

Evidence of climate-driven selection on tree traits and trait plasticity across the climatic range of a riparian foundation species

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Abstract

Selection on quantitative traits by heterogeneous climatic conditions can lead to substantial trait variation across a species range. In the context of rapidly changing environments, however, it is equally important to understand selection on trait plasticity. To evaluate the role of selection in driving divergences in traits and their associated plasticities within a widespread species, we compared molecular and quantitative trait variation in *Populus fremontii* (Fremont cottonwood), a foundation riparian distributed throughout Arizona. Using SNP data and genotypes from 16 populations reciprocally planted in three common gardens, we first performed Q_{ST} - F_{ST} analyses to detect selection on traits and trait plasticity. We then explored the environmental drivers of selection using trait-climate and plasticity-climate regressions. Three major findings emerged: (1) There was significant genetic variation in traits expressed in each of the common gardens and in the phenotypic plasticity of traits across gardens, both of which were heritable. (2) Based on Q_{ST} - F_{ST} comparisons, there was evidence of selection in all traits measured; however, this result varied from no effect in one garden to highly significant in another, indicating that detection of past selection is environmentally dependent. We also found strong evidence of divergent selection on plasticity across environments for two traits. (3) Traits and/or their plasticity were often correlated with population source climate (R^2 up to .77 and .66, respectively). These results suggest that steep climate gradients across the Southwest have played a major role in shaping the evolution of divergent phenotypic responses in populations and genotypes now experiencing climate change.

KEYWORDS

climate change, divergent selection, local adaptation, phenotypic plasticity, *Populus fremontii*, Q_{ST} - F_{ST}

1 | INTRODUCTION

Understanding the processes shaping phenotypic diversification in nature is a central objective of ecology and evolutionary biology (Bolnick et al., 2011; Schluter, 2000). Trait variation within widespread species can be extensive due to historic demographic processes and spatially and temporally heterogeneous landscapes exerting different selection pressures across a species' range (Whitlock, 2008). Over time, subpopulations can become genetically and phenotypically differentiated due to neutral processes, such as drift, gene flow, and mutation, as well as the adaptive process of natural selection (Holsinger & Weir, 2009; Leinonen et al., 2013; Spitze, 1993; Wright, 1931). Natural selection acts on both phenotypes and phenotypic plasticity, defined as the range of phenotypes a single genotype can express as a function of environmental change (Nicoltra et al., 2010). The strength and direction of selection may vary, creating a mosaic of trait means and differences in trait plasticity across species' distributions (Chevin & Lande, 2011). Adaptive evolution of individual traits and associated plasticity can therefore differentially affect a population's persistence on the landscape under a changing climate, as both alter the range of phenotypes a population can express (Kelly, 2019).

Phenotypic divergence is particularly evident in long-lived forest trees, which often show strong genetic differences and local adaptation among populations with ecological and evolutionary consequences for associated species and communities (Hereford, 2009; Leimu & Fischer, 2008; Savolainen et al., 2007; Whitham et al., 2020). One common hypothesis for the origins of phenotypic variation in trees is local adaptation in response to climate. For example, studies on *Populus* have shown evidence of adaptive population differences in growth, phenology, and physiological traits (Blasini et al., 2020; Fischer et al., 2017; Frewen et al., 2000), and the evolution of regionally adapted ecotypes (Bothwell et al., 2021; Cooper et al., 2019; Evans et al., 2014; Grady et al., 2011; Ikeda et al., 2017; McKown et al., 2014). To show that phenotypic variation among populations is due to divergent selection by their home climate, we need approaches that integrate molecular and phenotypic assessments of replicated genotypes. In order to test for selection in trait plasticity, phenotypic assessments must be repeated across multiple common garden environments (Liu & El-Kassaby, 2019).

In addition to understanding the role of natural selection in shaping trait differences, there has been an increasing interest in understanding if and how selection acts on phenotypic plasticity itself (Arnold et al., 2019; Josephs, 2018). Phenotypic plasticity is expected to evolve proportionally to the variability and predictability of the environment, with higher plasticity correlated with more predictable and more heterogeneous environments (Lande, 2009; Lind et al., 2011). For example, De Kort et al. (2020) found plastic responses to drought in woodland strawberry were higher in topographically variable sites, while Leung et al. (2020) experimentally determined that plasticity evolved to a lower degree in populations of a microalga experiencing less predictable salinity conditions after 500 generations. The evolution of decreased plasticity in

homogeneous environments could occur when there is a net cost to maintaining plasticity (DeWitt et al., 1998). Plasticity is also thought to increase in populations adapted to more benign climates relative to harsh ones because the fitness cost of maladaptive plasticity producing phenotype-environment mismatches will be greater when resources are limited (Alpert & Simms, 2002). This has been demonstrated in studies where lower elevation plants produced stronger plastic responses to drought compared to plants from harsher, high-elevation sites (Akman et al., 2021; Gugger et al., 2015). Higher plasticity under milder (yet variable) conditions may occur under the normal range of background environmental fluctuations, however when extreme events occur outside of this range, theory predicts rapid evolution of plasticity (Lande, 2009). Evolution of increased plasticity after extreme environmental shifts can allow mean phenotypes to approach new optima by accelerating phenotypic adaptation, which may enhance population persistence (Chevin & Lande, 2010; Lande, 2009). However, this depends on the shape of the reaction norm and the genetic variance and covariances available for selection to act upon after the extreme event (Chevin & Hoffmann, 2017). Finally, although plasticity is commonly studied on traits in isolation, species often respond to changes in environment with phenotypic plasticity in multiple traits, termed multivariate plasticity (Nielsen & Papaj, 2022; Schlichting, 1989). Plasticity in one trait can therefore alter plasticity in another trait, changing the optimal multivariate plastic response and fitness outcome to the new environment (Nielsen & Papaj, 2022). Correlations among trait plasticities may constrain the evolution of plasticity, resulting in discrete phenotypic strategies or solutions (Schlichting, 1989). Together, these processes combine to generate a heterogeneous phenotypic landscape, where selection gradients can produce marked differences in plasticity along environmental clines.

A common test for whether natural selection is the mechanism responsible for generating phenotypic divergence among populations is to compare Q_{ST} , the variation in quantitative traits, to F_{ST} , the variation in neutral genes (Lande, 1992; Spitze, 1993; Wright, 1951). Q_{ST} is the quantitative genetic analog to F_{ST} and measures the proportion of additive genetic variance in a trait attributed to among-population differences. If $Q_{ST} > F_{ST}$, there is evidence that directional selection is responsible for population-level divergence with respect to a trait of interest. If $Q_{ST} \approx F_{ST}$, the null model that population differences are due to genetic drift alone cannot be rejected. Finally, if $Q_{ST} < F_{ST}$, this suggests uniform or stabilizing selection acting to constrain among-population divergence (Spitze, 1993). Selection is expected to be uniform when populations share the same phenotypic optimum and divergent when phenotypic optima vary, such as across heterogeneous environments (Le Corre & Kremer, 2012). The surge in both experimental and theoretical Q_{ST} - F_{ST} studies has revealed a major role of natural selection shaping intraspecific variation in quantitative traits (Leinonen et al., 2008, 2013; McKay & Latta, 2002), with approximately 70% of all studies showing $Q_{ST} > F_{ST}$ (Leinonen et al., 2008).

Q_{ST} - F_{ST} comparisons can also be used to test for selection on phenotypic plasticity (Josephs, 2018). After calculating replicated

measures of plasticity across two or more environments for each genotype, the analysis can be conducted as for any other trait. Lind et al. (2011) used Q_{ST} - F_{ST} to test for selection on plasticity in development time among island populations of the common frog, *Rana temporaria*, which experience variable pool drying regimes. De Kort et al. (2016) performed a modified Bayesian Q_{ST} - F_{ST} analysis (Ovaskainen et al., 2011) to show selection for increased phenological plasticity in *Alnus glutinosa* with increasing latitude, possibly due to the higher temperature sensitivity associated with the evolution of frost tolerance. Alternatively, selection on plasticity can be assessed by regressing a genotype's plasticity against overall fitness or a fitness proxy (Arnold et al., 2019; Pigliucci & Schlichting, 1996). In Fremont cottonwood, for example, higher plasticity in bud flush is associated with higher survival when populations experience warmer temperatures (Cooper et al., 2019). Either approach can complement the use of environment-trait regressions (Whitlock, 2008) to test whether trait divergence among populations is systematically related to climatic gradients as selection pressures. Together, Q_{ST} - F_{ST} analyses and phenotype-climate regressions can be used to examine the evolutionary forces shaping trait and plasticity variation across the landscape (Josephs, 2018; Kelly, 2019; Whitlock, 2008).

The role of selection by past climate in shaping intraspecific variation is especially important to quantify in the American Southwest, where the effects of climate change are pronounced (Garfin et al., 2013; Williams et al., 2020). The Southwest is described as one of the most "climate-challenged" regions of North America, with warming temperatures and increasing drought events already contributing to massive forest mortality events (Breshears et al., 2005). Fremont cottonwood is especially sensitive to drought and high temperature, particularly in combination, as evidenced by stand-level mortality at the Bill Williams National Wildlife Refuge on the lower Colorado River (Figure 1). Recent studies by Hultine,

Allan, et al. (2020) and Blasini et al. (2020) suggest that these trees are at the edge of their thermal tolerance where water is essential for evaporative cooling. This mortality is associated with the mega-drought that Williams et al. (2020) identified as being the second worst drought in the past 1200 years in the American Southwest. Thus, current climatic gradients will be exacerbated by ongoing climate change, leading to new selection pressures on trees that may be locally adapted to an increasingly narrower range of habitable conditions.

In this study, we use trait data from the three experimental common gardens described in Cooper et al. (2019) to quantify divergence (Q_{ST}) in both genotype means within environments and genotype plasticities across environments for five traits of Fremont cottonwood (*Populus fremontii*). Common gardens are necessary to ensure that among-population variance components reflect genetic differences and are not inflated by environmental effects (Leinonen et al., 2013). Reciprocal common gardens can reveal traits that vary across environmental gradients as a result of phenotypic plasticity (Franks et al., 2014; Kawecki & Ebert, 2004). Plastic responses to environmental stress or release from stress may mask or amplify genetically determined trait differences that have emerged as a result of divergent selection (Oke et al., 2015). It is therefore important to assess phenotypes in multiple growing conditions to see how the environment can modify the degree to which we can detect evidence of selection. Our use of multiple common gardens adds to the Q_{ST} literature by examining how the detection of trait differences depends on environmental conditions (Akman et al., 2021) and by allowing for Q_{ST} - F_{ST} tests on trait plasticity across gardens.

Both the population collection sites and garden locations span an elevation gradient of almost 2000 m, consistent with the species' range and including a difference of 12°C mean annual temperature and >500 mm in mean annual precipitation across source locations and



FIGURE 1 Stand-level mortality event of Fremont cottonwoods along the Bill Williams National Wildlife Refuge on the lower Colorado River. Photograph taken by HF Cooper in March 2017

~350mm across gardens. These gardens have demonstrated genetic and environmental differences in phenology (Cooper et al., 2019), leaf litter traits (Jeplawy et al., 2021), and phytochemical defense compounds (Eisenring et al., 2022). The benefit of these experimental gardens is enhanced by the inclusion of genomic data based on the identification of >9000 single nucleotide polymorphisms (SNPs) for all genotypes planted across the three gardens. SNPs are an ideal marker for Q_{ST} - F_{ST} analyses because their mutation rates and the effects of drift are considered to be more similar to loci that control quantitative traits compared to other molecular markers, such as hypervariable microsatellites (Edelaar & Bjorklund, 2011). Thus, the only difference between quantitative trait loci driving Q_{ST} and the loci used in F_{ST} estimates should be that only the latter conform to neutral molecular evolution (Leinonen et al., 2013).

To address whether climate-driven natural selection drives trait and trait plasticity divergences in Fremont cottonwood, we evaluated three hypotheses: (1) Genetic variation in tree traits will be evident among populations and genotypes in each of the three common gardens, although the magnitude of the genetic effects may vary across environments and among traits. Likewise, populations will differ in the magnitude of plasticity of these traits measured across the garden environments. (2) Q_{ST} values will be significantly higher than the neutral expectation of F_{ST} , suggesting divergent selection has outweighed drift in shaping divergence in trait means and plasticities among populations. (3) Mean population phenotypes will show strong relationships with their climate of origin, as is expected when climate is a primary selective force. Similarly, the magnitude of trait plasticity will also be correlated with population source climate and may increase or decrease from hot-adapted to cool-adapted populations, depending on the trait. Such plasticity-climate relationships should emerge when population origins differ not only in mean climate conditions but also in climatic variability across seasons and years, as is the case in the Southwest.

2 | MATERIALS AND METHODS

2.1 | Collection sites and common gardens

To establish the common gardens, 16 populations of *Populus fremontii* were collected throughout Arizona, encompassing the environmental variation experienced by the Sonoran Desert ecotype, along with three populations located on the Mogollon Rim within the Colorado Plateau region of northern Arizona (Figure 2). These populations group genetically with and have been alternatively identified as the Mogollon Rim (Blasini et al., 2020) or Utah High Plateau ecotype (Ikeda et al., 2017; Table S1). This sampling design does not include the third described ecotype of the Central California Valley (Ikeda et al., 2017). Cuttings of ~0.2m were taken from individual tree genotypes located over 20m away from each other to ensure independent genotype sampling. The clonal replicates from 12 trees per population were grown in the greenhouse for approximately four months. Saplings were then planted in the summer and fall of 2014 in each garden when they were ~0.3m tall.

The three replicated experimental common gardens span broad elevation and climatic gradients, resulting in extreme climatic transfers for some populations. The northernmost garden represents the cold edge of the species' climatic range. It is located adjacent to Canyonlands National Park, Utah and is maintained by The Nature Conservancy's Dugout Ranch. The middle Arizona garden is located adjacent to the Agua Fria River in Agua Fria National Monument and is maintained by the Arizona Game and Fish Department. The southernmost garden is in Yuma, Arizona near Mitty Lake, and is maintained by the Bureau of Land Management. These gardens span over a 1500m elevation difference, a 12°C mean annual temperature range (10.7°C in Yuma, 17.2°C in Agua Fria, and 22.8°C in Canyonlands), and a precipitation difference of ~350mm (Table S1). Each common garden was planted with 4096 trees. These trees were arranged into four replicated blocks to account for within-garden environmental variance, with each block made up of 16 randomized population-level plots. Each population plot had 64 trees, made up of three to six replicates of the 12 genotypes collected for that population. Plots were arranged in a randomized 8×8 grid, with trees spaced 1.85m in each cardinal direction. The garden was designed using population plots instead of fully randomized by genotype to assess population-level effects on dependent community members such as arthropods and mycorrhizae, as well as ecosystem-level traits like carbon flux.

To examine the relationship between climate and traits, we downloaded 30-year normals (1961–1990 means) for 21 abiotic climate variables for each of the 16 provenance sites and the three common gardens using the program ClimateWNA (Wang et al., 2012). Because variation in both temperature and precipitation in the Southwest are very strongly correlated with elevation, these current climate variables are excellent proxies for the climates that trees have experienced during their local evolutionary histories ($r > .985$) for correlations between current mean annual temperature (MAT) and precipitation (MAP; WorldClim 2, Fick & Hijmans, 2017) and those variables estimated from 6000 or 22,000 years ago (WorldClim 1.4, Hijmans et al., 2005). To create a multivariate climatic index representing the environmental variation found throughout the 16 provenances, the ClimateWNA variables plus elevation, latitude, and longitude, were combined in a principal component analysis (PCA) using labdsv (Roberts, 2007) and vegan (Oksanen et al., 2016) packages in the R statistical language (R Core Team, 2014). Environmental variables and PCA loadings are reported in the supporting information (Tables S1 and S2, Figure S1).

2.2 | Trait analysis

We analysed five traits for phenotypic differentiation: fall bud set, spring bud flush, specific leaf area (SLA), height, and trunk basal diameter. Phenology of bud set and bud flush were measured in the fall of 2015 and the spring of 2016, respectively, as reported in Cooper et al. (2019). Bud set was recorded as the initiation of bud formation, where internode elongation had ceased and the newly emerged, bundled leaves were clustered at the same level on the stem, offset

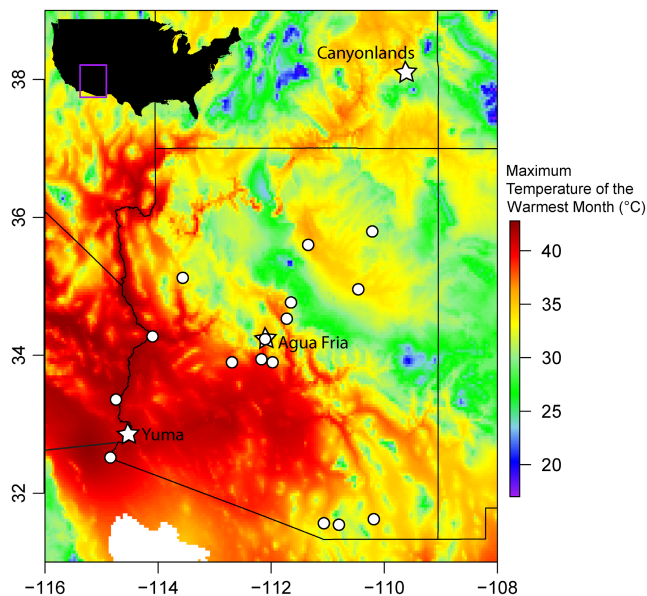


FIGURE 2 Map of the 16 collection locations (white circles) and three common gardens (white stars). The middle common garden of Agua Fria is also a collection site. Colour represents the maximum temperature of the warmest month (°C). Axes are labelled with degrees latitude and longitude. Inset is the map of the United States with a purple rectangle outlining the latitude and longitude presented in the full map

from the shoot axis (Frewen et al., 2000). Bud set was measured at 6–10 day intervals from September through December of 2015 on three replicates of all 12 genotypes per population in each garden. We scored trees based on the bud stage exhibited by 50% or more of the apical meristems. There was little within-plant variation in apical bud development, so we considered this metric a good approximation of whole plant progression towards dormancy. Spring bud flush was recorded using a categorical scale from 0 (no bud activity) to 4 (leaves out and flat), adapted from Vitasse et al. (2009). At stage 1, buds were swollen and/or elongating; at stage 2, buds were open and leaves were partially visible; at stage 3, leaves had fully emerged from the buds but were still folded or wrinkled; and at stage 4, at least one leaf was fully unfolded. Stages 1 to 4 were recorded as that category when 50% of buds reached this stage. 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, where colder temperatures persist later into the spring. All analyses were performed on the data from stage 3 bud flush observations. Bud set, bud flush, and height were assessed the full first year of growth (2015–2016) for every genotype in each of the common gardens.

Specific leaf area (SLA) was measured using the average of three to six fully expanded leaves that were free of or had minimal herbivore damage (if no leaves without damage could be found). To standardize for light availability, all leaves were collected from a single south-facing branch, collected approximately at breast height in May and June of 2020. Due to mortality in the gardens over the five years since planting, and the time required for sampling, SLA was only

measured on 12 populations in Yuma and Agua Fria, and seven populations in Canyonlands, with 3–7 genotypes measured within each population. Although early SLA analysis from 2015 showed similar patterns to the 2020 data, concern over residual maternal and greenhouse effects cautioned against using this first year of data. Leaves were scanned on site immediately after collection (before any water loss), and leaf area was measured using ImageJ software (Schneider et al., 2012). After the area scans, leaves were dried using silica beads and then weighed. Lastly, we used trunk basal diameter recorded at the end of the fourth year of growth (2018), which was measured as the diameter at root collar (DRC), ~10 cm from the soil, on every live tree in the gardens. Diameter at root collar was used instead of diameter at breast height because it allows us to track tree growth consistently from planting up to their current stature.

2.3 | Genetic analysis

Genomic DNA was extracted from ~0.2 g silica-dried leaf tissue from all 192 genotypes using the Thermo Scientific MagJET Genomic DNA Kit (Thermo Scientific). Double-digest restriction-associated DNA (ddRAD) libraries were prepared using 2–5 ng of DNA per sample in 20 µl reactions following a modified Peterson et al. (2012) protocol. Restriction digestion and ligation were carried out simultaneously in 20 µl reactions using restriction enzymes *MspI* and *EcoRI* and universal adapter sequences for indexing PCR. Ligation products were amplified using 25 cycles of PCR. After indexing, products were checked on an agarose gel and purified. Libraries were then pooled and size selected for fragments between 200 and 350 bp using a Pippin Prep (Sage Science, Inc.). The size-selected pool was quantified by qPCR and sequenced on an Illumina MiSeq Desktop Sequencer (Illumina, Inc.) in 2 × 75 mode. Sequence reads were processed using a modified Stacks pipeline (Andrews, 2018; Catchen et al., 2013). Potential chloroplast and mitochondrial sequences were filtered from the data set by comparing them to other *Populus* sequences downloaded from GenBank. Specifically, we removed sequences that matched chloroplast sequences from *P. fremontii* and mitochondrial sequences from *P. tremula* × *P. alba*. Parameter values for identification of informative loci were based on tests following parameterization in Mastretta-Yanes et al. (2015). The minimum stack depth for each individual was three and the minimum number of individuals per locus cluster was three. All loci used in the measure of F_{ST} were found to be in Hardy-Weinberg equilibrium. To calculate F_{ST} and a 95% confidence interval around F_{ST} , we bootstrapped population-level pairwise F_{ST} values 500 times using the *divPartCalc* function in the R package *diversity* (Keenan et al., 2013).

2.4 | Statistical analysis

To investigate the population and genotype variation in phenotypic traits, each garden was modelled separately using linear random effects models fit by maximum likelihood in the *lme4* package in R

(Bates et al., 2015; R Core Team, 2014). The tree traits were modeled as response variables, while population and genotype nested within population were random effects. Garden plot was included as a random variable to help account for within-garden environmental variance. Statistical significance was calculated using likelihood ratio tests for the random effects using the package lmerTest (Kuznetsova et al., 2015).

To model population and genotype variation in phenotypic plasticity, we first needed to obtain replicated estimates of plasticity for each genotype for each trait. Because all cuttings were taken from a single genotype, and are thus equally related, we considered two options for calculating plasticity with replication: (1) arbitrarily assign a single individual tree in one environment to be compared phenotypically with an individual tree in each of the other two environments, or (2) create a distribution of possible results using repeated randomized assignments (Lind et al., 2011). The latter is the approach we took here. For each genotype with at least one tree in each of all three gardens, we randomly assigned all available trees into genotype triplets, with one tree from each garden. We then calculated plasticity for each triplet as the absolute value of the maximum difference in those three trait values. This method produced a number of estimates of plasticity equal to the lowest number of trees available for that genotype in any garden. Thus, for each randomization, the replication is exactly the same as it would be for a single arbitrary comparison. We repeated this random triplet assignment 100 times to obtain a set of possible plasticity data sets. For each data set, we estimated the variance components necessary to calculate Q_{ST} using a linear random effects model as described above, where trait plasticity was the response variable, and population and genotype nested within population were the random effects.

For each trait and trait plasticity, we compared the quantitative trait variation (Q_{ST}) with genetic variance at neutral loci (F_{ST}). To calculate Q_{ST} we used the following formula:

$$Q_{ST} = \sigma_p^2 / (\sigma_p^2 + 2\sigma_G^2)$$

where σ_p^2 is the additive genetic variance among populations and σ_G^2 is the additive within-population variance (McKay & Latta, 2002; Spitze, 1993), that is, the variance among genotypes within populations. Each trait or plasticity was analysed using the models described above, and population and genotype variances were extracted to calculate Q_{ST} . Parametric bootstrap and Bayesian estimation are considered the best methods to obtain a precision estimate around Q_{ST} (O'Hara & Merilä, 2005). We performed parametric bootstrapping to obtain a 95% confidence interval for Q_{ST} , resampling the 16 populations with replacement 1000 times, and estimating Q_{ST} for each bootstrapped data set. This bootstrapping was performed in R using code provided by Evans et al. (2016). Resampling over the highest level in a hierarchical experimental design (here the population) is considered best practice (O'Hara & Merilä, 2005). Variance in Q_{ST} becomes quite large as the number of populations decreases (<20), especially if populations are highly differentiated (Goudet & Büchi, 2006; O'Hara

& Merilä, 2005). Goudet and Büchi (2006) recommend sampling many populations relative to the number of families. In using clonally replicated genotypes, our estimate of σ_G^2 includes both additive and nonadditive genetic effects, an approach that has been shown to lower Q_{ST} estimates and is thus a conservative test of $Q_{ST} > F_{ST}$ (Cubry et al., 2017). Conversely, lower Q_{ST} estimates derived from nonadditive genetic effects contribute to a more liberal test of convergent selection ($Q_{ST} < F_{ST}$; Cubry et al., 2017; Whitlock, 2008). To determine whether Q_{ST} was significantly different from F_{ST} , we compared the 95% confidence intervals for both, which provides much stronger inference than simply comparing Q_{ST} to the mean F_{ST} value (Leinonen et al., 2013; Whitlock, 2008). Broad-sense heritability (H^2) point estimates and confidence intervals were also calculated for each trait in each garden using the equation, $H^2 = \sigma_G^2 / (\sigma_G^2 + \sigma_E^2)$, where σ_E^2 includes both the plot variance and the error variance. Calculations of heritability for plasticity did not include plot-level variance since plasticity was measured across gardens.

To test whether phenotypes showed strong climatic relationships, we regressed population trait means and trait plasticities against the first principal component (PC1) from the environmental PCA. We tested these regressions and calculated an adjusted R^2 using a linear model in R (R Core Team, 2014). Here, we used a single estimate of plasticity for each genotype. Using all available replicates for each genotype, we first calculated the mean trait value for each genotype in each garden, and then calculated plasticity as the maximum difference between gardens. Systematic differences among populations seen in these trait-climate correlations are another, stronger test for evidence of divergent selection acting over genetic drift (Whitlock, 2008).

3 | RESULTS

3.1 | Genetic and phenotypic variation

Our data set of 192 genotypes analysed with ddRAD yielded 9195 SNP loci with an average read depth of 13 per locus. The 16 Arizona populations showed strong differentiation with an average pairwise $F_{ST} = 0.175$ and 95% confidence interval of 0.144–0.205. Consistent with our first hypothesis, we found significant within and among population variation for traits at each of the three common gardens (Table 1, Figure 3), with phenology traits exhibiting higher differentiation at the population than the genotype level in all but one case. For SLA, height, and diameter at root crown (DRC), the relative contribution of population versus genotype varied among gardens. Traits measured in the hottest common garden (Yuma) exhibited stronger population than genotype effects in four out of the five traits; for SLA, the proportion of variance explained by genotype was higher than the proportion explained by population, although it was very close (27% vs. 24%, respectively; Table 1). This garden thus produced higher values of Q_{ST} (the proportion of the genetic variance that is found among rather than within populations, see next section).

TABLE 1 Model variance and *p*-values for each trait measured in each garden, showing the population, genotype, and plot-level effects on trait variation

Trait	Garden	Variable	Proportion variance explained	<i>p</i> -Value
Bud set	Yuma	Population	30.19	<.001
		Genotype	13.12	<.001
		Plot	8.43	<.001
	Agua Fria	Population	17.70	<.001
		Genotype	24.97	<.001
		Plot	7.82	<.001
	Canyonlands	Population	29.53	<.001
		Genotype	16.57	<.001
		Plot	2.23	.003
	Plasticity	Population	30.00	<.001
Bud flush	Yuma	Population	86.59	<.001
		Genotype	6.42	<.001
		Plot	0	1
	Agua Fria	Population	78.08	<.001
		Genotype	6.59	<.001
		Plot	1.54	<.001
	Canyonlands	Population	2.97	.16
		Genotype	3.56	.08
		Plot	4.07	.02
	Plasticity	Population	23.25	<.001
SLA	Yuma	Population	24.28	.002
		Genotype	26.81	<.001
		Plot	10.91	<.001
	Agua Fria	Population	19.31	.02
		Genotype	8.3	<.001
		Plot	27.63	<.001
	Canyonlands	Population	61.21	<.001
		Genotype	8.16	<.001
		Plot	7.03	<.001
	Plasticity	Population	6.72	.2
Height	Yuma	Population	14.85	<.001
		Genotype	9.40	<.001
		Plot	7.57	<.001
	Agua Fria	Population	3.73	.5
		Genotype	11.55	<.001
		Plot	20.26	<.001
	Canyonlands	Population	16.39	.004
		Genotype	22.81	<.001
		Plot	8.57	<.001
	Plasticity	Population	45.51	<.001

(Continues)

TABLE 1 (Continued)

Trait	Garden	Variable	Proportion variance explained	p-Value
DRC	Yuma	Population	12.13	<.001
		Genotype	6.13	<.001
		Plot	12.92	<.001
	Agua Fria	Population	0.52	.9
		Genotype	7.90	<.001
		Plot	23.77	<.001
	Canyonlands	Population	0.71	.7
		Genotype	24.66	<.001
		Plot	4.03	<.001
Plasticity	Plasticity	Population	36.93	<.001

Note: In addition, model variance and *p*-values for each trait's plasticity across the three gardens, showing the population effect, are shown.

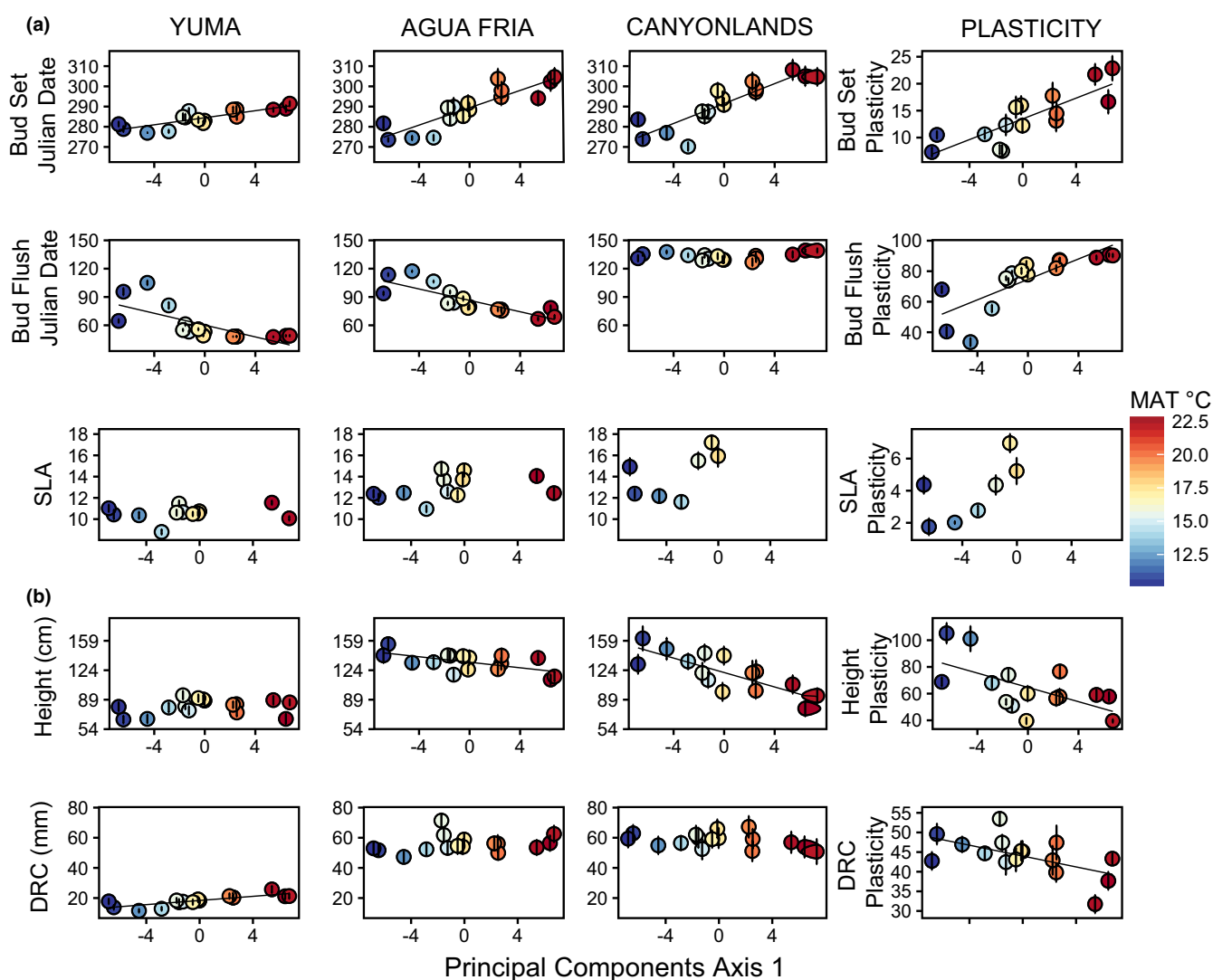


FIGURE 3 Population means ($\pm 1SE$) for (a) leaf traits and (b) growth traits measured in each garden as well as the population mean trait plasticity values, regressed onto their home climate (indicated by principal component axis 1 values). Populations are coloured by mean annual temperature (MAT °C). Regression lines are present when there is a significant relationship ($p < .05$) between the PC1 axis and the trait. SLA is in unit of mm^2/mg . Note the scale on the y-axis for the plasticity regressions are different than the trait regressions

Phenotypic plasticity across the three gardens showed significant population differences in all traits except SLA (Table 1, Figure 3). Here, the lower sample size of seven populations with no populations from the hottest locations may have contributed to this non-significant effect. Population explained more variance in plasticity in the growth traits compared to the phenology traits (Table 1). The direction of plasticity (trait values increasing or decreasing across gardens) varied by genotype and trait, however in most cases, trait values increased from hot to cooler climates. Bud flush and SLA consistently increased from hot to mid to cold gardens. Growth traits generally increased from hot to mid gardens, but not necessarily from the mid to cold gardens. Bud set did not exhibit a general trend across all genotypes. Thus, for all but one trait, genotypes varied in the magnitude of their plasticity more than the direction. A summary of reaction norms for each trait is presented in Figure S2.

3.2 | Q_{ST} - F_{ST} : Comparison of quantitative trait differentiation to neutral genetic expectation

We found evidence of selection (Q_{ST} - F_{ST}) driving phenotype differences in just over half of the traits measured across the three gardens (Table 2, Figure 4). For seven out of 15 cases, the Q_{ST} confidence interval was above the F_{ST} confidence interval, consistent with directional selection shaping trait differences and increasing local adaptation among these populations. One case showed evidence of stabilizing selection, where the Q_{ST} confidence interval fell below the F_{ST} confidence interval. Bud flush traits exhibited the highest levels of population differentiation. For example, Q_{ST} for bud flush in the hot and mid gardens was 0.87 and 0.86, respectively, while Q_{ST} values for bud set were more moderate (0.26–0.54). The confidence intervals for Q_{ST} crossed those of F_{ST} in two phenology measurements (bud set in Agua Fria and bud flush in Canyonlands), suggesting no difference from the neutral expectation of genetic drift of these traits in these environments. Divergent selection on specific leaf area was apparent in the mid and cold gardens, but not detectable in the hot garden of Yuma (Table 2, Figure 4). Tree growth traits showed relatively lower Q_{ST} values compared to leaf traits across gardens. Tree height showed significant divergent selection when measured at the hottest common garden in Yuma, but was not statistically different from F_{ST} in the two cooler gardens of Agua Fria and Canyonlands (Table 2, Figure 4). Contrary to our hypothesis, we found evidence of stabilizing selection for basal trunk diameter in the coldest garden, where the Q_{ST} value fell below the F_{ST} confidence interval. However, this result should be interpreted with caution since our Q_{ST} values were calculated using clonal replicates for within-population genetic variance, which includes nonadditive genetic effects like dominance. Dominance reduces estimates of Q_{ST} and is therefore a poor indicator of stabilizing selection (Cubry et al., 2017). This trait was indistinguishable from the neutral expectation of F_{ST} in the warm and mid gardens.

Mean Q_{ST} values for all trait plasticities except DRC were above the F_{ST} confidence interval (Table 2), suggesting overall divergent selection acting on plasticity. We found the strongest evidence for

divergent selection on plasticity for bud flush (mean Q_{ST} = 0.84) and height (mean Q_{ST} = 0.66) where the Q_{ST} 95% confidence interval distribution never crossed the F_{ST} confidence interval (Figure 5). In the analyses of bud set (mean Q_{ST} = 0.44) and SLA (mean Q_{ST} = 0.69), the lower Q_{ST} confidence interval distribution overlapped with F_{ST} , indicating that for some of the 100 possible plasticity data sets, trait plasticity differences among populations were not distinguishable from the neutral expectation of drift. Specifically, 67% of the permutations fell within the F_{ST} interval for bud set, while only 6% overlapped for SLA. Similar to DRC, the Q_{ST} values for DRC plasticity were much lower than the other plasticities (mean Q_{ST} = 0.07), however the upper confidence interval did overlap with F_{ST} 76% of the time (Figure 5). These three cases of plasticity Q_{ST} confidence interval distributions overlapping with F_{ST} represent a weaker detection of selection. However, these results do provide partial evidence for selection on SLA plasticity, where 94/100 permutations were non-overlapping.

3.3 | Climate as an agent of directional selection

The strength of the correlations between traits and provenance climate varied across gardens (Table 3, Figure 3), supporting our third hypothesis of strong associations between phenotype and climate for some traits in some environments. The first two axes explained 87.7% of the variation in provenance climate and were influenced primarily by temperature and growing season-related climate variables (Table S2, Figure S1). Populations sourced from areas with higher temperatures, lower precipitation, lower elevation, and longer growing seasons had higher PC1 scores. Bud set exhibited the strongest relationship with provenance climate across the gardens (R^2 = .67–.77), while bud flush showed significant correlations in the two warmer gardens (R^2 = .49 in Yuma and .66 in Agua Fria), but not in the cold garden (R^2 = -.01 in Canyonlands; Table 3, Figure 3a). In Canyonlands, population variation was constrained as all trees flushed at approximately the same time, late in the spring. Specific leaf area did not show significant trait-climate correlations in any garden, although we see overall SLA values increasing from the hot to the cold garden site (Figure 3a).

Tree growth traits were more likely to show garden-dependent relationships between population origin and performance (Table 3, Figure 3b). Tree height showed no climate relationships when planted in the hottest garden; however, the correlation became stronger in the mid- to cold gardens. When planted at the coldest garden, trees sourced from colder, wetter climates, including the three populations from the Colorado Plateau, were taller than populations from hotter, drier environments. Similarly, the DRC relationship in the hottest garden showed trees sourced from warm, hot environments had larger trunk diameters compared to trees from colder climates (Figure 3b). Together, tree height and basal trunk diameter act as indicators that overall tree performance is consistent with local adaptation, with hot, southern populations growing larger in the hottest Arizona garden, and northern, cold adapted populations growing larger in the coldest Utah garden.

Trait	Garden	Q_{ST}	H^2	Reported H^2
Bud set	Yuma	0.54 (0.40–0.86)	0.19 (0.05–0.26)	0.91 <i>P. trichocarpa</i> (Frewen et al., 2000)
	Agua Fria	0.26 (0.15–0.42)	0.30 (0.24–0.34)	
	Canyonlands	0.47 (0.46–0.57)	0.28 (0.18–0.24)	
	Plasticity	0.44 (0.18–0.82)	0.12 (0.03–0.21)	
Bud flush	Yuma	0.87 (0.69–0.93)	0.48 (0.36–0.60)	0.94 <i>P. trichocarpa</i> (Frewen et al., 2000)
	Agua Fria	0.86 (0.67–0.93)	0.30 (0.16–0.43)	
	Canyonlands	0.29 (0.00–1.00)	0.04 (0.00–0.07)	
	Plasticity	0.84 (0.64–0.95)	0.16 (0.04–0.27)	0–0.13 <i>A. glutinosa</i> (De Kort et al., 2016)
SLA	Yuma	0.31 (0.01–0.62)	0.35 (0.18–0.46)	~0.2–0.6 <i>P. nigra</i> (Guet et al., 2015)
	Agua Fria	0.54 (0.23–0.79)	0.10 (0.04–0.14)	
	Canyonlands	0.79 (0.70–0.93)	0.21 (0.09–0.23)	
	Plasticity	0.69 (0.37–0.98)	0.14 (0.01–0.26)	
Height	Yuma	0.44 (0.23–0.69)	0.11 (0.04–0.17)	0.03–0.42 <i>P. tremuloides</i> (Ding et al., 2020)
	Agua Fria	0.14 (0.00–0.50)	0.12 (0.05–0.19)	
	Canyonlands	0.26 (0.03–0.43)	0.27 (0.18–0.31)	
	Plasticity	0.66 (0.42–0.94)	0.09 (0.01–0.17)	
DRC	Yuma	0.50 (0.09–0.73)	0.07 (0.04–0.10)	0.09–0.25 <i>P. tremuloides</i> (Ding et al., 2020)
	Agua Fria	0.03 (0.00–0.26)	0.08 (0.05–0.10)	
	Canyonlands	0.01 (0.00–0.07)	0.21 (0.19–0.30)	
	Plasticity	0.07 (0.00–0.16)	0.18 (0.13–0.23)	

TABLE 2 Q_{ST} and broad-sense heritability, H^2 (+ 95% confidence intervals), for each trait in each garden and for the 100 plasticity permutations for each trait across gardens

Note: Previously reported broad-sense heritability estimates for other *Populus* species are included, in addition to a reported bud flush plasticity score for the riparian tree, *Alnus glutinosa*.

Phenotypic plasticity was significantly correlated with population source climate for all traits except SLA (Table 3, Figure 3). Populations sourced from hot, dry climates exhibited increased plasticity in leaf-level phenology traits relative to the colder populations, as previously reported in Cooper et al. (2019). Growth traits showed the opposite pattern of increased plasticity in populations sourced from the colder, high elevation environments. SLA showed a similar trend to phenology, with warmer populations exhibiting higher plasticity compared to populations sourced from cooler climates, but was not significant. Again, this may be due in part to the lower

sample size of seven populations that did not include populations from the hottest, driest sites (Figure 3a).

4 | DISCUSSION

We found evidence consistent with selection acting on both traits and trait plasticity across our three common gardens. In addition, regressions between traits and provenance climate indicate that the selection detected with Q_{ST} - F_{ST} analysis may be driven by climatic

FIGURE 4 Q_{ST} means and 95% confidence intervals (point and vertical lines, respectively) for the phenotypic traits measured at each of the three gardens. The average pairwise F_{ST} value (0.175) + 95% confidence interval (0.144–0.205) is shown as the grey band. Common gardens are abbreviated as Y, Yuma; A, Agua Fria; C, Canyonlands

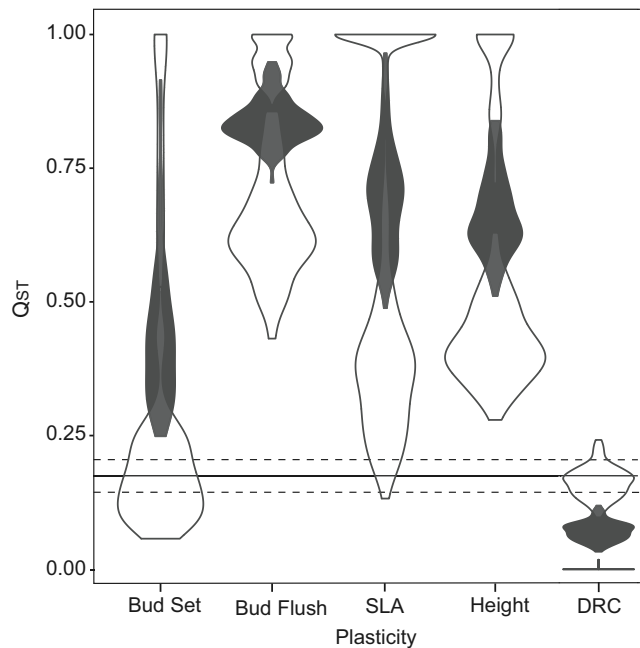
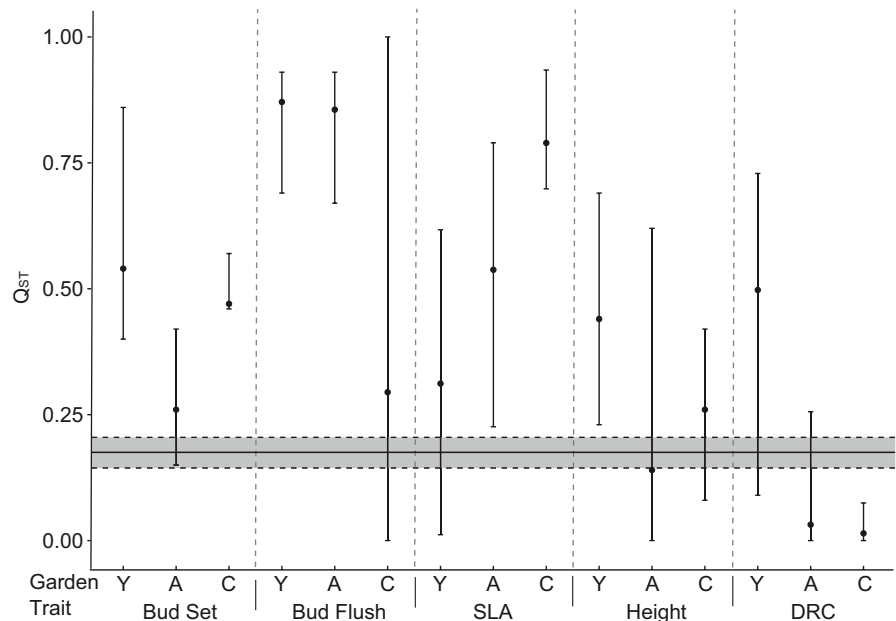


FIGURE 5 Trait plasticity Q_{ST} - F_{ST} distributions for each trait measured across the three common gardens. The filled shape is the mean Q_{ST} distribution and the open shapes are the 95% confidence intervals for the 100 plasticity data sets. As in Figure 4, the horizontal lines represent the average population pairwise F_{ST} and its 95% confidence interval. Any Q_{ST} distribution that crosses the F_{ST} confidence interval is interpreted as no different from neutral expectation and not under selection

clines to which these populations are locally adapted. The result of $Q_{ST} > F_{ST}$ for many ecological traits is consistent with other studies (Leinonen et al., 2013; McKay & Latta, 2002; Savolainen et al., 2007). However, our result of divergent selection acting on trait plasticity is quite striking in light of the relatively few examples of selection

TABLE 3 The adjusted R^2 and p -value output from the linear regression models of provenance climate (PC1 score) and population trait means at each common garden, as well as between PC1 and the population-level trait plasticity

Trait	Garden	Adjusted R^2	p -Value
Bud set	Yuma	.67	<.001
	Agua Fria	.76	<.001
	Canyonlands	.77	<.001
	Plasticity	.65	<.001
Bud flush	Yuma	.49	.002
	Agua Fria	.66	<.001
	Canyonlands	-.01	.36
	Plasticity	.62	<.001
SLA	Yuma	-.08	.69
	Agua Fria	.02	.28
	Canyonlands	.20	.17
	Plasticity	.33	.10
Height	Yuma	-.02	.42
	Agua Fria	.32	.013
	Canyonlands	.12	<.001
	Plasticity	.32	.017
DRC	Yuma	.62	<.001
	Agua Fria	-.01	.37
	Canyonlands	.05	.21
	Plasticity	.28	.02

on plasticity documented in the literature (Arnold et al., 2019). Combining Q_{ST} - F_{ST} analysis with phenotype-climate regressions can help uncover the evolutionary forces shaping both trait and plasticity differences across environmental gradients (Josephs, 2018; Kelly, 2019; Whitlock, 2008).

4.1 | Divergent selection shapes population trait differences

We interpret cases when both the Q_{ST} - F_{ST} analysis showed large divergences from neutral expectation and phenotype-climate correlations were significant as strong evidence for climate-driven selection. Cases with only one of these tests showing population differences provide partial evidence for climate-driven selection (Table 4). For instance, there were four cases showing $Q_{ST} > F_{ST}$, but nonsignificant trait-climate correlations. These inconsistencies between the two tests could be due to divergent selection that is not related to the climatic gradients we tested. There were also four cases showing Q_{ST} overlapping with F_{ST} , but significant trait-climate correlations. In these cases, bootstrap sampling of genotypes clearly included some cases where phenotypic variation was large within populations, even though the overall pattern of trait differentiation across the entire climate gradient was clear. For plasticity, there were also more significant plasticity-climate correlations (4 out of 5) than significant Q_{ST} - F_{ST} differences for plasticity (2 out of 5). Finally, there was a range of results across the three gardens within the Q_{ST} - F_{ST} analysis itself. Together, these tests provide a continuum of support for selection on traits and trait plasticity, and highlight which traits may be under the strongest selection and potentially the most important to investigate under climate change.

Consistent with other studies showing high phenological divergence across latitudinal clines (Evans et al., 2016; Hall et al., 2007; Howe et al., 2003; Hurme, 1999), we found the strongest evidence of selection for bud set and bud flush. Spring bud flush is highly differentiated among *P. fremontii* populations, with a difference of up to eight weeks observed in flush timing (Blasini et al., 2020; Cooper et al., 2019; Grady et al., 2015), and showed the highest Q_{ST} values in our study. We also found large population differences in fall bud set timing of ~2–5 weeks across the common garden gradient, reflected in moderate Q_{ST} values in two out of the three gardens. The strong population differences in phenology found here agree with Fischer et al. (2017), who showed leaf phenology accounted for >80% of the variation in tree and forest productivity among Fremont cottonwood genotypes. In comparison, genetic variation for phenology traits within populations (heritability) was lower in our study than that reported for its congener *P. trichocarpa* (Table 2).

Our detection of selection was partly dependent on the environmental conditions of each garden. For example, we observed the

highest population differentiation in both height and DRC expressed in the hottest garden, with decreasing mean Q_{ST} values in the cooler gardens (Figure 4). This variability in Q_{ST} across gardens suggests that phenotypes shaped by selection pressures across a species' range can be expressed differently in different growing environments, with some environments enhancing and others dampening population phenotypic differences (Akman et al., 2021; Oke et al., 2015). Particularly for growth traits, this may represent an interaction between the selection pressures that have shaped existing variation across the species range and novel selection pressures imposed in a common garden experiment or under future climate change.

Interestingly, for both growth traits, the hottest garden produced the highest Q_{ST} values but the lowest heritability values. This climate transfer from northern to southern Arizona represents an extreme warming treatment, a scenario that may be imposed on populations under severe heat waves with climate change (Cook et al., 2015). Because the very hot and dry conditions in this garden led to much lower growth and lower variation in growth overall (Figure 3), the values of Q_{ST} and H^2 depend entirely on the distribution of variation. In hot conditions, more variation was among populations (high Q_{ST}), whereas in the cold garden there was greater differentiation among genotypes within a population (higher H^2). This result has several important implications for population-level responses to climate change. Extreme heat conditions will clearly favour some populations over others, but within maladapted populations, selection may suppress genetic variation for growth, thus dampening their evolutionary response to climate change. This is an important avenue for further research, as the range of heritability values for growth and leaf morphology that we observed across gardens is similar to the range of values reported in other *Populus* studies (Table 2), suggesting that environmental effects on evolutionary potential are widespread.

4.2 | Divergent selection on plasticity

Our Q_{ST} - F_{ST} comparison indicates divergent selection acting on phenotypic plasticity in bud flush and tree height, and showed partial evidence for selection on plasticity in the other three traits (Table 2; Figure 5). These results are in contrast to previous studies that found no evidence of selection on trait plasticity using Q_{ST} - F_{ST} type comparisons (De Kort et al., 2016; Lind et al., 2011), and low overall

TABLE 4 Summary of the two tests for selection

Trait	Bud set				Bud flush				SLA				Height				DRC			
	Y	A	C	P	Y	A	C	P	Y	A	C	P	Y	A	C	P	Y	A	C	P
Selection tests	Trait				Bud set				Bud flush				SLA				Height			
	Garden				Y	A	C	P	Y	A	C	P	Y	A	C	P	Y	A	C	P
	Selection Tests																			

Note: Blue indicates a significant Q_{ST} - F_{ST} test and hatched lines indicate significant climate regressions for that trait or plasticity. Blank squares indicate nonsignificant results for both selection criteria. The Garden abbreviations are Y, Yuma; A, Agua Fria; C, Canyonlands; P, plasticity across gardens.

support for selection on plastic responses to temperature (Arnold et al., 2019). These studies, however, included mainly herbaceous annuals and birds (Arnold et al., 2019), with only one tree species reported (De Kort et al., 2016), suggesting differences in plasticity might be influenced by life-history traits. Our results suggest that for some traits, differences in the magnitude of plasticity among populations across a wide environmental gradient are larger than expected from neutral genetics. Conversely we found some evidence for stabilizing selection in DRC plasticity, indicating that the difference in the magnitude of plasticity for this trait across our populations was somewhat smaller than expected by F_{ST} . Finally, broad-sense heritability for the five trait plasticities ranged from 0.09–0.18. This is a similar result to bud burst plasticity found in another riparian deciduous tree, black alder ($H^2 = 0$ –0.13, De Kort et al., 2016). Our results of genetic variation in trait plasticity, evidence for selection based on Q_{ST} – F_{ST} analysis, and nonzero heritability estimates suggest that selection may lead to evolving plasticity across the range of Fremont cottonwood.

The mosaic of natural selection acting on trait plasticity across our populations shows how plasticity can evolve in response to different climates. We found significant plasticity-climate relationships in phenology and growth traits, where the sign of the correlation switched between these two types of traits (Figure 3). Specifically, we found trees sourced from hotter environments were significantly less plastic in height and DRC compared to the colder provenance populations, but had higher plasticity in bud set and bud flush (Figure 3). These plasticity-climate relationships partially agree with another study where populations of red spruce from warmer climates had greater plasticity in both bud break and growth compared to cold-adapted populations (Prakash et al., 2022). Our results may be an example of a multivariate plasticity response, where plasticity in one trait can affect the plasticity in another trait (Nielsen & Papaj, 2022). The higher plasticity in phenology traits measured in populations from hotter provenances is counterintuitive because colder source populations experience much more predictable fall freezing events and higher yearly temperature variation (see TD in Table S1), and theory predicts plasticity will increase under predictably variable environments (Chevin & Lande, 2010). It may be that interannual variation in climate is more important than seasonal variation for selection on leaf plasticity and is lower in these colder locations. Alternatively, the extreme climate transfer of southern Arizona populations to the northernmost cold garden (over 15°C colder in the coldest month, Table S1) may be too far outside of normal temperature ranges, resulting in large, but maladaptive plastic responses (Chevin & Hoffmann, 2017).

Importantly, the higher phenological plasticity seen in hot-adapted populations did not translate into increased growth or growth plasticity. Instead, high phenological plasticity pushed these trees outside of the appropriate growing season window (Cooper et al., 2019). Their high bud set plasticity meant that these trees did not set bud until late in the growing season, when freezing temperatures damaged nondormant tissues. The subsequent frost damage translated to lower growth compared to cold-adapted trees that set

bud earlier in the season, avoided frost damage, and thus grew much taller. When compared to the hottest garden where all populations experienced low growth, the colder populations showed greater plasticity in height than the hotter populations. This result can therefore be partially explained by the warm populations' maladaptive plasticity in phenology. Alternatively, the higher growth plasticity in cold-adapted populations could result from their higher intra-annual temperature variability (TD, Table S1). In contrast to phenological plasticity, this growth plasticity result would support the prediction that more predictably variable environments select for more plastic phenotypes (Lande, 2009).

4.3 | Local adaptation to climate

Whereas leaf phenology and morphology traits (bud flush, bud set, and SLA) had the highest degree of differentiation in our study, likely due to climate-related divergent selection, tree growth traits were less differentiated. This result suggests that the neutral processes of gene flow and drift may override weak selection on growth traits (McKay & Latta, 2002), or that growth is strongly constrained by the relative success dictated by the rest of a plant's phenotype (Saint-Laurent et al., 2003; Leinonen et al., 2013). In this case, the latter explanation is very likely. Although phenology and growth traits showed significant regressions with climate of origin (Figure 3), only the growth traits reversed the sign of that relationship across gardens. In contrast, the phenology trends were mostly constant across gardens, with warmer source populations setting bud later and flushing earlier regardless of growing environment (except for bud flush in Canyonlands, where all populations flushed at the same time). However, height and trunk diameter declined as populations were moved further in either a hotter or colder direction relative to their home sites. This indicates local adaptation, where the highest productivity is observed in populations whose source climate best matches that of the garden climate. In the hottest garden (Yuma), there was a positive relationship between trunk diameter and provenance climate. In the coldest garden (Canyonlands), the reverse was true, where trees from cooler provenances grew significantly taller than those from the warmer sites (Figure 3b). Importantly, because average growth was much higher in the cold garden than the hot garden, this pattern illustrates local adaptation by the stronger local versus foreign comparison, but not the weaker home versus away comparison (Kawecki & Ebert, 2004). Whether the higher performance of local populations is enabled by their leaf phenology and morphology traits measured here or by additional plant functional traits is an important area for further study.

4.4 | Management implications

When local adaptation and phenotypic differentiation in forest trees are closely tied to variation in climate, populations may become

increasingly maladapted as climate change continues (Aitken & Bemmels, 2015; Browne et al., 2019; Franks et al., 2014; Shaw & Etterson, 2012). However, the magnitude of climate change combined with the degree of genetic variation, heritability, and phenotypic plasticity of traits will all interact to determine the extent of adaptation or maladaptation. Maladaptation due to climate change is expected to be greatest in populations from the warmest extent of their range, while populations at the cold edge may benefit from slightly warmer temperatures (Aitken & Bemmels, 2015). This expectation corresponds with the maladaptive phenological plasticity we have observed in southern populations versus adaptive phenological plasticity in northern populations (Cooper et al., 2019). However, nuanced changes in temperature and precipitation patterns will produce novel genotype-climate associations, creating more complex climate responses than the poleward range shifts and vulnerable trailing edges traditionally associated with warming (Gougherty et al., 2021).

Changes in selection pressures associated with various environmental drivers will affect traits differently. For instance, Csilléry et al. (2020) showed silver fir populations exhibited adaptive divergence in growth and water use traits in response to drought selection, while phenology differences evolved independently in response to temperature variability. We saw the strongest evidence of past climate selection on phenology, bud flush plasticity, and height plasticity and moderate to low selection on growth traits and SLA (Table 4). However, the traits that most impacted by future selection pressures related to climate warming may be those with high heritability estimates in the hottest garden, such as bud flush and SLA. Traits with high heritability in the hot garden suggest these have more genotypic variation for selection to act upon under warming conditions.

Although our study does not encompass the full genetic and geographic range of Fremont cottonwood, our results of declining performance as climate transfer distance increases suggests that this species will likely experience maladaptation as local conditions become more arid, especially for southern populations that are close to their thermal tolerance (Ault et al., 2014; see Figure 1). Because these trees are important foundation species of riparian systems, more field trials aimed at selecting genotypes with sufficient performance under warming and/or drought conditions is essential for the management of healthy riparian communities and ecosystems (Whitham et al., 2020). Given the intensification of extreme events and climate variability going forward (Ganguly et al., 2009; Garfin et al., 2013; Jentsch et al., 2007; Williams et al., 2020), these types of field trials should be expanded to evaluate the correspondence between the degree of existing climate adaptation and the potential for future survival, through phenotypic plasticity, selection on remaining genetic variation, or a combination of the two (Josephs, 2018; Nicotra et al., 2010).

AUTHOR CONTRIBUTIONS

Hillary F. Cooper collected trait data, performed genetic and statistical analyses, and wrote much of the manuscript. Rebecca J. Best contributed to the development of the Q_{ST} plasticity calculation and helped with the theoretical development of the manuscript and

writing. Rebecca J. Best, Jaclyn P. M. Corbin, and Iris J. Garthwaite also assisted with some field collections and sample processing. Lela V. Andrews helped with RADseq processing. Gerard J. Allan, Catherine A. Gehring, Kevin R. Hultine, Kevin C. Grady, and Thomas G. Whitham designed the common garden experiment. Kevin C. Grady also assisted with data collection at the field sites. All authors provided critical edits to the manuscript and figures. All authors declare no conflicts of interest.

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CONFLICTS OF INTEREST

All authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The trait values from each garden and the R code for generating randomized plasticity replicates have been uploaded to the Dryad digital repository: <https://doi.org/10.5061/dryad.3r2280gk3>. The SNP dataset has been uploaded to NCBI BioProject ID PRJNA868761.

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