



## PRIMARY RESEARCH ARTICLE

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# Genotypic variation in phenological plasticity: Reciprocal common gardens reveal adaptive responses to warmer springs but not to fall frost

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## Abstract

Species faced with rapidly shifting environments must be able to move, adapt, or acclimate in order to survive. One mechanism to meet this challenge is phenotypic plasticity: altering phenotype in response to environmental change. Here, we investigated the magnitude, direction, and consequences of changes in two key phenology traits (fall bud set and spring bud flush) in a widespread riparian tree species, *Populus fremontii*. Using replicated genotypes from 16 populations from throughout the species' thermal range, and reciprocal common gardens at hot, warm, and cool sites, we identified four major findings: (a) There are significant genetic (G), environmental (E), and GxE components of variation for both traits across three common gardens; (b) The magnitude of phenotypic plasticity is correlated with provenance climate, where trees from hotter, southern populations exhibited up to four times greater plasticity compared to the northern, frost-adapted populations; (c) Phenological mismatches are correlated with higher mortality as the transfer distances between provenance and garden increase; and (d) The relationship between plasticity and survival depends not only on the magnitude and direction of environmental transfer, but also on the type of environmental stress (i.e., heat or freezing), and how particular traits have evolved in response to that stress. Trees transferred to warmer climates generally showed small to moderate shifts in an adaptive direction, a hopeful result for climate change. Trees experiencing cooler climates exhibited large, non-adaptive changes, suggesting smaller transfer distances for assisted migration. This study is especially important as it deconstructs trait responses to environmental cues that are rapidly changing (e.g., temperature and spring onset) and those that are fixed (photoperiod), and that vary across the species' range. Understanding the magnitude and adaptive nature of phenotypic plasticity of multiple traits responding to multiple environmental cues is key to guiding restoration management decisions as climate continues to change.

## KEYWORDS

bud flush, bud set, climate change, common garden provenance trial, phenology, phenotypic plasticity, *Populus fremontii*

## 1 | INTRODUCTION

As climate change continues to push the limits of plant species' physiological tolerances, they will acclimate, adapt, migrate, or die out (Aitken, Yeaman, Holliday, Wang, & Curtis-McLane, 2008). For those species that cannot migrate quickly, such as long-lived trees (Davis & Shaw, 2001), persisting in situ through natural selection and/or phenotypic plasticity may be critical for survival (Ghalambor et al., 2015; Lande, 2009; Pigliucci, 2005; Scheiner, 1993). Given that the predicted rates of evolutionary responses for long-lived species can be much slower than the predicted rates of climate change (Etterson & Shaw, 2001, but see Oddou-Muratorio & Davi, 2014), rapid plastic responses may be crucial for population persistence. Phenotypic plasticity, the ability of a genotype to produce distinct phenotypes when exposed to different environments, has been identified as an important response to climate change (Donelson, Munday, McCormick, & Pitcher, 2011; Franks, Weber, & Aitken, 2014; Merilä & Hendry, 2014; Nicotra et al., 2010), both within and across generations (i.e., transgenerational plasticity; Galloway & Etterson, 2007). When extreme climate events exceed historical levels of variation, locally adapted populations will experience environments for which current traits are poorly suited (Kim & Donohue, 2013; Wang, O'Neill, & Aitken, 2010). These climatic changes can prompt plastic trait responses ranging from adaptive to maladaptive in direction, and from small to large in magnitude, depending on the predictability of the environment (Ghalambor, McKay, Carroll, & Reznick, 2007; Hendry, 2016; Lande, 2009). Likewise, adaptive transgenerational plasticity is thought to be beneficial when the parental environment reliably predicts offspring environment (Herman & Sultan, 2011), a condition that may diminish with climate change. Although there has been substantial research on plasticity resulting from climate warming (Anderson, Inouye, McKinney, Colautti, & Mitchell-Olds, 2012; Cleland et al., 2012; Kramer, 1995), phenotypic responses to increasing climate variability will be impacted by both warming and freezing events. The responses of diverse genotypes to such divergent stressors may be best evaluated in replicated common gardens that differ from one another in multiple climatic characteristics.

A major component of local adaptation in deciduous temperate and boreal trees is the evolution of precisely timed phenological traits such as spring bud flush and fall bud set that match periods of plant activity, such as growth, reproduction, and dormancy, to suitable environmental conditions and cues (Harrington, Ford, & St. Clair JB, 2016; Kikuzawa, 1989; Körner & Basler, 2010). If species cannot shift their phenologies appropriately, the cost-benefit balance of maximizing growing season length while avoiding frost damage will become disrupted and may result in lower fitness. For instance, a review of phenologically plastic species that tracked warming temperatures by advancing spring phenology via earlier flowering or leaf emergence showed increased performance relative to less sensitive or canalized species (Cleland et al., 2012). Adaptive plasticity can be thought of as a shift in phenotype in the direction of the local optimum trait value, while genotypes that exhibit a shift in the opposite direction are considered non-adaptively plastic (Ghalambor et al., 2007).

Given the different environmental cues driving phenology in the spring versus fall, the expectation for how plasticity in bud flush and bud set has evolved differs (Franks et al., 2014). For temperate plants, spring phenology is typically activated by the accumulation of days above a certain base temperature following adequate chilling (Howe et al., 2003). Given increased warming trends, trees that are capable of plastic responses to temperature should shift to earlier bud flush dates (Franks et al., 2014). In contrast, fall phenology and cold acclimation are chiefly driven by photoperiod, with forest trees showing fine-scale adaptation to the length of the growing season of their local environment (Frewen et al., 2000). Since photoperiod is unaffected by climate change, traits such as fall bud set are predicted to show limited plasticity (Evans et al., 2016). However other environmental conditions such as drought and low temperatures may also affect fall phenology traits (Franks et al., 2014; Howe et al., 2003). This distinction in how species have evolved spring and fall phenology responses could result in uneven plastic shifts for bud flush versus bud set as climate change differentially affects environmental cues across a species' distributions. Increased climate warming, for example, can affect populations at leading and trailing edges differently due to earlier spring initiation or increased drought, respectively (Vitasse, Bresson, Kremer, Michalet, & Delzon, 2010). This can become important as warmer fall and winter temperatures disrupt cold hardiness traits in populations that have evolved with freezing, or in extreme cold snaps where populations have not evolved mechanisms to protect against freezing. Thus, in the same way that plasticity varies among phenology traits, the potential for plasticity can also vary across a species' distribution. Populations experiencing greater spatial and temporal environmental variation (Baythavong, 2011; Gianoli & González-Teuber, 2005), and those at range edge boundaries (Chevin & Lande, 2011) are expected to have evolved higher levels of plasticity (Hendry, 2016). Together these complex interactions necessitate a detailed examination of the interplay among species' traits, demography, and environmental change.

Fremont cottonwood (*Populus fremontii*) is a widespread foundation tree species found along riparian corridors throughout the western U.S. (Ikeda et al., 2017). As such, it is an ideal study system to investigate phenological plasticity across a gradient of environmental change. Despite its widespread distribution, less than 3% of Fremont cottonwood's historical range remains (Noss, LaRoe, & Scott, 1995; Lower Colorado River Multi-Species Conservation Program: LCR-MSCP, 2004). In addition to habitat loss, our study region of the American southwest is already experiencing dramatic climate change, with an average temperature increase of 0.9°C relative to the 1900–1960 average, with projections of up to 2°C by midcentury and 4.8°C by late-century (USGRP, 2017). When plant phenologies fail to track climate cues appropriately, associated species or entire dependent communities can become phenologically mismatched with their hosts (Visser & Both, 2005). Since Fremont cottonwood supports numerous dependent organisms and helps structure the riparian ecosystem (Whitham et al., 2006), the effects of climate change on its phenology could cascade into the extended phenotype (Whitham, Young, & Kuske, 2003), disrupting important species interactions and ecosystem-level

processes. In this study, we examine genetic and environmental variation in bud set and bud flush among 16 populations reciprocally planted across three common gardens, which encompasses a broad thermal range (10.4°C – 22.8°C) representative of the full species distribution. This experimental design of replicating clonally propagated genotypes across multiple natural environments is considered one of the best ways to ascertain the impact and adaptive nature of phenotypic plasticity by substituting space for time as a climate change proxy (Franks et al., 2014; Hendry, 2016). It also allows genotypes to experience much warmer and much colder temperatures compared to their source provenances, thereby simulating both warming and cooling climates.

We used this system to test four hypotheses. (a) There will be variation in phenological plasticity. Given previous evidence of genetic variation in functional traits in this species (Fischer et al., 2017; Grady et al., 2013; Grady, Kolb, Ikeda, & Whitham, 2015), coupled with the steep environmental gradient across the three gardens, we hypothesized that there will be significant genetic (G), environmental (E), and G×E effects on bud set and bud flush. (b) Phenotypic plasticity of individual genotypes will be related to their place of origin. We predicted that the magnitude of a genotype's plasticity will be related to the environmental conditions experienced in their home provenances. In this study, provenance environment ranges from hot deserts to montane forests spanning 5°C of latitude, 12°C mean annual temperature, 1,850 m of elevation, and vary substantially in the occurrence and frequency of frost. (c) Populations sampled in this study will be locally adapted. We hypothesized that populations are locally adapted to climate cues, and transplanting them beyond a threshold climate transfer distance away from their home environment will impact their survival. Measures of phenotypic plasticity and bidirectional transfers (i.e., transfer to both warmer and cooler climates) are incorporated to build on previous findings that populations transferred more than 3°C cooler than their home

climate suffered performance declines (Grady et al., 2015). (d) We predicted adaptive plasticity, defined as a phenotypic shift toward the local trait optimum (Ghalambor et al., 2007) will be beneficial, resulting in increased survival of genotypes transferred to new climates, while non-adaptive changes will lead to decreased survival. Our findings are discussed in the context of predicting responses to climate change and informing associated management strategies like assisted migration, which moves targeted genotypes across changing landscapes.

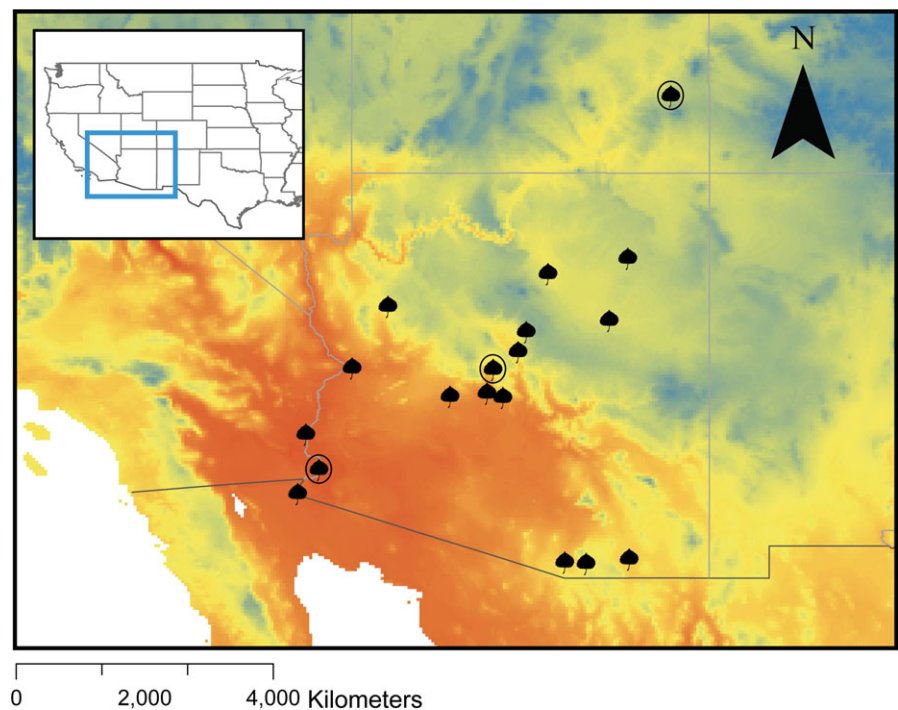
## 2 | MATERIALS AND METHODS

### 2.1 | Experimental design and trait measurements

To assess the genetic and environmental contribution of population differentiation in phenological traits, three common gardens were established in the fall of 2014. Cuttings from 16 populations of *Populus fremontii* from throughout Arizona encompassing the climate range of the Sonoran Desert Ecotype (Ikeda et al., 2017), with 12 genotypes per population, were collected. The cuttings were rooted in the greenhouse for up to four months and planted at the common garden sites when saplings averaged 0.3 m in height (Figure 1). Discrete genetic individuals were collected by ensuring a distance of at least 20 m between individual trees. In prior research using similar populations, it was found that this sampling approach resulted in discrete genotypes and avoided clones that may result from branch senescence and resprouting (Grady et al., 2017). Each tree was tagged, and geographic coordinate position taken with a GPS.

The three common gardens span a wide elevation gradient of almost 2,000 m and six degrees of latitude, encompassing the temperature and precipitation extremes experienced by *P. fremontii* (Table 1). The southernmost garden is located near Mittry Lake in Yuma,

**FIGURE 1** Location map of 16 provenance collection sites (leaf icon) of *Populus fremontii* and the three common garden locations (leaf with circle). The central garden is also a collection site. The shading corresponds to the degree-days above 5°C (DD5) throughout the region: red represents high DD5, blue low DD5 [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**TABLE 1** Common garden and source provenance environmental information

Common Garden	Code	Latitude	Longitude	Elevation (m)	MAT (°C)	MWMT (°C)	MCMT (°C)	MAP (mm)	AHM	DD>5	Total genotypes	Total trees
Mittry Lake, Yuma, Arizona	MYN-MLY	32.8498	114.4928	49	22.8	33.8	12.7	93	352	6,496	192	4,096
Agua Fria River, Horseshoe Ranch, Arizona	CAF-AUG	34.2567	112.0661	988	17.2	28.5	7.6	440	62	4,512	192	4,096
Canyonlands, Dugout Ranch, Utah	DIO-DUG	38.0925	109.5878	1,581	10.7	24.6	-3.2	225	92	2,798	192	4,096
<b>Provenance</b>												
Clear Creek, Bullpen	BCE-BUL	34.5397	111.6966	1,109	15.6	27.2	5.5	432	59	3,971	12	256
Agua Fria, Horseshoe Ranch	CAF-AUG	34.2567	112.0661	988	17.2	28.5	7.6	440	62	4,512	12	256
Cibola, CO River	CCR-COL	33.3621	114.6976	70	22.6	33.9	12.2	97	335	6,429	12	256
Cave Creek	CCU-CAV	33.89	111.951	696	19.9	31.3	10	349	86	5,439	12	256
Citadel Wash, Little CO River	CLF-LCR	35.6130	111.3190	1,299	14.1	27.2	0.8	176	137	3,635	12	256
Jack Rabbit, Little CO River	JLA-JAK	34.9600	110.4360	1,507	12.3	25.3	-0.7	212	105	3,140	12	256
Keams Canyon	KKH-OPI	35.8115	110.1695	1,920	10.7	23	-1.3	258	80	2,641	12	256
Willow Creek, Kingman	KWF-WIL	35.143	113.5428	1,126	15	26.6	5	243	103	3,760	12	256
Bill Williams, CO River	LBW-BIL	34.2760	114.0585	143	22.3	34.6	10.9	137	236	6,308	12	256
Rattlesnake Canyon	MRN-RAT	34.7830	111.6137	1,774	10.4	21.7	0.5	593	35	2,454	12	256
New River, Phoenix	NVR-NEW	33.9476	112.1361	666	19.9	31.4	10	337	89	5,460	12	256
Sonoita Creek, Patagonia	PSA-SON	31.5364	110.7631	1,234	15.7	25.2	7.1	471	55	3,957	12	256
San Luis, CO River	SCT-MEX	32.5270	114.8036	26	22.1	32.9	12.4	88	365	6,246	12	256
Santa Cruz, Tumacacori	TSE-TUM	31.5647	111.0447	986	17.5	27.2	8.8	402	68	4,584	12	256
San Pedro, Charleston	TSZ-SAN	31.6104	110.1668	1,219	16.9	26.4	7.7	322	84	4,373	12	256
Hassayampa, Wickenburg	WHY-HAS	33.9088	112.6764	575	19.6	31.4	9.4	284	104	5,343	12	256

Notes. Climatic variables are derived from ClimateWNA (Wang et al., 2012). "Total genotypes" and "Total trees" refers to total number of genotypes and trees in each garden.

AHM: annual heat-to-moisture index; DD >5: degree-days above 5°C; MAP: mean annual precipitation; MAT: mean annual temperature; MCMT: mean coldest monthly temperature; MWMT: mean warmest monthly temperature.

Arizona, and is maintained by the Bureau of Land Management. The central Arizona garden is located in Horseshoe Ranch adjacent to the Agua Fria River and is maintained by the Arizona Game and Fish Department. The northernmost garden is located near Canyonlands National Park on Dugout Ranch land adjacent to the Colorado River and is maintained by The Nature Conservancy's Canyonlands Research Center. The Yuma garden is the hottest, with a mean annual temperature (MAT) of 22.8°C. The garden at Agua Fria represents the middle thermal range with a MAT of 17.2°C, and Canyonlands is the coldest

garden with a MAT of 10.7°C. The Yuma site is flood irrigated with one-acre foot of water every two weeks between March and October and once per month for other months. The Canyonlands and Agua Fria gardens are drip irrigated with approximately five gallons per tree, three times per week, during the growing season (i.e., when freezing temperatures are not encountered). These gardens will be referred to as hot (Yuma), mid (Agua Fria), and cold (Canyonlands). Each common garden consists of four replicated blocks containing 16 population-level plots with 64 trees, for a total of 4,096 trees per garden. Within

each population plot, the 12 genotypes were replicated three to six times. Trees were spaced at 1.85 m in cardinal directions within each of the approximately 2 ha garden sites. Each garden was fenced with 2.5 m tall fencing to reduce potential for large ungulate grazing.

Survival was measured in the winters after the first and second growing seasons, when trees were dormant. Dead trees had lost all elasticity and were entirely dried out or absent from the plot. Fall bud set was assessed at 6–10 day intervals from September through December of 2015 on three replicates of all 12 genotypes per population at each garden. To measure fall bud set, we scored trees based on the bud stage exhibited by 50% or more of the apical meristems. This is a good approximation of whole plant progression toward dormancy as there was little within-plant variation in apical bud development. Bud set was recorded as the initiation of bud formation when internode elongation had ceased and the newly emerged, rolled up leaves were clustered at the same level on the stem and offset from the shoot axis (Frewen et al., 2000). Spring bud flush was recorded as the first sign of full leaf emergence on the tree. Bud flush was measured every two weeks from February through the end of April in the Yuma and Agua Fria gardens, and through the end of May in the Canyonlands garden.

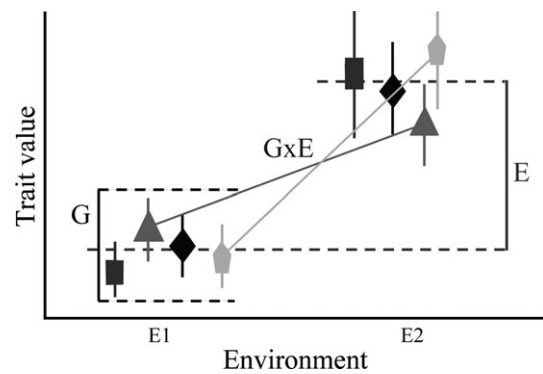
## 2.2 | Climate analysis

We downloaded 21 abiotic variables from each sampling location using the platform ClimateWNA (Wang, Hamann, Spittlehouse, & Murdock, 2012; Table 1 and Supporting Information Table S1). To reduce the dimensionality of intercorrelated climatic characteristics found throughout the 16 provenances, the abiotic ClimateWNA variables along with elevation, longitude, and latitude were analyzed in a principal component analysis (PCA) using the package *labdsv* (Roberts, 2007) and *vegan* (Oksanen et al., 2016) in R (R Core Team, 2014).

## 2.3 | Statistical analysis

To address our first hypothesis, we assessed genetic (at the population and genotype levels (G)), environment (E), and population-by-environment interaction (GxE) effects on bud set and bud flush among all 16 populations across all three gardens using linear mixed models fit by maximum likelihood with the *lme4* software package in R (R Core Team, 2014; Bates, Maechler, Bolker, & Walker, 2015). Individual phenology traits were modeled as response variables and environment (garden) was treated as a fixed effect with three levels, while population, genotype nested within population, and the population-environment interaction (GxE) were random effects. Statistical significance for these variables was calculated using likelihood ratio tests for the random effects and an *F*-test with Satterthwaite-approximated degrees of freedom for the fixed garden effect in the package *lmerTest* (Kuznetsova, Brockhoff, & Christensen, 2015). Variances are reported for all random effects.

To test our second hypothesis about the origins of plasticity, we determined whether the magnitude of plasticity observed in a



**FIGURE 2** A two-environment reaction norm showing the components of phenotypic variation of four genotypes: G = trait variation due to population genetics within a single environment, E = trait variation due to change in environment (plasticity), GxE = the variation in plasticity among genotypes. Phenotypic variation ( $V_P$ ) =  $V_G + VE + V_{G \times E}$

genotype was predicted by its provenance climate. Plasticity can be visualized as a reaction norm of phenotypic change along an environmental axis (e.g., Figure 2). If there are only two environments, then the plasticity of a genotype is either the slope of the reaction norm (Via et al., 1995) or simply the mean difference in trait values between environments (Scheiner & Lyman, 1989). In our study design using three gardens, plasticity was calculated as the difference between the earliest and latest day for each genotype mean across all environments. We then regressed plasticity scores for both phenology traits against the first axis of the environmental PCA.

To test our third hypothesis of the impacts of local adaptation in phenology and survival as a function of climatic transfer distance, we used linear regression, with the phenology trait as the predictor variable and survival as the response variable. Transfer distance is the difference between the climate of the source population and the garden location. The regression was fit separately for each of the three common gardens so we could compare local and nonlocal populations in each case.

Finally, to test our fourth hypothesis, we measured whether plasticity in phenology was in an adaptive direction, and whether such plasticity was related to increased survival. We hypothesized that “adaptive” in this sense indicates that plasticity should be beneficial, increasing population persistence and performance in the new environment. First, we grouped populations into three major provenance zones using the primary PCA axis of environmental variation, assigning each population to one of the three gardens (Supporting Information Figure S1). We assessed plasticity as the difference in number of days between a genotype's phenology at their assigned provenance zone garden and the garden of transfer. Negative plasticity values indicated an earlier season phenology response, whereas positive values indicated later phenology events compared to the local provenance garden. We then analyzed the relationship between plasticity and survival for genotypes from each provenance zone separately. Tests for significance



were conducted at the  $\alpha = 0.05$  significance level. For all regression models, we included population as a random effect and fit the model using the *lmer* package in R.

### 3 | RESULTS

#### 3.1 | Genetic, environmental, and GxE components of variation in phenology

Consistent with our first hypothesis, we found significant genetic and plastic variation in fall bud set and spring bud flush. Among all 16 populations planted across the three gardens, there were significant garden, population, genotype, and garden-by-population interaction effects (Table 2). The proportion of variation explained for bud set was ~45%, whereas these variables explained over 84% of the variation in

**TABLE 2** Genetic and environmental effects on each phenology trait

	Bud set		Bud flush	
	Variance	p-value	Variance	p-value
Population (random)	55.39 (20.4%)	<0.001	140.94 (51.2%)	<0.001
Genotype (random)	43.32 (16.1%)	<0.001	10.35 (3.8%)	<0.001
Population x Garden (random)	14.06 (8.9%)	<0.001	80.56 (29.3%)	<0.001
Garden (fixed)		<0.001		<0.001
Residual	158.58		43.34	

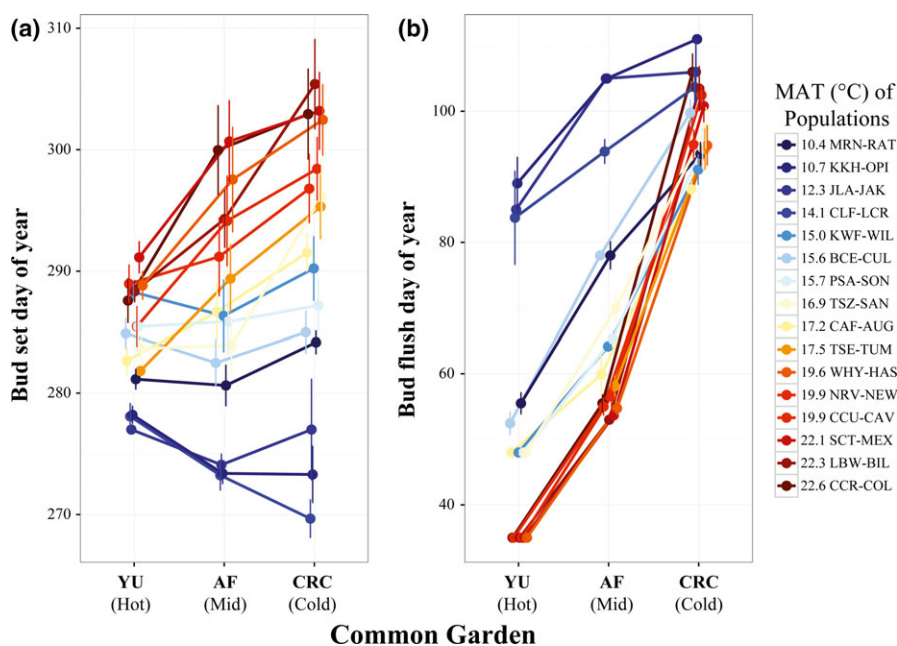
Note. For each factor, we report the variance, the proportion of total variance explained (in parentheses), and the *p*-value from the likelihood ratio test.

bud flush. The influence of population and population-by-environment was higher for bud flush, whereas genotype explained more variation in bud set, indicating more consistent within-population variation. Regardless of their growing environment, the more northern, frost-adapted populations set their buds significantly earlier in the fall compared to the central and southern populations (Figure 3a). Mean bud set dates were least variable among populations in the hot garden, with a difference of 14 days between first and last bud set, and most variable in the cold garden with a difference of ~36 days, more than doubling the duration of bud set timing. This suggests stronger environmental control on bud set in the hot garden, with larger genetic effects at the cold site.

Spring bud flush showed a similar pattern of relatively longer growing seasons for southern populations. In the two warmer common gardens of Yuma and Agua Fria, the southern populations flushed up to 70 days earlier in the spring than northern populations, and up to 14 days earlier than central populations. However, in the cold Canyonlands garden, both the southern and central populations exhibited a delayed flush phenology approaching the northern populations' late flush dates. Unlike bud set phenology, which was most variable among populations in the cold garden, bud flush was most variable in the warmer gardens, suggesting a harder environmental constraint on bud flush in areas with long, freezing winters. In Yuma (hot) and Agua Fria (mid), the duration of bud flush was 54 and 52 days, respectively, while Canyonlands (cold) produced a span of just over 22 days between the start and finish of flushing (Figure 3b).

#### 3.2 | Magnitude of plasticity in relation to provenance environment

After combining all environmental variables in a PCA, the first principal component axis (PC1) represented 95.8% of the variation among



**FIGURE 3** Population means ( $\pm 1$  SE) for (a) bud set and (b) bud flush across the three common gardens. Gardens are arranged from hottest to coldest: YU = Yuma, AF = Agua Fria, and CRC = Canyonlands Research Center. Populations are colored by the mean annual temperature (MAT °C) of their provenance [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]

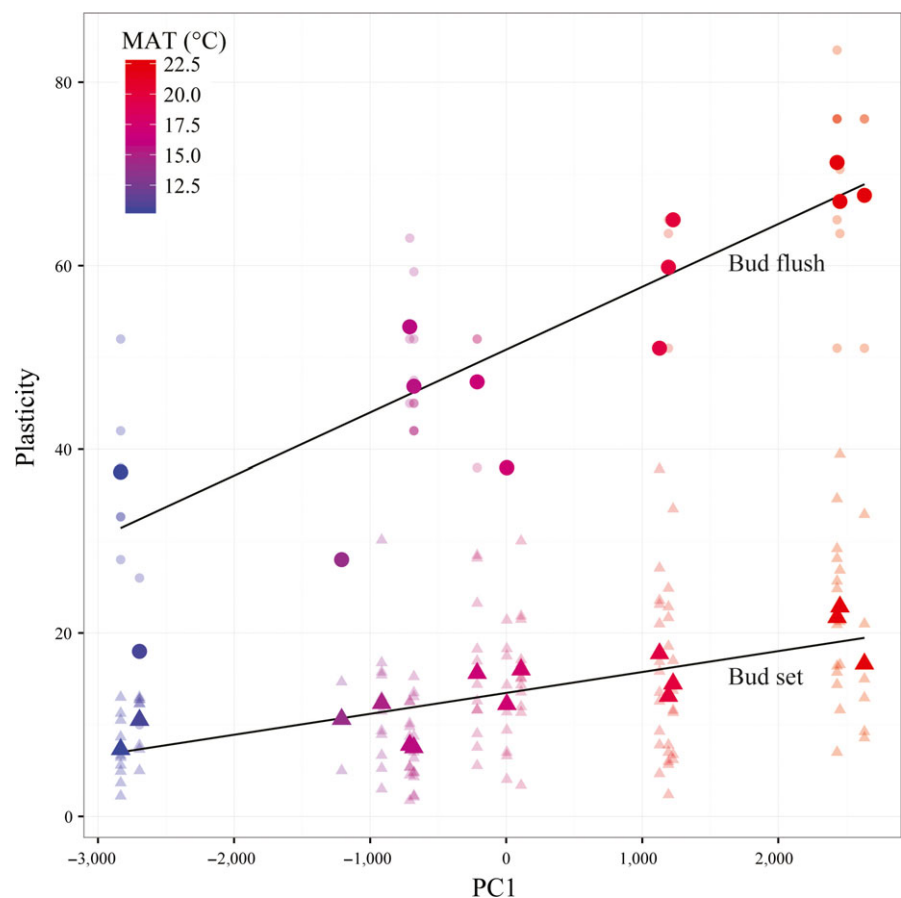
the 16 provenances, with four environmental variables (degree-days above 5°C, degree-days below 18°C, degree-days above 18°C, and summer heat-to-moisture index (Wang et al., 2012)) plus elevation comprising the majority of this axis (see variable PCA loadings in Supporting Information Table S1). The provenance environment, represented by PC1, was significantly related to fall bud set plasticity ( $R^2 = 0.22$ ;  $p < 0.001$ ;  $F_{1,156} = 45.6$ ) and spring bud flush plasticity ( $R^2 = 0.63$ ;  $p < 0.001$ ;  $F_{1,41} = 73.1$ ; Figure 4). This supports our second hypothesis that environmental conditions predict the magnitude of plasticity: greater plasticity in both traits was observed in populations from hotter and drier environments represented by more degree-days above 5°C and 18°C, lower elevation, and greater summer heat-to-moisture ratio.

### 3.3 | Local adaptation and mortality consequences of climate transfer distance

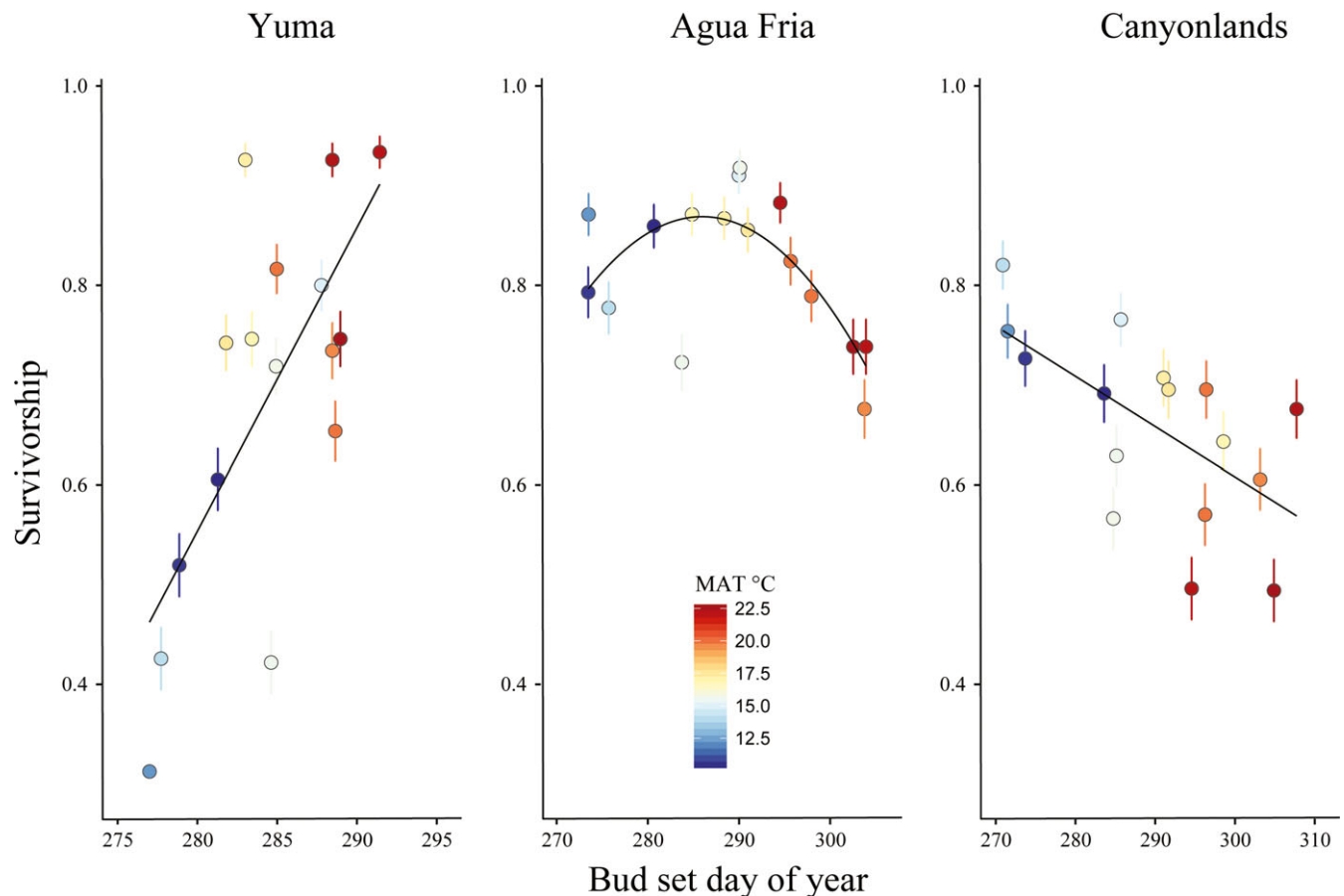
Population-level survival was significantly related to bud set phenology in each common garden, suggesting that the degree of mismatched phenology of non-local populations is one possible explanation for lower survival (Figure 5). This agrees with our third hypothesis that populations have locally adapted phenology traits, and increased mortality should correspond with increasing climate transfer distance between home and garden site. In the hot garden,

survival was positively correlated with bud set phenology ( $R^2 = 0.46$ ;  $p = 0.003$ ): populations exhibiting late bud set had the highest survivorship. In the middle garden, there was a quadratic relationship, with midseason bud set dates related to the highest survival ( $R^2 = 0.44$ ;  $p = 0.010$ ). In the cold Canyonlands garden, trees with the earliest bud set showed the highest survival ( $R^2 = 0.34$ ;  $p = 0.011$ ). For bud flush, the only significant relationship observed was in the hot garden, where earlier flush dates correlated with higher survival (in Yuma:  $p = 0.006$ ,  $R^2 = -0.44$ ; in AF:  $p = 0.807$ ; in CRC:  $p = 0.991$ ). This shows clear genotype  $\times$  environment interactions in Fremont cottonwood, with local trees exhibiting higher survival compared to non-local trees in each of the three common gardens.

We found that survival was a function of the transfer distance in growing season (measured as degree-days above 5°C, DD5; Wang et al., 2010) between provenance and garden transplant site. Survival was negatively correlated with DD5 transfer distance in the hot and cold gardens, but not the middle Agua Fria garden (Yuma:  $p = 0.013$ ; Agua Fria:  $p = 0.400$ ; Canyonlands:  $p = 0.015$ ). Although nonsignificant, we still observed a negative trend in the middle Agua Fria garden (Supporting Information Figure S2). A weaker pattern is expected in the middle garden since the maximum transfer distances are approximately half as great as those transferred between the hot and cold gardens.



**FIGURE 4** Bud flush (circles) and bud set (triangles) plasticity are significantly positively correlated with axis 1 of the climate PCA. Hotter, drier, lower elevation source environments (positive PC1) correlate with higher plasticity scores. Smaller transparent symbols represent genotypes, while larger, solid symbols indicate population means. Colors correspond to the mean annual temperature of the population, with reds indicating warmer temperatures and blues colder temperatures [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 5** Population-level mean ( $\pm 1$  SE) survival correlations with bud set date in each of the three common gardens. Populations are colored by the mean annual temperature (MAT °C) of their source provenance. In Yuma, survival is highest in the hotter source populations and is positively correlated with later bud set. The opposite is true in the coldest Canyonlands garden. A parabolic relationship was found at the mid garden of Agua Fria, where the highest survival correlated with midseason bud set of the central Arizona populations [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

### 3.4 | Consequences of adaptive versus non-adaptive plasticity

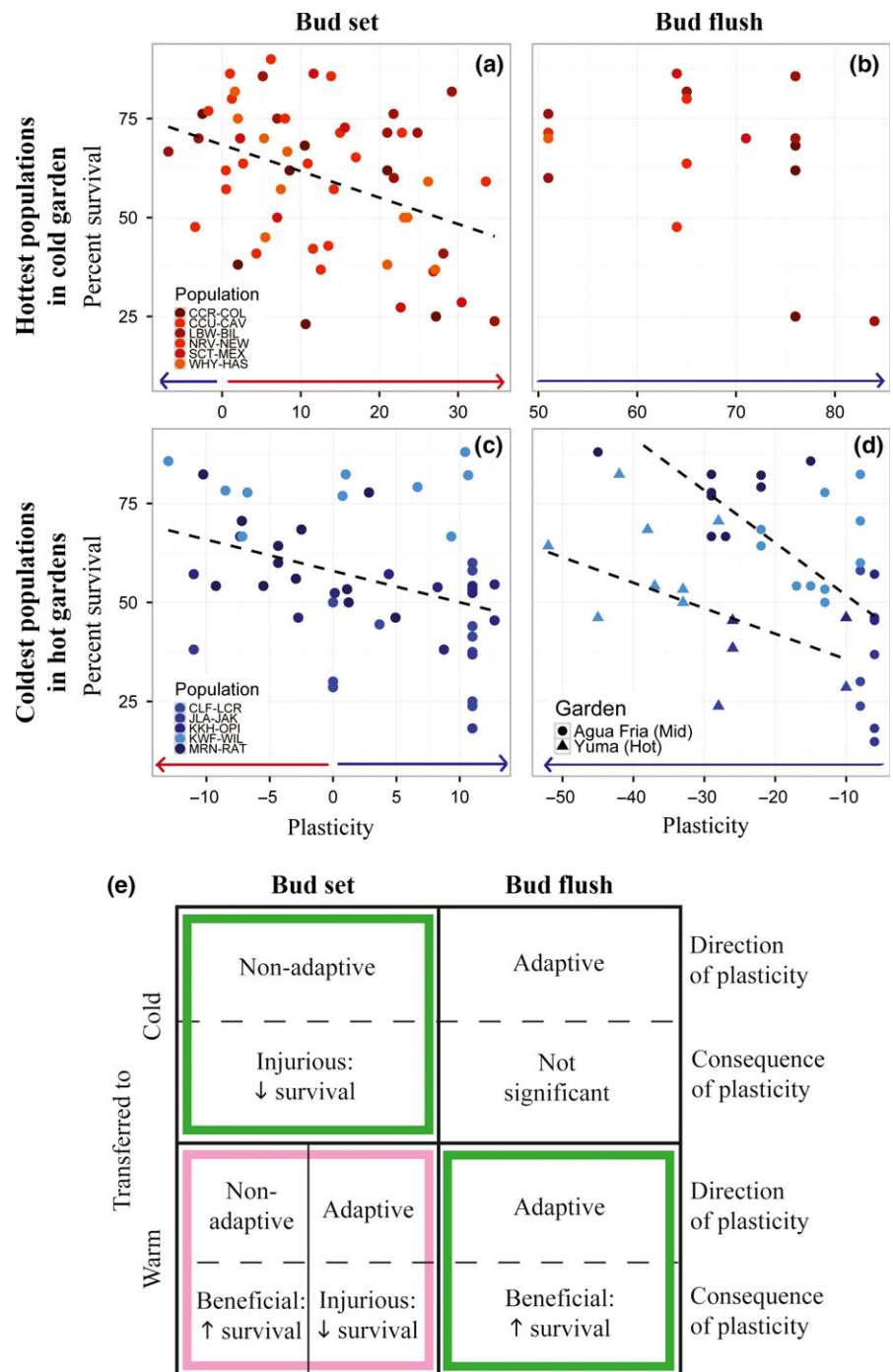
Shifts in bud set demonstrated either adaptive or non-adaptive plasticity depending on the source population and the direction of transfer (e.g., from hot to cold). The transfer of southern and central populations to the cold northern garden resulted in non-adaptive plasticity. Instead of setting bud *earlier* in the fall to match the phenology of the local genotypes and avoid frost damage in the cold garden, these genotypes delayed their bud set by up to 20 days *later* than in their native climates of Yuma and Agua Fria (Figure 3a). On average, the northern populations showed much less plasticity in bud set, with some genotypes exhibiting as little as three days difference between mean bud set dates across the three gardens. The direction and magnitude of plastic responses, however, varied widely among genotypes. Some northern genotypes exhibited non-adaptive plasticity by advancing bud set in the two hotter gardens by ~5 days compared to in the cold garden, effectively shortening their growing season even more, while others displayed adaptive plasticity in the hot garden, delaying bud set later in the season to approach local populations' phenology (Figure 3a).

In contrast to the mixed results for bud set, trends in bud flush plasticity were consistently in the adaptive direction. The southern and central populations showed increasingly delayed flush timing from the hot to mid to cold gardens, while the northern populations showed progressively earlier flush phenology from the cold to mid to hot gardens (Figure 3b). In every case, bud flush timing of the non-local trees shifted in the direction of the local phenology in each garden.

The ability of adaptive shifts in phenology to actually confer higher survival was supported for only some traits in some provenance zones. Genotypes transferred from the hot, southern provenance zone to the cold Canyonlands garden (Figure 6a,b) showed non-adaptive plasticity in bud set (shifting away from the local optimum), and experienced lower survival in proportion to that plasticity ( $R^2 = -0.32$ ;  $p = 0.013$ ; Figure 6a). Thus, non-adaptive plasticity had the expected negative effect. For bud flush, we did not find any corresponding significant relationship ( $R^2 = 0.11$ ;  $p = 0.173$ ; Figure 6b), perhaps partly due to the high overwinter mortality of southern populations in the northern garden, which lowered sample size.

Genotypes from the cold, northern provenance zone transferred to the hot Yuma garden (Figure 6c,d) showed adaptive plasticity in





**FIGURE 6** Survival-plasticity relationships for bud set (a, c) and bud flush (b, d). Plasticity is the difference in phenology (in days) between the population's assigned provenance zone garden and the garden of transfer. Negative plasticity scores indicate earlier season phenology events, while positive values indicate phenology events later in the year. Arrows show whether plasticity is in an adaptive direction (colored blue) or a non-adaptive direction (red). Genotypes are colored using the same provenance mean annual temperature schematic as in Figure 3. A summary of the direction and mortality consequences for each of these plastic shifts (a-d) is presented in (e). Here, green boxes identify expected results based on Hypothesis 4 that adaptive plasticity increases survival, while the pink box indicates a nonintuitive result not predicted by our hypothesis [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

bud flush (shifting toward the local optimum) and this increased survival (Figure 6d). Those genotypes that were able to flush over 50 days earlier in the spring in the hot garden and up to 45 days in the middle garden, relative to in the cold garden, showed the highest survival rates compared to those which had minimal flush change (in Agua Fria:  $R^2 = -0.65$ ,  $p = 0.0001$ ; in Yuma:  $R^2 = -0.27$ ,  $p = 0.072$ ). This finding again supports the expected relationship between adaptive plasticity and increased survival. This was the only significant phenology-plasticity relationship for an intermediate transfer involving the middle garden. However, for bud set, this transfer showed an unexpected, contradictory pattern: genotypes that advanced bud

set over 10 days earlier in the hot garden rather than delaying it to match local genotypes (a non-adaptive shift) had higher survival. In contrast, genotypes that did adaptively delay bud set had lower survival ( $R^2 = -0.361$ ;  $p = 0.011$ ; Figure 6c). This pattern reveals a contradiction in how adaptive plasticity is described. Northern genotypes that shift their phenology toward that of southern genotypes when planted in the south exhibit "adaptive plasticity" by the definition of Ghalambor et al. (2007), but this plasticity is not "adaptive" in the sense of increasing fitness (Dudley & Schmitt, 1996). Overall, these results suggest that plasticity in bud set can be in an adaptive or non-adaptive direction depending on the climate

transfer, while spring bud flush plasticity is generally adaptive. However, the consequences of the plasticity we observed were not always consistent with our hypothesis of adaptive shifts conferring beneficial survival and non-adaptive shifts resulting in injurious survival consequences (Figure 6e).

## 4 | DISCUSSION

### 4.1 | Patterns and drivers of phenological variation

The degree of genetic variation and the magnitude and direction of plastic responses in plant traits will determine the extent to which populations can persist and adapt under climate change, and are important determinants of how far individual genotypes and populations can be moved for restoration and reforestation projects. Given that phenology shifts are one of the biggest climate change impacts reported thus far (Munguía-Rosas, Ollerton, Parra-Tabla, & De-Nova, 2011; Parmesan & Yohe, 2003; Thackeray et al., 2010; Westerling, Hidalgo, Cayan, & Swetnam, 2006), there is a need to understand the responses of these traits to multiple phenological cues. This includes cues that are shifting under climate change such as temperature, and those, such as photoperiod, that are not. Here, we have evaluated the variation in bud phenology traits in terms of genetic, environmental, and GxE variation using replicated common gardens which represent a more realistic climate change experiment by exposing genotypes to changes in numerous climatic variables rather than examining single variables in isolation.

We found significant environmental and GxE effects on phenology for both traits, highlighting the consequences of phenotypic changes in response to environmental change. The magnitude of plasticity in bud set and bud flush varied dramatically among populations and was positively correlated with increasing temperature and aridity of the provenance climate. This result contrasts with that of Vitasse et al. (2010), who showed no difference in the magnitude of plasticity for leaf phenology among oak and beech populations along a ~1,500 m elevation gradient spanning ~7°C mean annual temperature, but agrees with the relatively high levels of plasticity in spring and fall phenological events observed in other woody species (Kramer, 1995; Vitasse et al., 2010).

Variation in bud set showed a higher influence of genotypic effects compared to bud flush, while bud flush variation showed larger population-level effects. These results corroborate the findings of Evans et al. (2016), who found among-provenance and provenance  $\times$  garden variance terms were larger than among-garden variance, emphasizing genetic effects over environment for bud set. In our study, population-level differences in bud set are related to increasing mortality as populations were transferred increasing climatic distances between their home and garden sites.

Understanding genetic variation within populations is critical to understanding the potential for adaptation to climate change in the absence of assisted migration (Kelly, Sanford, & Grosberg, 2012). The two basic conditions for the evolution of plasticity are that genetic variation in plasticity is present (significant GxE interactions)

and that correlations exist between plasticity and fitness (Crispo et al., 2010). In our study, both of these conditions have been met, especially for bud set. This could indicate potential for further adaptation: if plasticity increases fitness in a new environment, increased levels of plasticity would be expected to evolve. In contrast, decreased plasticity might evolve when non-adaptive plasticity leads to fitness declines (Crispo et al., 2010).

### 4.2 | Adaptive and non-adaptive phenotypic plasticity with global change

In general, our study shows that northern, cold-adapted populations exhibit phenotypic plasticity for bud set and bud flush in the right, adaptive direction (toward the local optimum) when moved into hotter climates, whereas southern populations exhibit plasticity in the wrong direction for bud set when moved into colder climates (Figures 3 and 6). Despite lower levels of plasticity compared to the central and southern populations, the northern populations extended their growing season via earlier flush and later bud set, providing evidence that populations will be able to partially adjust their phenology as the climate warms in the future. This trend of adaptive plasticity of northern populations toward the local trait optima when moved to hotter, drier climates, however, is not a perfect solution to a warming climate. Despite the most plastic genotypes exhibiting higher survival than the canalized genotypes in the hot garden (Figure 6), much like Cleland et al. (2012)'s findings on phenology shifts, these northern trees exhibited >30% higher mortality rates compared to the local populations. Southern populations, however, displayed much higher plasticity for both traits, but in the wrong direction for bud set when planted into colder climates. In the context of a warming Southwest, this finding that southern populations are unable to anticipate freezing temperatures by setting bud earlier is less important than our finding that northern populations appear constrained in their response to a warming climate. The northern populations transferred to the middle garden experienced an increase in mean annual temperature of ~2–7°C, and a 10–12°C increase when transplanted into the hot Yuma garden. The central populations transferred to the hot garden experienced a change of ~3–6°C. The warming increases associated with these intermediate garden transfers (cold to mid, and mid to hot) are more consistent with model projections for the end of the century, especially when taking extreme heat wave predictions into account (Garfin, Jardine, Merideth, Black, & LeRoy, 2013). As temperatures continue to warm and the threat of freezing temperatures diminishes, trees that can maximize their growing season through phenological plasticity (i.e., earlier bud flush and later bud set) will likely become the most productive, and may outcompete less plastic trees that do not respond to warming (Cleland et al., 2012). In general, the northern populations in the middle garden set bud later and flushed earlier, advancing and extending their growing season. The central populations transferred to the hot garden, however, had minimal bud set change or shifted toward earlier bud set, shortening their growing season. This non-adaptive plasticity in bud set by the central populations is

offset by adaptive plasticity in bud flush, shifting these populations to an earlier growing season, but not extending growing season length. This result supports Kramer's (1995) finding of advanced growing season with warming temperatures due to equal shifts earlier in fall and spring phenology. The ability to shift phenology earlier and extend the growing season, trends that we observed for populations experiencing the intermediate warming garden transfer, will become increasingly important as rising temperatures force an earlier spring (Thackeray et al., 2010; Westerling et al., 2006).

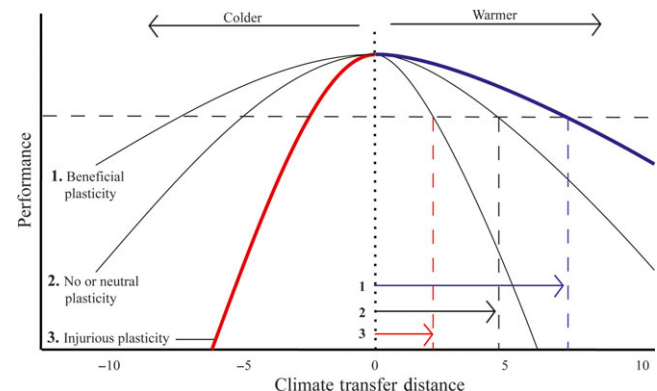
The large differences in adaptive and non-adaptive plastic responses among populations moved from cold to hot climates versus hot to cold climates may be a result of different evolutionary histories in phenology cues relating to cold hardiness. The onset of growth in the spring is regulated mainly by temperature, while fall growth cessation and the development of buds are initiated by photoperiod and chilling requirements (Chuine, Aitken, & Ying, 2001; Howe et al., 2003; Howe, Hackett, Furnier, & Klevorn, 1995). In our study, southern populations naïve to freezing temperatures may be photoperiod-insensitive and initiate bud set using only temperature cues, since it is advantageous to have the longest growing season possible in southern latitudes where temperatures rarely dip below freezing. Alternately, northern populations that have evolved with freezing temperatures may be highly sensitive to photoperiod, setting bud using day length cues, so as to avoid frost damage by tracking temperatures at the "wrong" time of year (Körner & Basler, 2010). This is consistent with our finding that the hottest, southern populations set bud latest in all sites, while the northern, cold-adapted populations exhibited consistent early-season bud set. In the cold Canyonlands garden, the southern populations waited until the first freeze date on November 1st (Day 305 of the year, Utah Climate Center; Figure 3) to set bud, resulting in frost damage and likely contributed to their high mortality in this cold garden. Interestingly, a similar pattern of delayed spring phenology in a northern-most common garden was also recorded for an annual European aster (Lustenhower, Wilschut, Williams, Putten, & Levine, 2017). Consistent early bud set timing across the three gardens supports the importance of day length cues for northern populations. The four coldest populations all set their buds in early October across the three common gardens. In Canyonlands and Agua Fria the average bud set date was October 2nd, and in Yuma it was October 5th; at these dates the three locations had nearly identical day lengths ( $\leq 5$  min difference; NOAA Solar Calculator).

The reduced plasticity in phenological traits of the northern populations may be linked to physiological adaptations to freezing temperatures. In this case, adaptations to large seasonal shifts in growth and dormancy (i.e., when winters predictably involve periods of freezing) may represent a trade-off against adaptations or plastic responses to climate shifts within growing seasons that stay above freezing temperatures. In some ways, this is opposite to the evidence that more variable environments facilitate the evolution of greater plasticity when environmental cues are predictable (Hendry, 2016; van Tienderen, 1991; Via & Lande, 1985). Indeed, we found the greatest plasticity expressed in populations experiencing

unpredicted winter freezing. However, early theory papers point to the degree of cold hardiness of a species as related to the degree of the seasonal variation it experiences (Allee, Emerson, Park, Park, & Schmidt, 1949), and the probability of surviving climatic extremes increasing with greater seasonal climatic deviations from the mean (Janzen, 1967). It follows then, that populations that do not experience predictable freezing winters would not shift phenology to survive freezing temperatures. This plasticity pattern, however, may be limited to specific phenology traits such as bud set, which is partially determined by fixed cues like photoperiod, as well as in species that experience variable freezing frequencies across their distributions.

### 4.3 | Management implications: plasticity and assisted migration

Although our results suggest that adaptive phenotypic plasticity may allow plants to cope with a warming climate to some degree, it is important to evaluate its limits. This is especially true as plasticity can encompass phenotypic changes that are beneficial to performance and survival as well as changes that are injuriously plastic, resulting in reduced survival (Figure 7). Given the rapid rate of climate change, especially in the American Southwest (Garfin et al., 2013), even beneficial plasticity cannot be expected to maintain population productivity beyond a certain climate transfer distance. Prior to a critical mortality or fitness threshold being reached, alternative strategies may become important for the continued survival of species experiencing climate change.



**FIGURE 7** Three potential consequences of phenotypic plasticity of a genotype transferred increasing climate distances (e.g., mean annual temperature) to both warmer and colder climates. Climate transfer distance can also represent in situ climate changes. The dashed horizontal line represents a theoretical performance level, below which active management practices may be required to maintain a population's productivity. Beneficial plasticity results in the greatest climate transfer distance experienced before active management is needed (arrow 1), nonplastic or neutrally plastic genotypes represent a midrange of climate transfer distance (arrow 2), and injurious plasticity results in the shortest climate transfers (arrow 3) before populations fall below the performance threshold. Bolded curves represent our overall results for bud flush (blue) and bud set (red) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

Assisted migration has been proposed as a way to mitigate the effects of climate change and has led to the development of seed transfer zone guidelines where warmer seed sources are being planted northward or at higher elevation (Rehfeldt et al., 2014; Wang et al., 2010). Increases in the upper elevation boundary of seed transfer standards have been recommended for numerous commercial tree species in British Columbia (O'Neill et al., 2008) to maintain forest resiliency and productivity by planting genotypes "preadapted" to warmer climates (O'Neill et al., 2017). Our results showing adaptive, beneficial plasticity of northern populations moved to hotter, lower elevation gardens suggest these trees can experience relatively large amounts of warming before the population reaches a mortality threshold and active management of the area such as assisted migration is needed (Figure 7). Conversely, the non-adaptive, injurious plasticity responses of southern populations moved up in latitude and elevation to colder common garden sites points to caution in moving populations or genotypes to much higher, colder environments (Figure 7). This may be especially important in managing those species whose populations have variable exposure to predictable freezing. Our observed non-adaptive shift in bud set constrains the climate transfer distance for *P. fremontii* in the context of assisted migration and reinforces the idea of small, step-wise transfers over shorter time periods to keep pace with warming (Grady et al., 2015; O'Neill et al., 2008). However, as climate change pushes the frost-line north, planting genotypes from lower elevations or latitudes adapted for long growing seasons might be the best restoration practice, especially in areas that do not experience freezing winters.

Using common gardens distributed over five degrees of latitude, we have shown that reciprocally transplanted genotypes of Fremont cottonwood exhibit considerable phenological plasticity for both bud flush and bud set. We have also demonstrated that plasticity can be both adaptive and non-adaptive resulting in either beneficial or injurious survival consequences. This suggests that trade-offs in trait responses and/or plant performance may accompany plasticity in the context of climate change. Overall, our results suggest that plasticity may represent an inherent flexibility that long-lived trees and plants may use to adapt to a rapidly changing environment. Such flexibility may constitute an important tool for land managers seeking to optimize conservation of widespread species, and in the case of Fremont cottonwood, to better manage arid lands currently experiencing the greatest impact of a warming and drying climate.

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## CONFLICT OF INTEREST

The authors declare no conflict of interests, commercial, financial, or otherwise, associated with this publication.

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## SUPPORTING INFORMATION

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

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