points (i.e. phenotypes with higher frequency of occurrence). Plot D shows fitness relation for only late apical shoot elongation in 2004 because no other period was statistically significant ($P < 0.05$) in relation to unconditional expected height. Dotted lines represent 95% confidence intervals.

Figure S4 Relationship of unconditional expected height with survival and mean height in 2012 in Experiments 1 (Exp. 1) and 2 (Exp. 2) Open circles indicated population performance.

Appendix S1 R script of aster selection analysis for shoot elongation in 2002 with mortality between 2002 to 2012 (Fig. 3a and c).

Appendix S2 R script of aster selection analysis for shoot elongation in 2002 with mortality between 2003 to 2012 (Fig. 3b and d).

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