

Evidence for population differentiation among Jeffrey and Ponderosa pines in survival, growth and phenology



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ABSTRACT

Ecological restoration projects that include reforestation require that land managers select appropriate source of seeds for long-term persistence. In California, the standard approach for making this choice is based on seed zone and elevational band, both geographically-based measures. However, given the pace of contemporary climate change, populations previously adapted to local conditions may become increasingly mismatched to the changes in climate. If there is a lag in adaptation, current seed zones which assume local is best, would be less useful for reforestation guidelines. Here we use a historic provenance test to evaluate genetic differences among provenances of two species of pine, *Pinus ponderosa* and *P. jeffreyi*, and assess performance following seedling transfer across an elevational gradient. Growth in Ponderosa pine shows evidence of a lag in adaptation: trees transferred from lower elevations had consistently increased growth when compared to those trees from higher elevations. In contrast, Jeffrey pine showed no evidence of a lag in adaptation for height. However, survival of Jeffrey pine provenances showed a significant quadratic relationship with transfer distance, consistent with local adaptation. In particular, Jeffrey pine trees from cooler, higher elevation sites had increased survival at high elevation. Jeffrey pine trees from higher elevation also exhibited earlier bud burst than trees from lower elevation grown in the same site, consistent with counter-gradient adaptation in phenology. Together, our results show that genetic variation within species is important for tree survival, growth and phenology in different climates. However, species-specific responses to elevational transfer indicates generalizing seed transfer guidelines across conifer species may be challenging and additional information is necessary to inform managed relocation in a changing climate.

1. Introduction

Successful forest restoration involves identifying and selecting appropriate genetic material to promote long-term persistence and resilience of native tree populations under current and future climates. In California, current seed transfer guidelines specify seeds should only be moved only within a 150 m elevation band in a seed zone, with the aim to preserve locally adapted traits and forest genetic structure (Buck et al., 1970). Where geography correlates with local environments, this strategy assumes that local seed sources are adapted to local climates. However, this geographically-based approach does not consider current or future shifts in climate along elevational and latitudinal gradients, where the pace of contemporary climate change may lead to population mismatches with local environmental conditions (Anderson, 2016;

Hamilton et al., 2016; Wadgymar et al., 2018).

In the face of ongoing climate change, local populations that cannot rapidly track shifting phenotypic optima through adaptive evolution and/or phenotypic plasticity may decline in mean fitness (Aitken et al., 2008; Chevin et al., 2010; Kopp and Matuszewski, 2013). This is particularly true for tree species, where generation length may limit populations' ability to adapt to climate *in situ* (Aitken et al., 2008; Wilczek et al., 2014; Aitken and Bemmels, 2016). To compensate for potential adaptational lag, species distributions have been modeled using past, contemporary and future climates to identify source populations that may perform well under future climatic conditions (Wang et al., 2010; Rehfeldt et al., 2014a). In addition, assisted gene flow, moving seedlings within their range, but beyond current geographically-based seed zones (ie: moving seedlings to cooler regions, or up in elevation) has

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been proposed for forest seedling transfer (Ledig and Kitzmiller, 1992; Millar et al., 2007; Schwartz et al., 2012; Aitken and Whitlock, 2013; Aitken and Bemmels, 2016). Inclusion of data from long-term provenance trials provides an additional means to evaluate population changes in fitness-related traits across space and time. More specifically, replicate provenance trials in which genotypes are transferred across a range of environments can test directly for local adaptation. These trials may provide evidence of the scale and extent of local adaptation, indicate the relative performance of different source populations across a range of environmental conditions, and may identify trends that indicate current lags in adaptation to contemporary environments.

Despite their broad geographic distributions, trees are often adapted to local environmental conditions with more narrow climate tolerances relative to range-wide distributions (Petit and Hampe, 2006; Savolainen et al., 2007; Kremer et al., 2012). In *Pinus*, the scale and extent of local adaptation varies substantially across species and varieties with differential growth and survival associated with latitudinal and elevational gradients (Alberto et al., 2013; Rehfeldt et al., 2014a). Genetic clines have been observed for several pine species, where temperature variation associated with elevation accounts for substantial growth variation across populations (Rehfeldt et al., 1999; Wang et al., 2006; Chmura et al., 2011; Rehfeldt et al., 2014a; Rehfeldt et al., 2014b). Previous studies have shown that pine trees with increased height often come from areas with mild winters, including low elevation sites, while those from cold environments, or high elevations, tend to have higher cold hardiness, but reduced height accumulation (Rehfeldt et al., 2002; Mimura and Aitken, 2010; Rehfeldt et al., 2014b; Aitken and Bemmels, 2016). At high elevations or latitudes, there is a substantial trade-off between tolerance to low winter temperatures and growth with strong selection influencing the length of active growth (Hamilton et al., 2016). Finally, in California, reduced summer moisture at lower elevations can have large effects on survival and growth, as shown previously in Ponderosa pine (Sorensen et al., 2001; Rehfeldt et al., 2014a; Rehfeldt et al., 2014b; Rother et al., 2015). The combination of genetic differences both across species and between populations within species for both survival and growth will likely reflect the evolution of resource-allocation strategies in response to climate variation (Akalusi and Bourque, 2018).

The seasonal timing of bud burst and bud set are critical traits associated with adaptation to local climates. Optimal phenological transitions in the spring are determined by a selective trade-off between growth and the maintenance of dormancy and cold hardiness mediated primarily by chilling requirements, temperature and photoperiod (Howe et al., 2003; Savolainen et al., 2007; Basler and Korner, 2012; Hamilton et al., 2016). Trees from cooler climates may burst bud later relative to those from low elevations or latitudes due to varying heat sum requirements necessary to achieve bud burst (Howe et al., 2003; Chmura et al., 2011; Lenz et al., 2013). However, the timing of bud burst will also be sensitive to heat sum accumulated following autumnal chilling in the form of degree days, where the depth of dormancy attained may contribute to variance in phenological transitions (Rehfeldt, 1990; Cregg et al., 2000; Mimura and Aitken, 2010). In addition, bud burst may be influenced by moisture availability in dryland areas, characteristic of low elevation mediterranean climates of California (Walker et al., 2015). Provenance-specific development and growth associated with phenological transitions will be sensitive to changes in climate, however, they have rarely been considered alongside tree relocation strategies (Hamilton et al., 2016; Liepe et al., 2016). Moreover, since the timing of bud burst is closely tied to the timing of reproduction (Delpierre et al., 2016), if there is a phenological mismatch between transplanted trees and local ones, reduced fitness following reforestation may be expected.

Managed relocation of pine tree populations has been proposed as a viable option to mitigate some of the consequences of a changing climate (Park et al., 2014; Aitken and Bemmels, 2016). However, forest

management faces the challenge of designing strategies that keep forests functional today and prepares them for future climate conditions. Few provenance tests have integrated assessment of traits needed to successfully relocate tree populations within a spatial and temporal framework (Aitken et al., 2008; Ukrainetz et al., 2011). Our study includes long-term data on tree survival, growth performance and phenological transitions for a set of genotypes across an elevational gradient under multiple common garden conditions, providing a comprehensive assessment of the effects of relocating tree populations beyond current seed transfer guidelines (Aitken et al., 2008; Ukrainetz et al., 2011; Akalusi and Bourque, 2018). Evaluation of extreme transfer distances will be incredibly valuable to anchoring transfer functions associated with future climatic conditions (Wang et al., 2006; Wang et al., 2010).

Here we present the results from a long-term provenance study of two pine species, Jeffrey and Ponderosa pine, planted at 3 elevations in California's mediterranean climate to provide information for seed transfer in future reforestation projects. We address the following questions: (1) How is genetic variation and/or phenotypic plasticity for survival, growth, and bud phenology expressed in common gardens with provenances from different climates and elevations, and how do genetic and plastic responses depend upon planting site elevation and species identity? (2) Is there evidence of a lag in adaptation, such that provenances transplanted from warmer, lower elevation sites have higher relative performance?

2. Methods

2.1. Study species

This project focuses on two three-needled yellow pine species commonly found in the Sierra Nevada of California: Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) and Ponderosa pine (*P. ponderosa* Lawson & C. Lawson). Both species are fire-adapted. In general Jeffrey pine produces larger cones (25 cm vs 12 cm). Jeffrey pine is distributed only in California, while Ponderosa pine is widespread across the American West. In California, Jeffrey pine is generally found at higher elevations than Ponderosa pine, though their distributions overlap at intermediate elevations (Lanner, 1999; Baldwin et al., 2012). While previous ecological genetics studies have examined variation in phenotypic traits important to adaptation for Ponderosa pine (Jenkinson, 1980; Cregg et al., 2000; Sorensen et al., 2001; Kitmiller, 2005; Gerson et al., 2009), there remains a lack of data for Jeffrey pine.

2.2. Provenance test design

A provenance test focusing on adaptation across elevational gradients was established by the USDA Forest Service, Pacific Southwest Research Station, Institute of Forest Genetics in 1973. Seeds were collected from approximately 10 maternal trees from three different provenances of Jeffrey pine and four different provenances of Ponderosa pine, respectively, spanning a contiguous elevational gradient of the two species along the western slopes Sierra Nevada mountain range. Seeds were then planted into each of three different planting sites. The three planting sites included a 2010 m high elevation site, Angora Creek in the Tahoe Basin (AC-2010), a 1360 m middle elevation site, Lincoln Hill on the Eldorado National Forest (LH-1360), and a 1030 m low elevation site, Mt. Danaher outside the town of Camino (MD-1030) (Table 1). The names of the provenances are coded as follows: the first letter indicates the species name (J – Jeffrey pine, P – Ponderosa pine), followed by the initials of the source of origin (FH – Forest Hill, LV – Lake Valley, HM – High Meadows, SF – Salmon Falls, SI – Silver Fork, and EB – Emerald Bay) and a number indicating the approximate elevation in meters for that particular source. Four provenances of Ponderosa pine were used, including one from the Tahoe Basin. There were three provenances of Jeffrey pine, including two from the Tahoe Basin.

Table 1

Location and climate information; including mean annual temperature (MAT), mean annual precipitation (MAP), frost free period (FFP), Hargreaves climatic moisture deficit (CMD), water balance index calculated as $MAP - CMD$ (WBI_{cmd}) and years of thinning for planting sites and seed sources for Jeffrey and Ponderosa pine provenance tests.

	Lat.	Long.	Elev. (m.a.s.l.)	MAT (°C)	MAP (mm)	CMD (mm)	WBI_{cmd} (mm)	FFP (days)	Thinnings
<i>Planting Sites</i>									
MD-1030	38.72	120.65	1036.3	13.5	1271	727	544	210	1975, 1983, 1985, 2012
LH-1360	38.66	120.50	1365.5	11.4	1363	665	698	194	1976, 1984, 1990
AC-2010	38.87	120.04	2011.7	6.7	938	551	387	108	1975, 1988
<i>Seed sources</i>									
<i>Jeffrey pine</i>									
J-FH-1170	39.10	120.77	1170.4	12.3	1521	609	912	200	
J-LV-1920	38.90	120.02	1920.2	7.3	842	677	165	110	
J-HM-2460	38.90	119.90	2462.8	4.2	946	455	491	69	
<i>Ponderosa pine</i>									
P-SF-150	38.75	121.07	145.4	16.2	633	915	-282	291	
P-FH-1170	39.10	120.77	1170.4	12.3	1521	609	912	200	
P-SI-1200	38.77	120.32	1204.0	12.1	1139	683	456	191	
P-EB-1920	38.95	120.10	1920.2	7.0	911	625	286	104	

These sources span the elevational range of Jeffrey and Ponderosa pine, though the planting sites are closer to the range of Ponderosa Pine (Table 1). The LH-1360 and MD-1030 planting sites were surrounded by Ponderosa pine trees. While the AC-2010 site is near populations of Ponderosa pine, the planting site itself was surrounded by Jeffrey pine trees. Thus all the planting sites represented present-day ecological distributions for Ponderosa pine. For Jeffrey pine, only the high-elevation planting site is relevant to present-day ecological conditions, whereas the lower elevation sites serve as proxies for conditions that existing populations might experience under predicted future climate warming.

Trees were planted in a randomized block design including 9–10 open-pollinated maternal half-sib seed families from each of the seven provenances from both species at each planting site. Approximately 16–24 seedlings from each family were initially planted in each site for a total sample size of 2882 for Ponderosa and 1921 for Jeffrey pine. Tree spacing was 1.82×1.82 m in AC-2010, 3.04×3.04 m in MD-1030, and 3.04×1.52 m in LH-1360. The number of blocks varied by site. Initially two trees were planted into each planting spot, and in 1975–76 each spot was thinned to one tree per spot. Selective thinnings were carried out in all sites (Table 1), where the worst performing trees in each provenance were removed. Intensity of thinnings varied by site and year. The AC-2010 test site was burned in 2007 causing around 10% mortality, and a subsequent randomized silvicultural thin was performed to avoid future fire risks.

2.3. Survival and growth measurements

To focus our survival analyses only on trees that died due to natural causes, we assessed the survival of trees at all three planting sites from 1975 to 76 after thinning to one per planting spot, including the trees that were alive in 1982 for MD-1030 and LH-1360, and 1983 for AC-2010. Growth data were collected on individual trees at the different test sites in 1982 (9 years growth), 1990 (17 year growth) and 2014 (41 year growth), including basal diameter (mm), diameter at breast height (mm) and height measurements (cm).

2.4. Phenological data: Spring bud burst

Bud phenology was recorded for both pine tree species weekly from mid-April to the end of May 2014 at the low elevation site, MD-1030. This included 62 Jeffrey pine trees spanning three provenances and 93 Ponderosa pine trees from all four provenances. Data was collected weekly on three different branches within each individual tree by recording a video using a GoPro camera attached to a 10 m long pole. The videos were analyzed in the lab to extract information on the

phenological stage of the bud. Bud images were classified into six different stages with stage 1 being a closed bud and stage 6 fully elongated needles (Appendix 1 - visual guide of the phenological stages).

2.5. Climate data

We obtained mean annual temperature (MAT, measured in °C), mean annual precipitation (MAP, measured in mm), and frost free period (FFP, measured in days) estimated using the method developed by Crookston and Rehfeldt (2008) for each collection and planting site location (i.e. Latitude, Longitude and Elevation). Hargreaves climatic moisture deficit index (CMD, measured in mm), an annual index of moisture availability necessary to support plant growth, was obtained from ClimateWNA (Wang et al., 2012) and used to calculate the Water Balance Index (WBI_{cmd}) by taking the difference between mean annual precipitation (MAP) and CMD. We chose to limit the number of climate variables we analyzed because we did not have enough provenances and planting sites for multivariate analyses. These variables each describe very different things, temperature, precipitation and growing season length. However, we note that less precipitation at a site does not imply that that site is the “driest” site, as water availability is a product of both precipitation and temperature. We use these variables over multivariate summary statistics as these measurements reflect climate variables that can be compared across species and landscapes and may be directly interpretable for seed transfer purposes (Hamilton et al., 2013).

2.6. Statistical analyses

2.6.1. Survival analyses

We calculated site and provenance means from the proportion of trees that survived in each maternal seed family, and calculated relative survival for each provenance by dividing each provenance mean by the test site mean. We estimated general transfer functions (Campbell, 1974) as univariate quadratic regressions of relative survival on the difference in elevation, MAT, MAP, FFP and WBI_{cmd} between the test site and the provenance site (lm function in R). We used ANOVA (lm function in R) to test for the effects of provenance, test site and their interaction on family absolute survival proportions on the survival responses among provenances across test sites (i.e. population response functions in Rehfeldt et al. 1999) for each pine species. We used least-squares means to analyze survival differences among provenances within test sites (lsmeans function in R).

2.6.2. Height and growth performance analyses

To estimate general transfer functions (Campbell, 1974; Campbell,

1991; Ying and Yanchuk, 2006) for growth, we calculated the relative height for each tree by dividing its height by the test site mean for each year (1982, 1990 and 2014) within each species. From these data we calculated provenance mean relative heights from the average relative height of the maternal seed families. We then performed univariate linear regressions of provenance mean relative height on the difference in elevation, MAT, MAP, FFP and WBI_{cmd} between the test site and the provenance site (transfer distance). Additionally, to understand how each provenance performed in each test site independently we did a univariate linear regression within each test site for the 2014 data. Finally, we performed a Pearson correlation between height and diameter at breast height (DBH).

To test for plasticity of height to test site and differences among provenances in plastic response of height to climate across sites, we used a linear mixed effect model to analyze differences between absolute (not relative) tree heights including two factors (test site and seed provenance) and their interaction (lmer function in the lme4 package in R). The model also included the random effects of block within planting site as well as family for the 1990 and 2014 data. We used least-squares means to analyze the effect of factors (lsmeans function in R).

2.6.3. Bud phenology analyses

We performed a Kruskal-Wallis test on the number of days to stage five to assess whether there were differences in the phenological transitions between the different provenances for Jeffrey and Ponderosa pine. The Kruskal-Wallis test is a non-parametric, categorical test appropriate for comparing bud stage data.

3. Results

3.1. Survival analyses

Transfer functions (relative performance) – In Jeffrey pine, the survival transfer function for elevation, MAT, MAP, WBI_{cmd} and FFP was significantly concave downward, with an intermediate optimum (Table 2, Fig. 1a, and Sup. Fig. 1a). Jeffrey pine trees transferred to an elevation ~500 m lower than their site of origin (the optimal transfer distance) had highest relative survival, with a similar pattern for MAT and FFP. Thus, there was no evidence of a lag in adaptation for survival, which would have resulted in positive optimal transfer distance to higher elevation. The quadratic relationship was driven by greater relative survival of the higher elevation sources at the higher elevation planting site, as well as the greatly reduced relative survival of the lowest elevation source at the highest elevation planting site, as would be expected if provenances were adapted to local climate. The optimal transfer distance for Jeffrey pine, based on the WBI_{cmd} transfer function, was moving to environments with approximately 270 mm greater

Table 2

Quadratic regressions between relative survival and elevation transfer, MAT, MAP, WBI_{cmd} and FFP difference between the test site and the provenance site for Jeffrey and Ponderosa pine early survival. β_{linear} and $\gamma_{quadratic}$ are the linear and quadratic coefficients, respectively, boldface indicates significant individual coefficients (P -value < 0.05). The P -value is for the whole model.

Species	Variable	β_{linear}	$\gamma_{quadratic}$	r^2	d.f.	P
Jeffrey	Elevation	−0.0001	−0.0000001	0.69	6	0.03
	MAT	0.021	−0.003	0.68	6	0.03
	MAP	0.0001	−0.0000005	0.75	6	0.01
	WBI_{cmd}	0.0001	−0.0000005	0.63	6	0.05
	FFP	0.001	−0.00001	0.69	6	0.03
Ponderosa	Elevation	−0.00001	−0.00000005	0.24	9	0.29
	MAT	0.005	−0.002	0.24	9	0.29
	MAP	−0.00008	0.0000001	0.06	9	0.75
	WBI_{cmd}	−0.00008	0.0000004	0.07	9	0.72
	FFP	0.0003	−0.000004	0.23	9	0.30

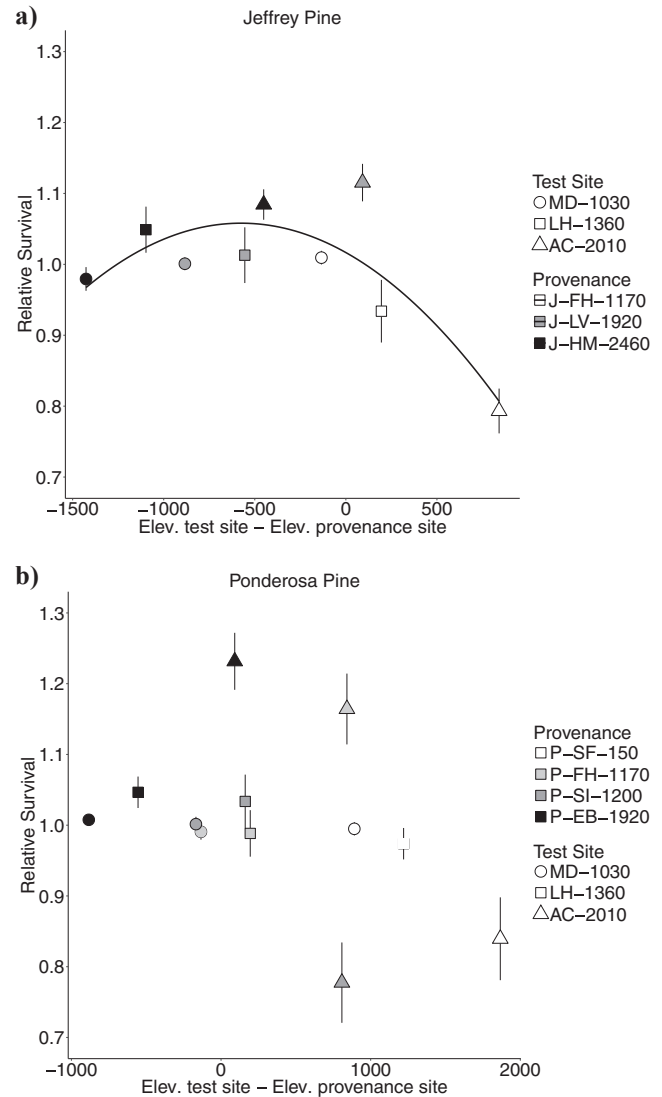


Fig. 1. Early relative survival for Jeffrey pine (a) and Ponderosa pine (b) trees and elevation transfer. Test sites are represented by different shapes, and seed provenance is represented by different shading. Quadratic regression line from the model for all three test sites combined (Table 2) shown when significant.

water availability to support plant growth. This transfer function was driven by the water availability at the site of origin: both J-LV-1920 and J-HM-2460 had low WBI_{cmd} and had high relative survival as all the test sites had higher WBI_{cmd} values. In contrast, the lower elevation provenance J-FH-1170 that had the highest WBI_{cmd} value at its site of origin had lower survival as it was transferred to test sites with lower WBI_{cmd} values. In contrast, Ponderosa pine exhibited no impact of transfer distance on relative survival (Fig. 1b and Sup. Fig. 1b).

Population response functions ($G \times E$ in ANOVA of absolute performance) – ANOVA of absolute family-level values for survival revealed significant effects of test site, provenance and their interaction on survival for both Jeffrey and Ponderosa pine (Table 3a). In both species, survival differences among provenances were greatest at AC-2010, the high elevation test site, where provenances from low elevation sites had lower survival (Table 3b), but provenances differed in survival responses across sites, indicating plasticity for the trait.

3.2. Height and growth analyses

Transfer functions (relative performance) – We found no significant regressions between climatic variables and relative height in Jeffrey

Table 3a

ANOVA table for the effect of test site, provenance and their interaction for survival proportions of Jeffrey and Ponderosa pine.

Species	Source	DF	F	P
Jeffrey	Test site	2	25.62	< 0.001
	Provenance	2	19.17	< 0.001
	Test site × Provenance	4	11.10	< 0.001
Ponderosa	Test site	2	240.75	< 0.001
	Provenance	3	19.30	< 0.001
	Test site × Provenance	6	16.36	< 0.001

Table 3b

Jeffrey and Ponderosa pine provenances survival proportions at each test site. Letters indicate significant differences between provenances within the test site.

Species	Test Site	Provenance	N(fam)	Surviving proportion	
Jeffrey	MD-1030	J-FH-1170	10	0.979	a
		J-LV-1920	10	0.971	a
		J-HM-2460	10	0.950	a
	LH-1360	J-FH-1170	10	0.813	b
		J-LV-1920	10	0.881	ab
		J-HM-2460	10	0.913	a
	AC-2010	J-FH-1170	10	0.658	b
		J-LV-1920	10	0.926	a
		J-HM-2460	10	0.900	a
Ponderosa	MD-1030	P-SF-150	10	0.975	a
		P-FH-1170	10	0.971	a
		P-SI-1200	10	0.981	a
		P-EB-1920	10	0.988	a
	LH-1360	P-SF-150	10	0.838	a
		P-FH-1170	10	0.850	a
		P-SI-1200	9	0.888	a
		P-EB-1920	10	0.900	a
	AC-2010	P-SF-150	10	0.571	b
		P-FH-1170	10	0.792	a
		P-SI-1200	9	0.529	b
		P-EB-1920	10	0.838	a

Table 4

Regressions between 2014 relative height and elevation, MAT and FFP difference between the test site and the provenance site for Ponderosa pine.

Variable	Test Site	B	r ²	d.f.	P
Elevation	All sites	0.00005	0.51	10	0.006
	MD-1030	0.00007	0.93	2	0.02
	LH-1360	0.00006	0.37	2	0.24
	AC-2010	0.00007	0.87	2	0.04
MAT	All	−0.0080	0.44	10	0.011
	MD-1030	−0.014	0.96	2	0.013
	LH-1360	−0.014	0.65	2	0.12
	AC-2010	−0.015	0.96	2	0.012
FFP	All	−0.0005	0.54	10	0.004
	MD-1030	−0.0007	0.99	2	0.005
	LH-1360	−0.0005	0.66	2	0.19
	AC-2010	−0.0006	0.90	2	0.05

pine in 1982, 1990 or 2014 (See [Supplementary Data](#), Tables S1a – S1e). In contrast, Ponderosa pine trees that were transferred to a higher elevation site (cooler temperature and shorter growing season) than their site of origin had greater relative height than those transferred to a lower elevation (warmer temperature and longer growing season) than their site of origin (Table 4, Table SI S1a, Fig. 2a and b). This pattern reflects elevational clines within each test site; relative height generally decreased with increasing elevation of origin. For Ponderosa pine we also found a significant positive relationship between relative height and climate transfer distance for MAT and FFP (Table 4, Fig. 2b, Tables SI S1b and S1e). Interestingly, there was no significant regression between relative height and the transfer distance of precipitation (MAP)

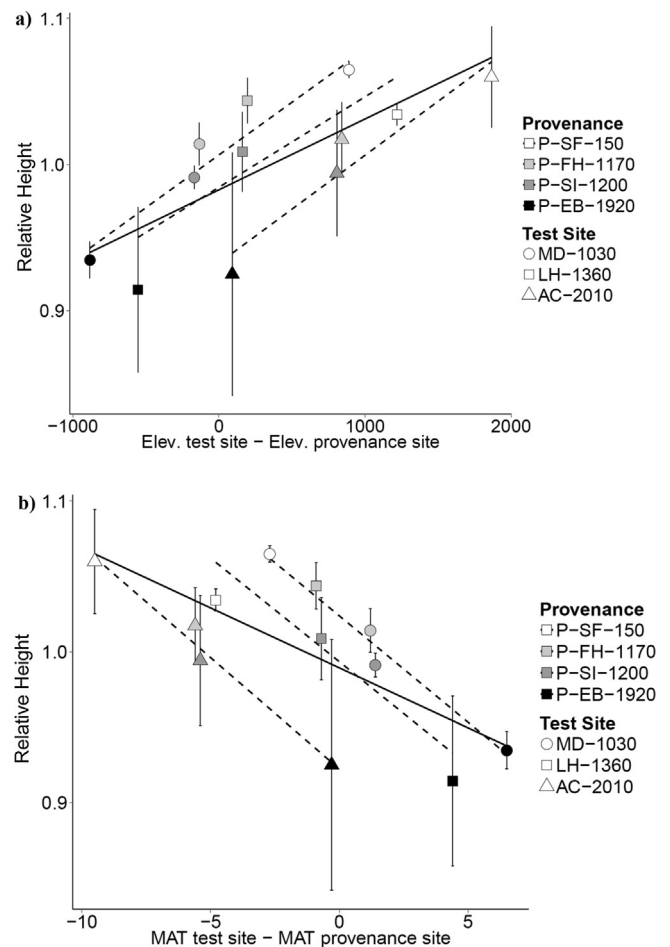


Fig. 2. Regression of relative height (mean $\pm$ s.e.) on elevation (a) and MAT (b), for Ponderosa pine for the 2014 data. Overall regression is indicated as a solid line, and within site regressions are indicated as a dashed line. Test sites are represented by different shapes, seed provenance is represented by different shading.

and of the water balance index (WBI_{cmd}) in Ponderosa (Table S1c and S1d). It should be noted that no trees were planted in their “home site” and all comparisons are relative differences in growth compared to the differences in the climates between where the trees originated and where they were planted.

Population response functions ($G \times E$ in ANOVA of absolute performance) – In Jeffrey pine we found significant differences among test sites and provenances in absolute tree height in 1990 and 2014 (Table 5). Trees were taller overall at lower elevation sites and the high-elevation provenance was the shortest in most test sites (Table 6). However, the high elevation provenance was tallest in the mid elevation site, and a significant test site $\times$ provenance interaction indicated variation in plastic responses among provenances to test site environments (Table 6). For Ponderosa pine we found a significant effect of test site, provenance and their interaction in 1990, and a significant effect of test site and provenance in 2014 on tree height. In both years, Ponderosa pine trees were taller at lower elevation sites. In 1990, height differences among provenances were greatest in the low elevation site and insignificant in the high elevation site, resulting in a significant site $\times$ provenance interaction (consistent with a $G \times E$ interaction). In 2014 Ponderosa pines were taller in low elevation sites, and the highest elevation provenance was the shortest in all plantings (Table 6).

Finally, we found a positive significant Pearson correlation between height and DBH for both Jeffrey and Ponderosa pine species

Table 5

ANOVA table for the fixed effects of test site, provenance, and the interaction of test site $\times$ provenance (from a mixed-model analysis with family and block as random factors) on tree height for Jeffrey and Ponderosa pine for 1990 and 2014 data.

Year	Species	Source	DF	F	P
1990	Jeffrey	Test site	2	2999.19	< 0.001
		Provenance	2	13.93	< 0.001
		Test site $\times$ Provenance	4	8.06	< 0.001
	Ponderosa	Test site	2	10683.4	< 0.001
		Provenance	3	31.7	< 0.001
		Test site $\times$ Provenance	6	148.41	< 0.001
2014	Jeffrey	Test site	2	297.08	< 0.001
		Provenance	2	7.40	< 0.001
		Test site $\times$ Provenance	4	12.51	< 0.001
	Ponderosa	Test site	2	1329.86	< 0.001
		Provenance	3	11.10	< 0.001
		Test site $\times$ Provenance	6	1.96	0.07

(Supplementary Information, Table S2).

3.3. Bud phenology analyses

Bud burst timing did not differ among different Ponderosa pine provenances and they burst bud earlier than the Jeffrey pine trees. We found evidence of counter-gradient variation in bud burst (i.e. days to stage 5) among Jeffrey pine provenances ($\chi^2 = 16.5$, $df = 2$, $P = 0.0003$) which were only tested at the low-elevation planting site (MD-1030). Trees from the low elevation provenance (J-FH-1170) transitioned more slowly to stages 5 and 6 than trees from the mid and high elevation provenances (Fig. 3a), consistent with the idea that lower elevation trees have higher heat-sum requirements for bud burst and that higher elevation sources responded more quickly to spring warmth. In contrast, we did not find significant differences in bud burst between Ponderosa pine provenances ($\chi^2 = 3.23$, $df = 3$, $P = 0.36$; Fig. 3b) at the low-elevation planting site (MD-1030).

4. Discussion

In a rapidly warming climate, populations previously well-adapted to local conditions may become increasingly mismatched to the change

Table 6

Jeffrey and Ponderosa pine provenances height (cm) (mean $\pm$ s.e.) at each test site. Letters indicate significant differences between provenances within the test site.

Species	Test Site	Provenance	1990			2014		
			N	$X \pm$ s.e.		N	$X \pm$ s.e.	
Jeffrey	MD-1030	J-FH-1170	96	910.8 $\pm$ 16.4	a	60	2062.7 $\pm$ 30.0	a
		J-LV-1920	95	1003.0 $\pm$ 9.9	a	63	2129.8 $\pm$ 30.0	a
		J-HM-2460	96	908.9 $\pm$ 9.8	a	55	2027.4 $\pm$ 38.0	a
		J-FH-1170	40	846.0 $\pm$ 19.5	ab	40	1833.2 $\pm$ 50.5	a
		J-LV-1920	40	892.7 $\pm$ 16.4	a	39	1728.2 $\pm$ 50.3	a
		J-HM-2460	40	810 $\pm$ 16.9	b	38	1242.1 $\pm$ 92.5	b
	AC-2010	J-FH-1170	142	191.2 $\pm$ 5.0	a	10	743.0 $\pm$ 21.5	a
		J-LV-1920	221	199.9 $\pm$ 5.0	ab	20	710.0 $\pm$ 35.5	a
		J-HM-2460	216	212.34 $\pm$ 3.8	b	16	801.9 $\pm$ 38.3	a
Ponderosa	MD-1030	P-SF-150	106	1264.3 $\pm$ 11.2	a	57	2694.7 $\pm$ 23.0	a
		P-FH-1170	180	1193.9 $\pm$ 9.9	b	53	2564.7 $\pm$ 31.5	b
		P-SI-1200	186	1201.2 $\pm$ 10.4	b	59	2520.28.5	b
		P-EB-1920	115	1150.2 $\pm$ 10.6	c	59	2379.0 $\pm$ 28.8	c
		P-SF-150	40	1165.5 $\pm$ 14.6	a	40	2471.7 $\pm$ 27.9	a
		P-FH-1170	40	1132.7 $\pm$ 16.2	a	40	2501.5 $\pm$ 31.1	a
	LH-1360	P-SI-1200	40	1127.2 $\pm$ 24.6	a	42	2395.7 $\pm$ 48.5	a
		P-EB-1920	40	1034.0 $\pm$ 34.6	b	41	2264.9 $\pm$ 58.6	b
		P-SF-150	96	214.7 $\pm$ 4.6	a	11	790.9 $\pm$ 29.2	a
		P-FH-1170	96	200.5 $\pm$ 4.1	a	14	771.4 $\pm$ 31.4	a
	AC-2010	P-SI-1200	95	200 $\pm$ 6.0	a	16	760.6 $\pm$ 22.8	a
		P-EB-1920	96	210.5 $\pm$ 4.4	a	16	704.4 $\pm$ 45.0	a

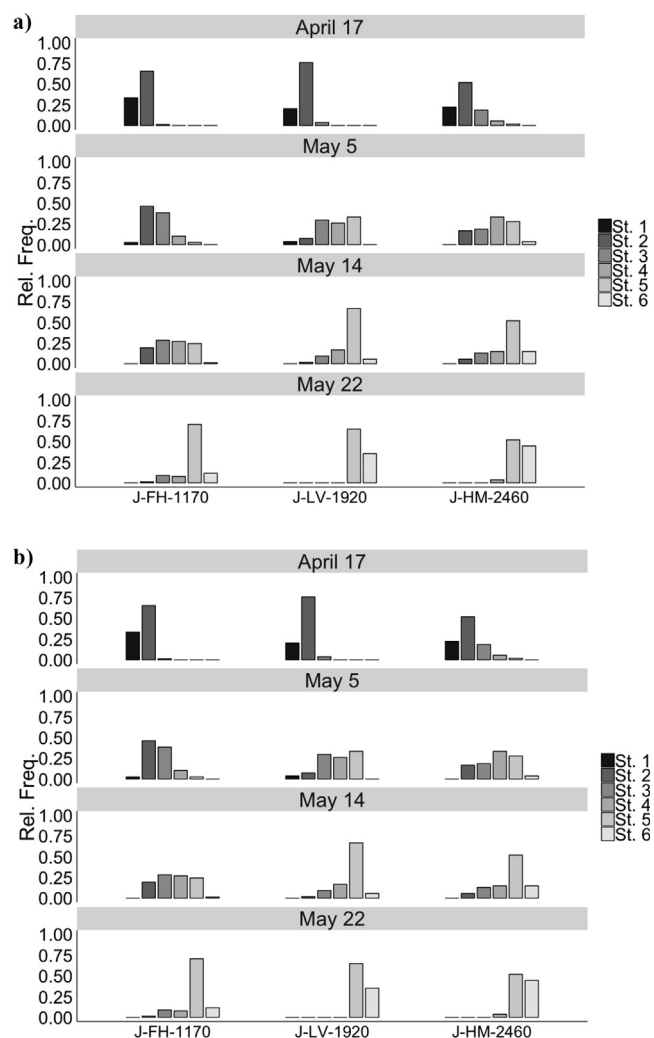


Fig. 3. Bud burst stage proportions (Stages 1 – 6) for a) Jeffrey and b) Ponderosa pine provenances for each week sampled from April to May 2015 at MD-1030, the low elevation site.

in conditions as the population mean phenotype lags behind a shifting optimum (Aitken et al., 2008; Kopp and Matuszewski, 2013; Wilczek et al., 2014; McGraw et al., 2015). We used a historical provenance test for Ponderosa and Jeffrey Pine to test for evidence of adaptation to local climates, plasticity and signatures of adaptational lag. We observed genetic differences among populations originating from different source elevations and interactions between provenance and site between species indicating the maintenance of genetic variation and plasticity for select traits. In the lower-elevation species, Ponderosa pine, we found little population differentiation in survival or phenology but strong evidence for adaptational lag associated with relative height, which was greatest in lower elevation provenances transferred to higher elevations. In contrast, in Jeffrey pine, the higher-elevation species, we found evidence of local adaptation for survival, as well as counter-gradient variation in bud burst phenology, but no difference among provenances in relative growth or evidence of a lag in adaptation. These differences raise important questions for generalized seed transfer guidelines across species in a rapidly changing world.

4.1. Evidence of a lag in adaptation in Ponderosa pine: Relative heights were higher for provenances from warmer, lower elevation sites transferred to cooler high elevation sites

In this study, relative height of Ponderosa pine within a planting site increased significantly with elevational transfer distance, as well as mean annual temperature and frost free period (Fig. 2). Trees transferred from lower elevation sites (that were warmer and had longer growing seasons) exhibited greatest relative height at all three planting sites. Trees transferred from lower elevations may be better able to take advantage of a longer growing season than trees adapted to cooler temperatures. Previous studies have found that populations from northern latitudes and high elevations exhibit a trade-off between active growth and development of cold tolerance and dormancy in the fall influencing length of growing season (Rehfeldt et al., 1999; Rehfeldt et al., 2002; Hamilton et al., 2016). Provenance tests in Ponderosa pine have found similar growth patterns where populations from milder environments having increased growth but reduced cold tolerance relative to those from higher latitudes or elevations (Rehfeldt et al., 2014b). Higher elevation provenances may be unable to take advantage of a lengthening growing season. This raises concern for growth potential of high elevation provenances under predicted future warming if the growing season shifts, as local genotypes will be increasingly mismatched with their local growing season, leading to adaptational lag.

4.2. Evidence of local adaptation in Jeffrey pine: Population differentiation in relative survival and phenology

4.2.1. Local adaptation in survival

In contrast with our results for Ponderosa pine, we found no effect of climate or elevation of origin on relative growth of Jeffrey pine in the test sites, and no evidence for a lag in adaptation. However, a significant quadratic regression of relative survival on elevation of origin, as well as four climatic variables, suggests Jeffrey pine may be locally adapted. The intermediate optimum transfer distance of approximately 500 m lower (Fig. 1) indicates that relative performance was lower for longer transfer distances of high elevation provenances to much lower elevations (a proxy for climate warming). At the cool, dry, high elevation site, there was a pronounced reduction in relative survival for the low elevation provenance. The Jeffrey pine provenances from mid and high elevations that were moved to lower elevations had higher survival. While the quadratic relationship is primarily driven by an extreme transfer distance, these extreme points become quite valuable as increased transfer distance provides a better understanding of the transfer function. Anchored points reflected in tails of the distribution become valuable as they improve the development of the transfer function for individual species (Wang et al., 2006; Wang et al., 2010;

O'Neill et al., 2014).

In addition to phenological and growth measurements, differential water use as calculated from a Water Balance Index (WBI_{cmd}), may influence survival. At mid and high elevations, there was increased water availability between provenance origin and test site to lead to increased survival for Jeffrey pine. However, the low elevation Jeffrey pine provenance, originating from greater water availability (~ 900 mm), had low survival across those test sites that had reduced water availability. While similar trends were not observed for ponderosa pine, these results suggest that water availability has species-specific consequences on survival. Similar to previous research in Mediterranean pines, transfer from wet to drier environments may lead to differential success in drier environments between local and non-local genotypes (Veltas et al., 2008). These results indicate that response to hydric stress may impact species success, particularly as drought and seasonality become increasingly extreme, although species will exhibit differential responses to variation in water availability.

There is little evidence in the literature of cold damage leading to tree death because extreme cold temperatures occur sporadically (Wagener, 1960) and test sites are generally located in areas of high productivity in order to assess optimal tree growth (Allen and Breshears, 1998; Leites et al., 2012). However, in California, Wagener (1960) reported that during an extreme cold event both Ponderosa and Jeffrey pine showed cold damage, although it could have resulted from a combination of cold damage followed by an insect attack. Understanding the negative effects of low temperatures on pines is relevant as one of the predicted effects of climate change is early snowmelt, potentially leading to higher frost damage on pine trees (Mellander et al., 2007; but see Lenz et al., 2013).

Ponderosa and Jeffrey pine survival in Mediterranean Californian forests are influenced by temperature, but precipitation as snowmelt will also interact to contribute to hydric stress (Guarin and Taylor, 2005; Gworek et al., 2007; Allen et al., 2010; Ganey and Vojta, 2011; Williams et al., 2013). This interaction will likely be more prevalent at low elevation sites, where increasing extremes contribute to differential survival, as currently observed in Jeffrey pine (Allen and Breshears, 1998; Gworek et al., 2007; Allen et al., 2010). Currently, California is experiencing a much higher than normal rate of tree mortality (McIntyre et al., 2015) and while the data collected in this study predates the current trend for elevated tree mortality, understanding patterns of tree survival has become a high priority in California (for example: https://www.gov.ca.gov/docs/10.30.15_Tree_Mortality_State_of_Emergency.pdf).

Contrasting results for Jeffrey and Ponderosa pine are also explained by the sampling design: Jeffrey pine provenances came from sites ranging from 1170 to 2460 m. a. s. l., and thus the majority of transfers for this species were from higher to lower elevations. While the range of elevation sampled for Ponderosa pine provenances went from 150 to 2000 m. a. s. l. and test site locations ranged from 1030 to 2010 m. a. s. l. so a majority of transfers for this species were to a higher elevation than their site of origin. The varying direction of primary transfer may explain different results for Jeffrey and ponderosa pine. Transfer from higher to lower elevation on average for Jeffrey pine likely led to increased hydric stress contributing to reduced survival. This contrasts with ponderosa pine, where transfer from lower to higher elevations may have provided a competitive advantage for lower-elevation provenances relative to local provenances.

4.2.2. Counter-gradient differentiation across elevations in Jeffrey pine budburst phenology

For trees at high elevations, lower degree-day requirements may allow budburst at the appropriate time in spring, leading to counter-gradient adaptive differentiation for thermal sensitivity. Our results showed that bud burst timing, after 41 years of growth in the same environment, did not differ among different sources of Ponderosa pine. However, for Jeffrey pine, the low elevation provenance burst bud later

at the low elevation test site than the mid and high elevation provenances, suggesting counter-gradient adaptation to elevational differences in spring forcing temperatures. Phenological differences between these species can be explained by the different selective pressures experienced at different latitudes and elevations (Lopushinsky and Max, 1990; Rehfeldt, 1990; Cregg et al., 2000). In our study we found that Ponderosa pine provenances commenced growth earlier than Jeffrey pine indicating species-specific responses to phenological cues.

Trees vary in their thermal threshold associated with timing of bud burst (Lopushinsky and Max, 1990; Kramer et al., 2000; Bronson et al., 2009; Basler and Korner, 2012). The interaction between daylength and temperature/elevation summarized in degree-days is a good predictor for budburst across species (Basler and Korner, 2012). Within species, common-garden studies have shown that high elevation populations may burst earlier than those from lower elevations due to lower thermal thresholds (Lopushinsky and Max, 1990; Samela et al., 2013). Indeed, Basler and Korner (2012) suggested that high elevation provenances may have reduced degree day requirements relative to low elevation provenances. In the case of Jeffrey pine, the two provenances from higher elevations had earlier bud burst, which may reflect different thermal requirements. Distributed across higher elevations, reduced thermal thresholds at higher elevations may accelerate phenological transitions in Jeffrey pine to maximize potential growing season. This contrasts with Ponderosa pine, which is the most common pine species in the dry forest of North America. Dry forest phenology is also partly determined by water availability, where individuals will experience low spring temperatures and hydric stress in summer (Kramer et al., 2000; Mutke et al., 2003; Maseyk et al., 2008; Walker et al., 2015). Consequently, the impact of water availability may more adequately reflect phenological transitions in Ponderosa pine not captured in this current assessment.

5. Conclusions

This long-term study integrates information on survival, growth and phenology in two pine species, allowing for a more comprehensive understanding of the influence seed transfer may have on traits important to adaptation in a changing climate. Our results suggest Ponderosa pine may already be experiencing adaptational lag in response to warming temperatures, and that managed relocation of trees to higher elevational zones beyond current limits may be necessary (Ledig and Kitzmiller, 1992; Schwartz et al., 2012). This contrasts with Jeffrey pine, which exhibited no evidence of adaptational lag, appeared locally adapted and exhibited counter-gradient population differences in budburst phenology. In this species, the ability of local populations to survive in warming future climates will likely depend on their ability to withstand both hydric and temperature stress. Overall, substantial differences across species in response to elevational transfer points towards the need for species-specific data to inform potential seed transfer and suggests that long-term provenance tests will be incredibly valuable for informing management decisions in the face of future climate change.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2018.12.009>.

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