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RESEARCH ARTICLE

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Genetic divergence along a climate gradient shapes chemical plasticity of a foundation tree species to both changing climate and herbivore damage

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Abstract

Climate change is threatening the persistence of many tree species via independent and interactive effects on abiotic and biotic conditions. In addition, changes in temperature, precipitation, and insect attacks can alter the traits of these trees, disrupting communities and ecosystems. For foundation species such as *Populus*, phytochemical traits are key mechanisms linking trees with their environment and are likely jointly determined by interactive effects of genetic divergence and variable environments throughout their geographic range. Using reciprocal Fremont cottonwood (*Populus fremontii*) common gardens along a steep climatic gradient, we explored how environment (garden climate and simulated herbivore damage) and genetics (tree provenance and genotype) affect both foliar chemical traits and the plasticity of these traits. We found that (1) Constitutive and plastic chemical responses to changes in garden climate and damage varied among defense compounds, structural compounds, and leaf nitrogen. (2) For both defense and structural compounds, plastic responses to different garden climates depended on the climate in which a population or genotype originated. Specifically, trees originating from cool provenances showed higher defense plasticity in response to climate changes than trees from warmer provenances. (3) Trees from cool provenances growing in cool garden conditions expressed the lowest constitutive defense levels but the strongest induced (plastic) defenses in response to damage. (4) The combination of hot garden conditions and simulated herbivory switched the strategy used by these genotypes, increasing constitutive defenses but erasing the capacity for induction after damage. Because Fremont cottonwood chemistry plays a major role in shaping riparian communities and ecosystems, the effects of changes in phytochemical traits can be wide reaching. As the southwestern US is confronted with warming temperatures and insect outbreaks, these results improve our capacity to predict ecosystem consequences of climate change and inform selection of tree genotypes for conservation and restoration purposes.

KEYWORDS
climate change, common garden, environmental stress, functional traits, herbivory, intraspecific variation, phenotypic plasticity, riparian ecosystem

1 | INTRODUCTION

Terrestrial ecosystems are increasingly confronted with higher temperatures and less reliable precipitation as consequences of anthropogenic climate change (Li et al., 2018; Nolan et al., 2018). Rapid changes in environmental conditions pose threats to the persistence of many plant and animal species, particularly sessile, long-lived organisms such as trees (Brodribb et al., 2020; Kijowska-Oberc et al., 2020). Moreover, rapid environmental changes will be especially disruptive if the trees affected are foundation species, which structure associated communities and ecosystem processes via their functional traits (Ellison et al., 2005; Whitham et al., 2006).

Phytochemistry is a principal means by which foundation species modulate the communities and ecosystems in which they are imbedded. For example, tree metabolites can govern communities of soil microbes (Madritch & Lindroth, 2011) and canopy insects (Barbour et al., 2009; Barker et al., 2018; Visakorpi et al., 2019), structure ground-layer vegetation (Iason et al., 2005), and alter soil nutrient cycling (Chomel et al., 2016; Schweitzer et al., 2008) and stream water conditions (Thompson & Bärlocher, 1989). The expression of tree phytochemical traits is affected by genetic divergence among and within populations due to selection and drift as well as environmental factors (Holopainen et al., 2018; Westerband et al., 2021). Consequently, understanding how past climate-driven selection interacts with current climate change to shape tree functional traits is fundamental for assessing the persistence of forest ecosystems under future climates and riparian restoration scenarios. Surprisingly, however, few climate change studies have attempted to disentangle the impact of multiple environmental and genetic drivers on tree trait expression in general, and phytochemical expression in particular (Foster et al., 2016; Niinemets, 2010; Seidl et al., 2017).

Climate change influences phytochemical traits directly, via changes in abiotic factors such as temperature and precipitation that can drive tree trait expression, fitness, and habitat shifts (Anderegg et al., 2019; Boisvert-Marsh et al., 2014; Lévesque et al., 2013; Zimmermann et al., 2009). Climate change can also affect trees indirectly, by altering the frequency and magnitude of disturbance events (Seidl et al., 2017). For example, outbreaks of insect herbivores are often promoted by warm and dry conditions, and are expected to increase in frequency and intensity in coming years (Netherer & Schopf, 2010; Pureswaran et al., 2018; Seidl et al., 2017). To better assess climate change impacts on tree populations and the communities they support, research is needed that addresses the independent and combined effects of direct climatic factors and indirect biotic factors on functional traits.

Functional trait expression can also differ among tree populations adapted to habitats with divergent environmental conditions (hereafter “provenances”) (Stahl et al., 2014; Van Nuland et al., 2020; Xu et al., 2020). This is especially true for widespread tree species spanning large climatic gradients. Such provenance effects are partially the product of selective environmental adaptations (Turnbull & Griffin, 1985) and have been demonstrated for multiple functional traits in numerous tree species (Abdala-Roberts et al., 2016; Arend et al., 2011; Cooper et al., 2019; Nabais et al., 2018). Trees may also exhibit considerable variation in trait expression within provenances, as a consequence of local genetic and environmental variation (Damestoy et al., 2019; Moreira & Abdala-Roberts, 2020; Paaso et al., 2017). Such trait differences are the product of genotypic, developmental, and microenvironmental variation, and their interactions (Westerband et al., 2021).

In addition to constitutive (i.e., permanently expressed) trait variation, plants from different provenances may also vary with respect to trait plasticity, that is, the ability of a single genotype to produce different phenotypes under different environmental conditions (de Villemereuil et al., 2018; Pellissier et al., 2016). This variation in environmental response across trees from different provenances (i.e., Provenance × Environment interactions) or different genotypes (i.e., Genotype × Environment interactions) is often linked to provenance climate or biotic stressors (Lande, 2009; Nicotra et al., 2010). For example, plants growing in warmer, low-elevation environments also tend to experience higher and less variable levels of herbivory than high-elevation plants (Galmán et al., 2018; Moreira et al., 2018; Rasmann, Pellissier, et al., 2014; Scheidel & Bruelheide, 2001). As a consequence, low-elevation environments may select for plant genotypes with high levels of constitutively expressed defenses (Bakhtiari et al., 2019; Galmán et al., 2019; Zangerl & Rutledge, 1996). In contrast, cooler, high-elevation environments with comparatively low levels of herbivory should select for genotypes with high plasticity in defenses (Galmán et al., 2018, 2019; Zangerl & Rutledge, 1996), that is, enhanced capacity to induce chemical defenses after attack (Agrawal et al., 2002). Multiple studies, however, have found varying relationships between defense expression and elevation (Alonso-Amelot et al., 2007; Defossez et al., 2018; Moreira et al., 2014). Hence, a clear consensus on how chemical defense plasticity changes along gradients of both climate and herbivory has remained elusive (Carmona et al., 2020; Moreira et al., 2018; Murren et al., 2014).

In addition to phytochemical defenses (i.e., compounds with deterrent or toxic effects on herbivores), plants produce a diverse array of compounds used for structural support (e.g., fiber, comprised of cellulose and lignin) or for primary metabolic processes (e.g., proteins, carbohydrates). Like defense chemicals, these compounds also influence ecological interactions (e.g., herbivory, decomposition; Awmack & Leather, 2002; Li et al., 2018). Relatively, few studies have explored whether divergent climate conditions select for different constitutive and plastic expression patterns of structural and primary compounds. For example, the effects of elevational gradients on fiber and lignin are inconsistent, ranging from decreases to increases with elevation (Rasmann, Pellissier, et al., 2014; Richardson, 2004). A meta-analysis on leaf nitrogen (a proxy for protein and therefore an important nutrient for herbivores; Awmack & Leather, 2002) showed that plants from warmer, low-elevation provenances, and cool high-elevation habitats have similar constitutive levels (Read et al., 2014). Moreover, low- and high-elevation plants also do not differ in plastic responses to climate differences (Henn et al., 2018). The inconsistent or minimal elevational patterns in structural compounds and nitrogen, and the fundamental importance of these compounds to plant function suggest that their concentrations are driven by factors that vary independently of elevation-related climate. Hence, elevational variation in climate metrics and herbivory may not select for structural compounds and protein (N) levels. The small body of published research on these compounds, however, precludes definite conclusions.

Fremont cottonwood (*Populus fremontii*), a riparian tree species, provides an excellent model system to study the independent and interactive effects of tree genotype, provenance, and abiotic and biotic factors on phytochemical traits. *Populus fremontii* and other members of the genus *Populus* are frequently the dominant tree species of riparian ecosystems in the southwestern United States (Driebe & Whitham, 2000). *Populus* produces a diversity of phenolic metabolites that link intraspecific genetic variation with higher-order structure and function, including organismal interactions, community organization, and ecosystem processes (Bailey et al., 2006; Bangert et al., 2006; Barker et al., 2018; Schweitzer et al., 2004; Whitham et al., 2006, 2008, 2020). Fremont cottonwood spans a broad climatic range throughout the southwestern US, but is genetically highly variable within this range, comprising multiple ecotypes and distinct populations within them (Ikeda et al., 2017). These populations exhibit local adaptation along a steep climate gradient, with local populations showing much higher survival than foreign populations in the same garden (Cooper et al., 2019; Grady et al., 2015). Over recent decades, the species has suffered substantial habitat loss due to drought and other environmental changes (Noss & Scott, 1995; Smith & Finch, 2017; Stromberg, 1993). Thus, understanding how genetic and environmental factors interact to influence tree traits has important consequences for ongoing conservation and restoration efforts (Grady et al., 2011; Hultine et al., 2020).

Elevation gradients are widely used to test how multi-factor environmental variation affects ecological processes (Lortie & Hierro, 2021; Moreira et al., 2018; Schemske et al., 2009), and are powerful surrogates for assessing climate change impacts on ecosystems (Descombes et al., 2020; Rasmann, Pellissier, et al., 2014; Sundqvist et al., 2013). We used a system of three *P. fremontii* common gardens that span a steep climatic gradient. All gardens contained the same genotypes, which originated from different environmental provenances throughout Arizona. In each garden, we imposed the same simulated damage treatment to mimic herbivore attacks. Across this factorial tree provenance × garden climate × herbivory experiment, we analyzed multiple phytochemical traits, known to mediate diverse ecological dynamics. We tested the following hypotheses: (i) genotypes from low-elevation provenances that are adapted to hot, dry climates and high herbivore pressure will invest more in constitutive defenses than genotypes from high-elevation provenances. (ii) High-elevation genotypes, adapted to cool, wet climates will instead show more plastic responses in defense chemistry to changes in garden climate and herbivory (via induced defenses). In other words, we expect to see interactions between genetics (provenance and genotype) and environmental conditions. (iii) In contrast to defense chemistry, structural compounds and leaf nitrogen concentrations will show limited differentiation among provenances in both mean trait values and plastic responses to changes in garden climate and herbivory. By testing these hypotheses, we assess the relative importance of genetic differentiation across multiple scales, both abiotic and biotic environmental changes, and genetic by environmental interactions, for determining multiple tree leaf traits known to have major ecological effects. Improved understanding of the mechanisms that shape foundation tree chemistry is important for climate-ready ecosystem restoration strategies in a changing world.

2 | MATERIALS AND METHODS

2.1 | Experimental design, common gardens, and damage treatment application

To separate genetic and environmental effects on chemical traits in *P. fremontii*, we used three reciprocal common gardens. The gardens were planted at three elevations, spanning a temperature gradient of 12°C and an elevational gradient of more than 1500 m reflecting the precipitation and temperature extremes of *P. fremontii* (Table 1). Hereafter, we refer to the three gardens as hot (mean annual temperature [MAT]: 22.8°C, mean warmest monthly temperature [MWMT]: 33.8°C, mean coldest monthly temperature [MCMT]: 12.7°C), moderate (MAT: 17.2 °C, MWMT: 28.5°C, MCMT: 7.6°C), and cool gardens (MAT: 10.7°C, MWMT: 24.6°C, MCMT: −3.2°C). Because we used garden location as a surrogate for climate, we will refer to garden effects as "climate effects." We acknowledge that climate effects could be confounded with other factors such as soil composition, but these are less likely to change in a consistent way from the hot to moderate to cool garden locations. All three gardens received regular watering, but initial growth in the warmest garden was lower than that has been observed at other hot sites with unlimited water (Grady et al., 2011). Thus, the hot garden likely represents a type of climate stress increasingly common under prolonged drought in the Southwest (Williams et al., 2020). That is, hot temperatures with insufficient water for optimal evapotranspiration.

All gardens were planted between fall 2014 and spring 2015 with replicated clones of 12 genotypes (i.e., individual trees) collected from each of 16 *P. fremontii* populations (i.e., 12 genotypes × 16 populations = 192 genotypes). All plantings were established using saplings grown from cuttings taken from randomly selected trees

TABLE 1 Geographic and climatic information for the three gardens and home provenances of the 12 genotypes used in the experiment. Climate data are from ClimateWNA (Wang et al., 2012)

Garden name	Location	Elevation (m)	Latitude (decimal degrees)	Longitude (decimal degrees)	MAT (°C)	MWMT (°C)	MCMT (°C)	MAP (mm)
Hot	Mittry Lake, Yuma, Arizona	49	32.8498	−114.4928	22.8	33.8	12.7	93
Moderate	Agua Fria River, Horseshoe Ranch, Arizona	988	34.2567	−112.0661	17.2	28.5	7.6	440
Cool	Canyonlands, Dugout Ranch, Utah	1581	38.0925	−109.5878	10.7	24.6	−3.2	225

Home population	Nr. selected genotypes	Provenance group	Elevation (m)	Latitude (decimal degrees)	Longitude (decimal degrees)	MAT (°C)	MWMT (°C)	MCMT (°C)	MAP (mm)
San Luis, CO River	1	Low	26	32.5270	−114.8036	22.1	32.9	12.4	88
Cibola, CO River	1	Low	70	33.3621	−114.6976	22.6	33.9	12.2	97
Bill Williams, CO River	2	Low	143	34.2760	−114.0585	22.3	34.6	10.9	137
Agua Fria, Horseshoe Ranch	2	Middle	988	34.2567	−112.0661	17.2	28.5	7.6	440
Willow Creek, Kingman	2	Middle	1126	35.143	−113.5428	15	26.6	5	243
Jack Rabbit, Little CO River	1	High	1507	34.9600	−110.4360	12.3	25.3	−0.7	212
Keams Canyon	3	High	1920	35.8115	−110.1695	10.7	23	−1.3	258

Abbreviations: MAP, mean annual precipitation; MAT, mean annual temperature; MCMT, mean coldest monthly temperature; MWMT, mean warmest monthly temperature.

in the source populations. The populations were randomly selected from throughout Arizona. The establishment and maintenance of the gardens is described in detail by Cooper et al. (2019) and Hultine et al. (2020). In addition, all genotypes have been sequenced using double-digest restriction-associated DNA (ddRAD) resulting in approximately 9000 loci. These genomic data, together with population genetic data based on simple sequence repeats (Cushman et al., 2014) support substantial genetic divergence among populations, especially between low-elevation Sonoran Desert populations and higher elevation Colorado Plateau populations first identifed in Ikeda et al. (2017) and more recently identified in Bothwell et al. (2022). For our study, we chose 12 genotypes from a total of seven populations spanning the full environmental range. We were restricted to genotypes for which enough replicates were available in all three common gardens. Among these genotypes, we selected four genotypes originating from low-elevation provenances (26–143 m; hot climatic conditions), four genotypes originating from middle-elevation provenances (988–1126 m; moderate climatic conditions), and four genotypes originating from high-elevation provenances (1507–1920 m; coolest climatic conditions) (Table 1). For each provenance group (i.e., low, middle, and high elevation), genotypes were randomly selected from 2–3 climatically similar populations (Table 1).

We randomly selected 8–10 experimental trees of each genotype in each common garden (8–10 replicates × 12 genotypes × 3 gardens = 335 trees), and randomly subjected half of them to a damage treatment. The other half served as undamaged controls. Damage treatments in the hot, moderate and cool gardens were applied on April 27th, May 16th, and June 16th 2019, respectively, approximately 80 days after initial leaf flush at each site (Cooper et al., 2019). After this period of time, *Populus* leaves should be mature and phytochemically stable (Falk et al., 2018).

To apply the damage treatment, we first marked on each tree a branch section that contained 25–35 fully expanded, mature leaves. Half of the marked leaves were punctured with the self-cleaning plate of a metal garlic press, mimicking the shotgun-like (many small holes) damage pattern (Figure 1a,b) left by developing *Coptodisca* spp. larvae (Lepidoptera: Heliozelidae) (Figure 1c). These larvae were the dominant leaf herbivore found in all three gardens. Marked branch sections were then sprayed with a 1 mM jasmonic acid (JA) solution known to induce plant defense responses elicited by herbivory (Arnold & Schultz, 2002; Thaler et al., 1996). The JA solution was created by dissolving 250 mg ± JA (≥95%; Sigma-Aldrich) in 2.38 ml 99% EtOH to create a 500 mM stock solution. This stock solution was then further diluted with 1186.5 ml deionized water to create a 1 mM JA solution. Triton-X 100 detergent (0.1% v/v; Sigma-Aldrich) was added to help penetrate the leaf cuticles (Arnold & Schultz, 2002).

Branch sections of control trees were not physically damaged, but were sprayed with an identical solution that lacked JA. Three weeks after damage application, leaves were collected (without petioles) and dried in silica desiccant. For damaged trees, we collected only leaves that were artificially damaged and sprayed with JA. In a very few cases, damage application caused premature wilting of individual leaves. Those leaves were not collected. For control trees, all leaves within the marked branch sections were collected.

2.2 | Phytochemical measurements

We quantified chemical defenses, structural compounds, and nitrogen of the leaf samples. Salicinoid phenolic glycosides are the signature defense compounds in *Populus* and exhibit biological activity against a wide range of insect and mammalian herbivores (Boeckler et al., 2011; Lindroth & Clair, 2013). Condensed tannins comprise the second major class of secondary metabolites in *Populus* (Lindroth et al., 1987; Palo, 1984). Fiber and its constituent lignin represent structural plant compounds. They are particularly relevant for the formation of cell walls and therefore important for plant growth and tissue rigidity (Liu et al., 2018). Because fiber and lignin contribute

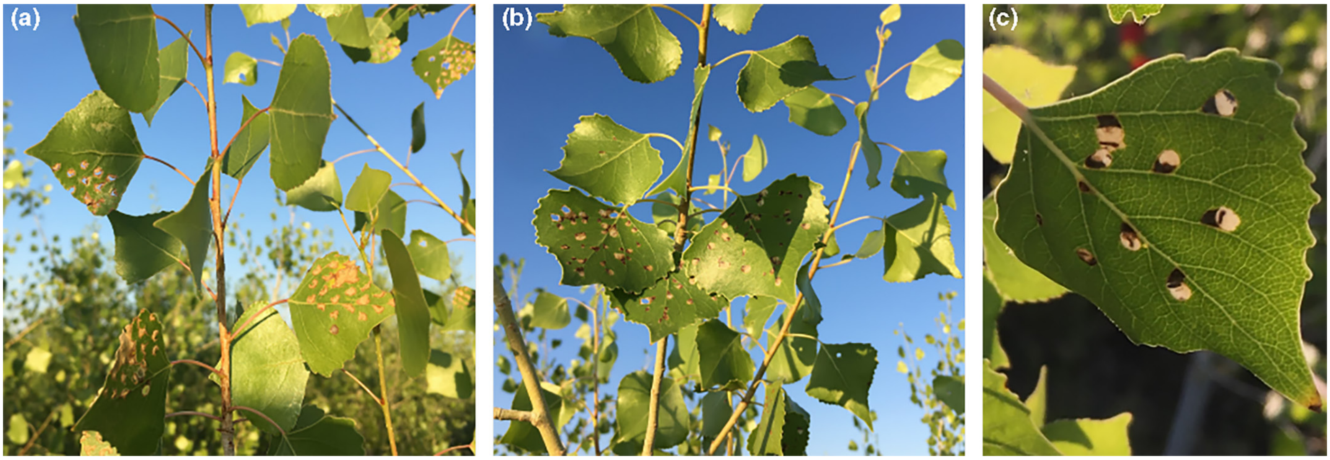

FIGURE 1 Visual comparison of leaf damage. Including (a) leaves that were punctured with a metal garlic press and sprayed with jasmonic acid to simulate herbivory, (b) the natural shotgun-like feeding pattern of *Coptodisca* spp. larvae (lepidoptera: Heliozelidae), and (c) developing *Coptodisca* spp. larvae.

to leaf toughness (Gessner, 2005), both constituents are also associated with herbivore feeding deterrence (Choong, 1996). Finally, leaf nitrogen is an index of leaf protein, and therefore an important proxy for insect food quality (Awmack & Leather, 2002). Dried leaves were ground using a Wiley® minimill (20-mesh screen). A subsample of the ground material was used for fiber and lignin analyses. The remaining ground leaf material was then pulverized in a ball mill and used for all additional phytochemical analyses.

The main *P. fremontii* salicinoids, salicortin and HCH-salicortin (Rehill et al., 2005), as well as salicin, were quantified using ultra-high-performance liquid chromatography-mass spectrometry after Rubert-Nason et al. (2017). Concentrations of "total phenolic glycosides" were calculated as the sum of the three constituents. Salicortin and HCH-salicortin standards were purified from *Populus tremuloides* and *P. fremontii* tissue, respectively. The salicin standard was obtained from Sigma-Aldrich. Condensed tannins were quantified via an HCl-butanol spectrophotometric method (Porter et al., 1985), with purified *Populus angustifolia* condensed tannins as standard. Levels of fiber (reported as the total amount of cellulose and lignin) and lignin were measured gravimetrically by sequential extraction in a hot acid-detergent solution in an Ankom 200 Digestor and then incubation in 72% H_2SO_4 (Rowland & Roberts, 1994). Due to limited leaf material, we were able to analyze fiber and lignin levels only from control leaves. Quantifications of total foliar nitrogen were performed with combustion gas chromatography (Thermo Flash EA1112 elemental analyzer; Thermo Finnigan).

2.3 | Statistical analysis

We used linear mixed models (LMMs) to test for the effects of tree provenance (low, middle, and high elevation), garden climate (hot, moderate, cool garden), leaf damage (damaged, undamaged), and their interactions on individual chemical traits. Chemical traits were coded as response variables, and provenance, garden climate, leaf damage, and their interactions were fixed effects. Tree genotype and the interactions genotype × garden climate, genotype × damage treatment and genotype × garden climate × damage treatment were used as random intercepts to account for genetic variation within provenances.

We quantified the relative explanatory power of the individual fixed and random effects using three steps. First, we calculated semi-partial R^2 to assess the relative importance of each fixed effect while accounting for all other fixed and random effect terms (Jaeger et al., 2017). The semi-partial R^2 is the most important indicator of relative effect size because our main variables of interest are fixed. Second, we calculated the proportion of total variance explained by all fixed effects (R^2_{marginal}) and all random effects ($R^2_{\text{conditional}} - R^2_{\text{marginal}}$). Lastly, the proportion of total variance explained by each individual random effect was calculated by dividing the variance for that effect by total variance. Note that the semi-partial R^2 values do not sum to the total fixed effects variance (R^2_{marginal}), because semi-partial R^2 values assess variance explained by a predictor after accounting for other predictors while total R^2 assesses the joint variance explained when all predictors are included together.

After assessing effects on mean chemical trait values, we quantified the magnitude of plastic responses to both garden climate (climate plasticity) and simulated herbivory (damage plasticity). For climate plasticity, we used trait expression from only undamaged trees. For each trait and each genotype, we calculated climate plasticity as the difference between the maximum and the minimum trait mean value among the three garden climates divided by the maximum trait mean value (Valladares et al., 2000, 2006). This approach resulted in an index ranging from zero to one. To test whether climate plasticity differed among low, middle, and high provenance genotypes, we used linear models (LMs) with plasticity scores as the response and a continuous index of home climate as the explanatory variable. For the continuous climate index, we used the first axis (PC1) from a principal component analysis of latitude, longitude, elevation, and 21 climate variables extracted from GIS layers (climate WNA; Wang et al., 2012). PC1 explained 71.5% of the variation among home provenance climate characteristics.

In addition to climate plasticity across gardens, we also quantified damage plasticity within each garden. For each chemical trait and each genotype, damage plasticity was calculated as the absolute difference between the damage and the control treatment means divided by the larger of the two treatment mean values. To test whether damage responses differed among provenances and gardens, the relationship between damage plasticity and provenance climate was explored for each garden separately. For this analysis, we used LMs with plasticity scores as responses and the continuous climate index as the explanatory variable.

All analyses were conducted with R 4.1.2 (R Core Team, 2022). LMMs were fit using the lmer function of the "lme4" package v. 1.1–26 (Bates et al., 2015). If necessary, response variables were ln- or power transformed using the powerTransform function of the "car" package, v. 3.0–10 (Fox & Weisenber, 2018) to meet the model assumptions of normality and homoscedasticity. For each LMM and LM, we calculated *F* and *p* statistics with the Anova function of the "car" package. For models that included variable interactions, type 3 Wald *F*-tests with Kenward–Roger approximations for the denominator degrees of freedom were applied. Type 2 tests were used when no interactions were present. The significance of random effects was tested with likelihood ratio tests implemented using the ranova function of the "lmerTest" package v.3.1–3 (Kuznetsova et al., 2017). We used the getvariance function of the "insight" package v. 0.13.1 (Lüdecke et al., 2019) to calculate proportions of model variances explained by the total fixed effects, the total random effects, and the model residuals as well as for quantifying individual variance contributions of each random intercept of an LMM. The r2beta function in the package "r2glmm" was used for calculating semi-partial R^2 statistics for individual fixed model effects v. 0.1.2 (Jaeger et al., 2017). The PCA was conducted using the command prcomp in the base R package.

3 | RESULTS

3.1 | Effects of garden climate, tree provenance, damage treatment, and tree genotype on phytochemistry

For most traits, the effect of provenance varied among gardens (provenance × garden interactions). Trees from high-elevation provenances showed 55% lower levels of total phenolic glycosides than middle- and low-elevation trees in the cool garden and 49%–68% lower total phenolic glycoside levels in the moderate garden. However, these among-provenance differences were not detected in the hot garden (Figure 2b; Table S1). Differences in total phenolic glycoside concentrations could be attributed mainly to variation in HCH-salicortin levels (Figure S1a). These results support our hypothesis (i) of higher constitutive defenses in low-elevation genotypes growing at home than in high-elevation genotypes growing at home. Interestingly, high-elevation trees at home invested more in fiber, exhibiting 18%–20% higher levels than middle- and low-elevation trees in the cool garden, but only 6%–11% higher levels in the moderate and hot gardens. This finding does not align with hypothesis (iii), which posited that genotypes from different provenances have similar constitutive levels of fiber. In support of hypothesis (iii), however, we found that leaf nitrogen concentrations were mostly affected by garden climate regardless of provenance. Across all genotypes, nitrogen levels were almost twice as high in

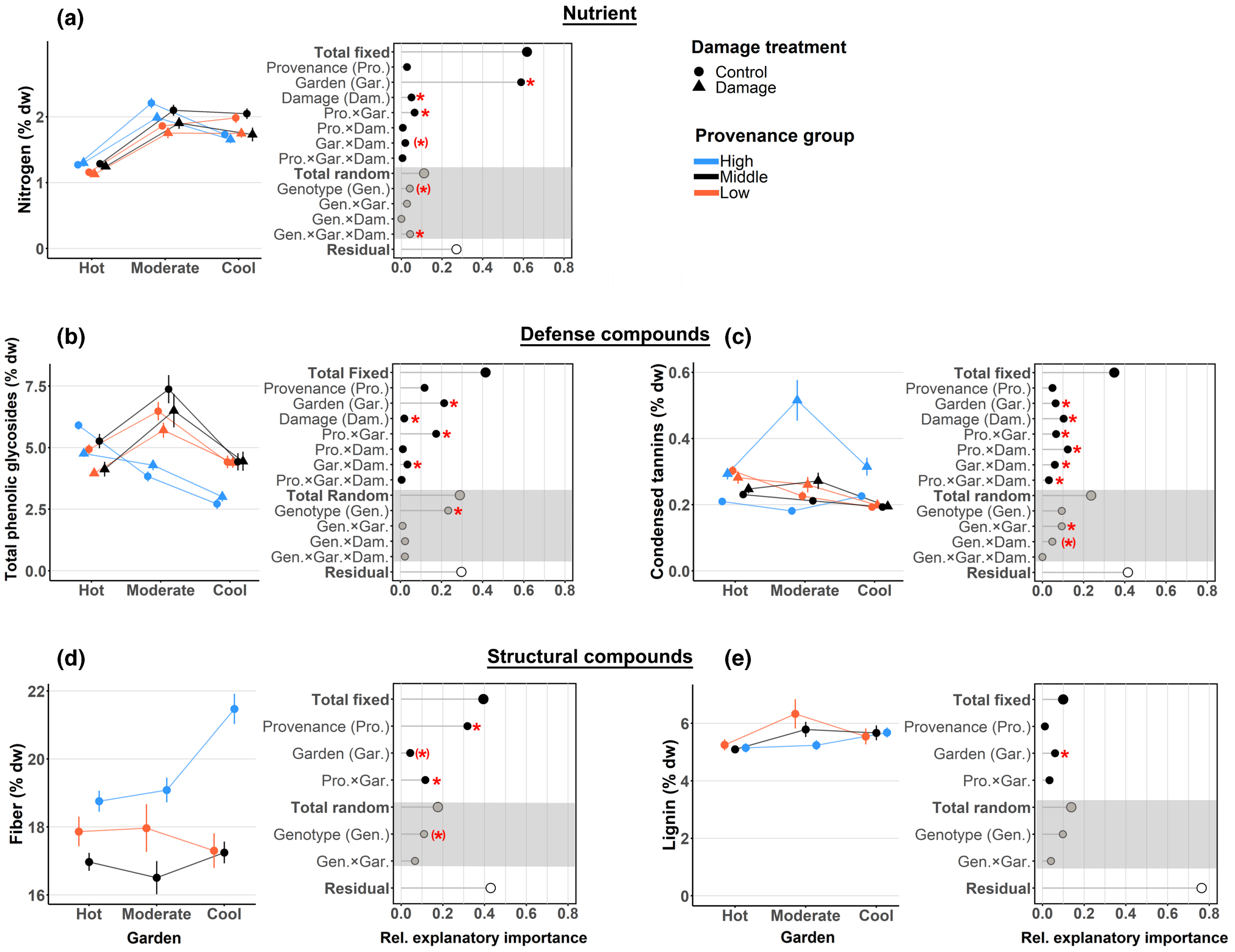

FIGURE 2 Line and effect size plots illustrating the effects of provenance, garden climate (garden), and damage treatment on (a) leaf nitrogen (a proxy for leaf protein and therefore an important nutrient for herbivores), (b) the defense compounds total phenolic glycosides and (c) condensed tannins, as well as the structural compounds (d) fiber, and (e) lignin. Line plots represent trait values (mean ± 1 SE) averaged across all genotypes of the same provenance group when growing under different climatic conditions (garden) and experiencing different damage treatments. Data points are horizontally jittered to reduce overlap. The corresponding effect size plots show the relative explanatory importance of each fixed effect as the partial R^2 value and the proportion of variance explained by total fixed effects, total random effects, and each random effect in the trait model. Due to limited leaf material, we were able to analyze fiber and lignin levels only from control trees. Asterisks without parentheses: $p < .050$, asterisks in parentheses: $p = .051–.100$. *F*, *p*, and df values of fixed and random effects are provided in Table S1.

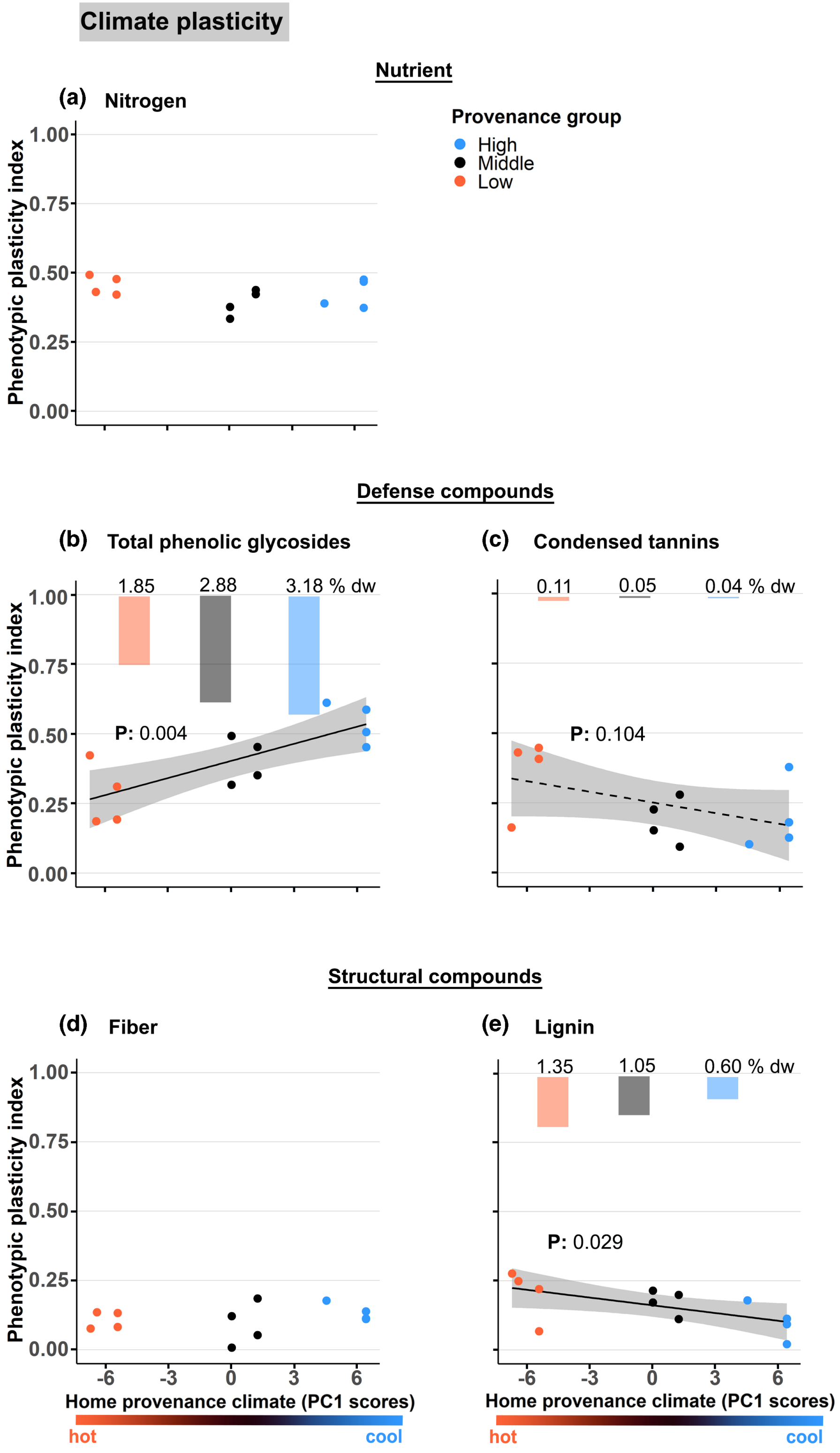

FIGURE 3 Relationships between climate plasticity (trait change across gardens) and the first axis from a principal component analysis explaining 71.5% of the climatic variation among home provenance climate characteristics. Climate plasticity of (a) leaf nitrogen, (b) total phenolic glycosides, (c) condensed tannins, (d) fiber, and (e) lignin are expressed as a phenotypic plasticity index. Each dot represents a mean plasticity response of a genotype using only control trees. For each genotype, phenotypic plasticity was calculated as the difference between the maximum and the minimum mean value of a metabolite measured in the three gardens divided by the maximum mean value of the metabolite. Gray areas represent 95% confidence interval bands. *p* values and trend lines are shown only for relationships with $p \leq .10$. Bars at the top of each panel represent the absolute difference (the actual difference in concentrations measured as % dry weight) between the maximum and minimum trait mean value among the three gardens, averaged over all genotypes within a provenance group. The vertical scale for these bars is consistent across all panels to show relative magnitude of plasticity across traits.

the moderate and cool gardens when compared with the hot garden, and garden explained almost 60% of the observed variation in nitrogen. Compared to garden and provenance interactions, the damage treatment added small effects on chemical traits (Figures 2 and 4; Table S1). The most pronounced treatment effects were found for condensed tannins. For high-elevation trees in the moderate climate garden, damage from simulated herbivory more than doubled the levels of condensed tannins (significant provenance × damage and garden × damage effects) (Figure 2c). This result supports our hypothesis (ii) of higher capacity for induced defenses in high-elevation genotypes. Damage minimally reduced the levels of nitrogen and affected phenolic glycosides in garden-specific ways (garden × damage interactions). Phenolic glycoside levels were 25% lower in damaged trees than in undamaged trees in the hot garden. In contrast, we

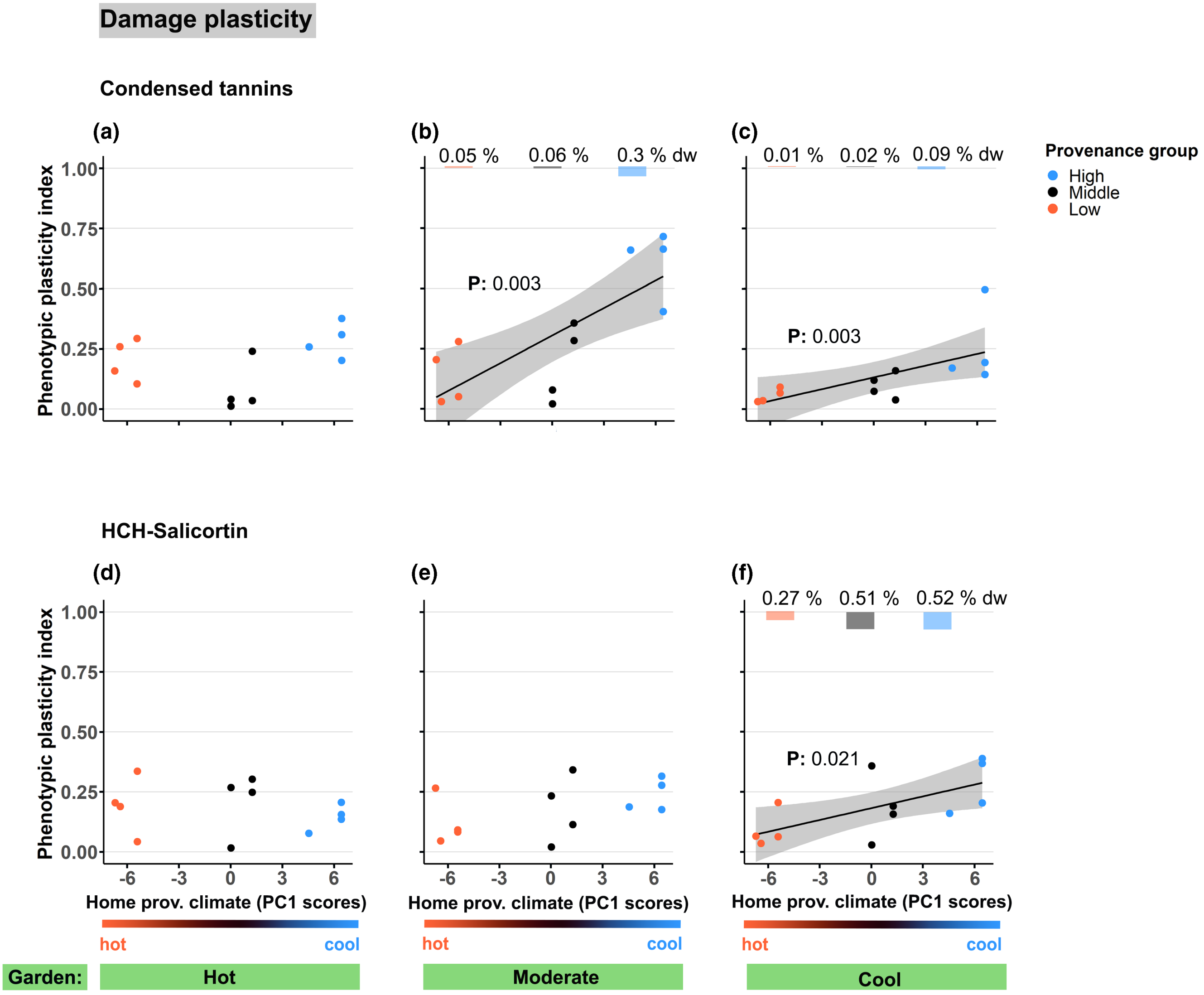

FIGURE 4 Relationships between plastic responses to leaf damage and jasmonic acid treatment and the first axis from a principal component analysis explaining 71.5% of the climatic variation among home provenance climate characteristics. Damage plasticity of condensed tannins in the (a) hot, (b) moderate, and (c) cool garden and HCH-salicortin in the (d) hot, (e) moderate, and (f) cool garden is expressed as a phenotypic plasticity index. Each dot represents a mean plastic response of a genotype assigned to a provenance group. For each garden and genotype, plasticity was calculated as the absolute difference between the damage and the control treatment means divided by the larger of the two treatment mean values. Gray areas represent 95% confidence interval bands. *p*-values and trend lines are shown only for relationships with $p \le .10$. Bars at the top of each panel represent mean absolute differences (the actual difference in concentrations measured as % dry weight) between undamaged and damaged trees, averaged over all genotypes within a provenance group. The vertical scale for these bars is consistent across all panels to show relative magnitude of plasticity across traits.

found only minimal changes (<5%) in phenolic glycoside levels between damaged and undamaged trees in the moderate and cool gardens.

Genotypic differences were important drivers of variation in phenolic glycosides but had only small effects on structural compounds (Figure 2d,e) and nitrogen (Figure 2a). Genotypic differences were particularly important for explaining total phenolic glycoside levels, accounting for over 20% of the variation in PGs observed across all factors (Figure 2b, effect size plot). When averaged across garden and damage treatments, genotypic differences in phenolic glycoside levels varied by twofold (Figure S2b). Interestingly, in the cases of total phenolic glycosides and fiber, we also found that genotypic variation within a provenance group was similar to or even exceeded among-provenance differences (Figure S2b,d).

3.2 | Importance of provenance climate for climate plasticity

Provenance climate affected the plastic responses to garden climate for total phenolic glycosides (Figure 3b) and lignin (Figure 3e), and marginally so for condensed tannins (Figure 3c). For phenolic glycosides in particular, trees from high-elevation provenances with the coldest climatic conditions showed plasticity scores nearly twice as high as trees from hot, low-elevation provenances (Figure 3). This supports our hypothesis (ii) that high-elevation genotypes would show higher phenotypic plasticity in response to climate as well as damage, and that changes in plasticity are related to provenance climate. Climate plasticity in total phenolic glycosides was driven by HCH-salicortin (p = .023), while salicortin and salicin showed no relationship between plasticity and home-provenance climate (data not shown). Lignin (Figure 3e) and condensed tannins (Figure 3c) showed smaller or non-significant effects, respectively, of provenance climate on plasticity across garden climates. The lignin effect contradicts our hypothesis (iii) that for structural compounds, genotypes from different elevation provenances should show similar plastic responses to climatic changes. The lignin effect was also in the opposite direction to that for phenolic glycosides, with trees from low-elevation provenances responding more strongly to garden climate than those from high-elevation environments.

3.3 | Impact of provenance climate on damage plasticity

As reported above, our hypothesis (ii) of higher induction in high-elevation genotypes was supported for both condensed tannins and phenolic glycosides (specifically HCH-salicortin) in the cool garden (Figure 4c,f). However, this greater capacity for induction was clearly limited to the moderate and the cool garden (Figure 4b,c,f). When grown under hot and dry conditions, there was no difference among provenances in their capacity for plastic responses to simulated herbivory (Figure 4a,d). Reduction of nitrogen levels in response to leaf damage (i.e., plastic responses) was equal among genotypes from different elevational provenances and in different gardens (Figure S3), supporting our hypothesis (iii) of limited population differentiation in the plasticity of non-defense compounds.

4 | DISCUSSION

Tree metabolites comprise important mechanistic linkages through which foundation tree species interact with, and influence, their environment (Jackrel et al., 2016; Whitham et al., 2006). Here we disentangle how garden climate and simulated leaf herbivory, as aspects of a tree's environment, interact with tree provenance and tree genotype to influence different phytochemical traits in Fremont cottonwood, an iconic foundation species. This study is one of the first to elucidate the interplay between abiotic and biotic stressors, tree provenance, and genotypic effects on various, functionally different phytochemical compounds.

Our results suggest that for many compounds, plastic responses to leaf damage and garden climate depend on the climate from which a population or genotype originates. An important outcome of our study is that trees from cool, high-elevation habitats showed stronger defense chemical responses to both abiotic and biotic environmental change than trees from hotter habitats. Trees from high-elevation provenances showed the highest plastic responses of total phenolic glycoside levels to variation in garden climate (Figure 3b). They also showed stronger induction from simulated herbivory (i.e., higher plasticity) of HCH-salicortin and condensed tannins than trees originating from low- and middle-elevation provenances (Figure 4). However, the capacity for induction was reduced under hot and dry climate conditions. Taken together, garden climate modulated defense strategies against leaf damage of cool-adapted trees. The latter relied on constitutively expressed defense compounds in hot environments and on plastic defense responses in cooler environments.

4.1 | Provenance effects: The evolution of inducible vs. constitutive chemical responses along climate gradients

Research on the relationship between elevational clines and chemical defenses has produced divergent results. Bakhtiari et al. (2019) reported that high-elevation *Cardamine pratensis* ecotypes showed stronger plastic responses in indole glucosinolate production to changes in growing climate than low-elevation *C. pratensis*. Similarly, Galmán et al. (2019) found that oak species adapted to cool, high-elevation environments showed stronger chemical defense induction upon feeding damage than trees from lower elevations. In contrast to induced defenses, however, constitutive defenses were lowest in high-elevation populations (Bakhtiari et al., 2019; Galmán et al., 2021). This contrast between high plasticity in high-elevation populations and high constitutive defenses in low-elevation populations is broadly consistent with our hypotheses and findings.

In studies comparing defense production across rather than within species, results have often been opposite. For example, Moreira et al. (2014) showed that pine species originating from high-elevation environments had higher constitutive defense levels than low-elevation species and the inducibility of direct defenses did not vary among high- and low-elevation pine species. Pellissier et al. (2016) reported that low-elevation *Cardamine* species showed higher inducibility of chemical defense than high-elevation species. Finally, several studies found no relationship between elevation and defense expression (reviewed in Carmona et al., 2020). Reasons for variation in the impact of elevation on plant defenses are unresolved and may relate to contrasting spatial and taxonomic scales among studies, differences in methodologies and traits, or the influence of abiotic factors that correlate with elevation (Carmona et al., 2020; Moreira et al., 2018). Alternatively, the inconsistency may simply reflect differences in responses among classes of secondary metabolites (Holopainen et al., 2018; Pellissier et al., 2016) or individualized responses among plant species.

The among-provenance differences observed in defense allocation patterns in our study align with two ecological and evolutionary expectations. First, predictable variation in environmental conditions should favor the evolution of adaptive phenotypic plasticity (Leung et al., 2020). In the context of climate stresses, this can lead to higher plasticity in populations from areas with a history of frequent, predictable exposure to different temperatures (Chevin & Hoffmann, 2017; Cooper et al., 2019). However, variation in climate occurs not only temporally but also spatially. Spatial heterogeneity in climate can increase with elevation (Rasmann, Alvarez, & Pellissier, 2014) and could select for greater ability of individuals to alter their phenotype in response to environmental changes (Baythavong & Stanton, 2010; Ernande & Dieckmann, 2004; Sultan & Spencer, 2002). Second, plastic defense responses (induction) are favored over constitutive strategies in environments of low or unpredictable herbivory (Karban, 2011; Mertens et al., 2021), such as high-elevation habitats (Galmán et al., 2018; Rasmann, Pellissier, et al., 2014). For example, Galmán et al. (2019) found that the inducibility of chemical defenses in oak is stronger in species with ranges that extend to high elevations.

In view of these two hypotheses, Fremont cottonwood trees adapted to high-elevation environments might optimize their fitness by allocating fewer resources to high constitutive defense levels and relying more on induced defense responses. This strategy allows plants to invest more resources in growth and reproduction, which can trade-off with defense production (Cole et al., 2021; Obeso, 2002; Züst & Agrawal, 2017). When growing in a warmer, low-elevation environment, however, having a high constitutive defense is beneficial as herbivore pressure tends to be high. Across the range of Fremont cottonwood studied here, the most common leaf herbivore (*Coptodisca* spp.) is most abundant at low-elevation populations (Bothwell et al., 2022).

In contrast to higher plasticity in chemical defenses, trees from high-elevation provenances showed the lowest climate-related plasticity in lignin (Figure 3e). However, trees from high-elevation provenances had the highest constitutive levels of fiber across all gardens. These among-provenance differences were especially large in the cool garden (Figure 2d). This result contradicts our hypothesis (iii) that plasticity and constitutive levels of fiber and lignin are not affected by provenance. Our results align with those of Rasmann, Pellissier, et al. (2014) who showed that constitutive levels of leaf toughness (a proxy for leaf fiber and lignin concentrations) in different tree species increase with elevation. Fiber and lignin are important for diverse biological functions (Liu et al., 2018) such as increasing leaf toughness and providing structural defense against herbivore and mechanical damage (Lucas et al., 2000). Lignin may also be relevant for cold acclimation (Liu et al., 2018) and UV protection (Sadeghifar & Ragauskas, 2020). Many of those functions are especially important in high-elevation habitats, suggesting that expression of high constitutive levels of fiber and lignin could be adaptive.

Leaf nitrogen levels were strongly affected by garden climate, and minimally affected by provenance, damage, and genotype (Figure 2a). These results support our hypothesis (iii), that genotypes from all elevation provenances show similar constitutive nitrogen levels and similar plastic responses to changes in climate or damage. The observed garden effects on nitrogen levels contrast the findings of a meta-analysis by Read et al. (2014) showing that leaf nitrogen concentration is not related to elevation-driven changes in temperature. However, our results align with previous research demonstrating that leaf nitrogen levels in Salicaceae species are strongly driven by environmental variation (Barker, Holeski, & Lindroth, 2019) but conserved across genotypes (Donaldson et al., 2006; Lindroth & Hwang, 1996). Our among-garden differences in leaf nitrogen levels may have been linked to environmental variation in Rubisco, the carboxylating enzyme of photosynthesis that comprises a large fraction of leaf nitrogen (Björkman, 1968; Hollinger, 1996). Generally, plants close their leaf stomata to minimize evaporation when experiencing arid conditions, as existed in our hot garden (Table 1; (Cornic & Massacci, 1996). Reduced photosynthesis eventually results in lower leaf Rubisco, and therefore nitrogen levels (Bota et al., 2004; Parry et al., 2002). Alternatively, the low foliar nitrogen concentrations in the hot garden may be related to the low soil nitrogen in that garden (Jeplawy et al., 2021).

4.2 | Environmental effects: Chemical defense strategies under novel stressors

Although genotypes from high-elevation provenances produced the lowest constitutive phenolic glycoside levels in their home conditions (cool garden), they increased these defenses with increasing garden temperatures (Figure 2b), to the point where they matched or exceeded all other genotypes in the hot garden. This result is consistent with our hypothesis (ii) that high-elevation genotypes not only show high phytochemical plasticity in response to damage, but also in response to changes in climate. Because populations from cold environments have higher survival in the cool garden and populations from hot environments have higher survival in the hot garden, we predict that trees growing in conditions most similar to their provenance climates are demonstrating more optimal trait strategies (Cooper et al., 2019). Plasticity that moves a foreign genotype's trait values closer to the local value is likely to increase fitness (Ghalambor et al., 2007).

Genotypes from high-elevation, cold provenances, however, appeared to lose their higher capacity to induce defenses following damage when grown in the hot garden (Figure 4). Thus, trees from cool environments were able to adjust some of their strategies in an adaptive direction but may have sacrificed some flexibility to do so. In the moderate garden, however, high-elevation trees were able to produce both elevated constitutive phenolic glycosides and the highest damage-caused inducibility in condensed tannins. This pattern could exist because a high level of chemical defense is optimal in these conditions, or because a more moderate climate shift relative to home conditions facilitated growth while providing more resources to invest in secondary metabolites (Monson et al., 2022). Climate-driven changes in defensive investments are particularly important to understand given that the southwestern US is predicted to experience increased warming, drought, and insect outbreaks in coming years (Gonzalez et al., 2018). Genotypes from colder provenances can adapt their defense strategy when experiencing climate warming. Rather than relying on induced defense responses in hot environments they invest in higher constitutive phenolic glycoside levels, thereby using the same defense strategy as well-adapted genotypes from low-elevation, hot provenances. This result suggests that trees from colder provenances may have unrecognized capacity to cope with potential increases in herbivore numbers in a warming climate.

4.3 | Genotypic variation within a provenance can equal among-provenance variation

Genetic variation underlying phenotypic differences can occur both among and within populations and climate regions, and all levels can be important for future adaptation and assisted migration. In previous work on *Populus*, genetic variation in defense compounds has been demonstrated at a range of scales, from within to across species and their hybrids (Barker, Holeski, & Lindroth, 2019; Eisenring et al., 2021; Holeski et al., 2012). Here, we found that in addition to genetic variation among provenances, genotypes within provenance groups also varied substantially in their levels of phenolic glycosides and condensed tannins (Figure S2b,c). In fact, for phenolic glycosides, condensed tannins and fiber, we found that phytochemical variation due to genotypic differences within a provenance equaled among-provenance variation (Figure S2b–d, Figure 2b–d). This result is important because it suggests that selection on genetically determined chemical traits could facilitate adaptation both across and within regions, with varying levels of natural or human-assisted dispersal.

4.4 | Implications for riparian ecosystems under climate change

Understanding the future persistence and phenotypic variation of foundation species is key to predicting the functioning of ecosystems in which they are imbedded. For foundation tree species, chemical traits are of particular importance. For example, intraspecific phytochemical variation in eucalyptus (*Eucalyptus globulus*) (Barbour et al., 2009), oak (*Quercus robur*) (Visakorpi et al., 2019) trembling aspen (*P. tremuloides*) (Barker et al., 2018; Barker, Riehl, et al., 2019), and Eurasian aspen (*Populus tremula*) (Robinson et al., 2012) can structure herbivore and fungal community composition. Variation in aspen (*P. tremuloides*, *P. tremula*) and oak (*Quercus laevis*) leaf litter chemistry can impact microbial community structure and soil nutrient dynamics (Kelly et al., 2010; Madritch & Hunter, 2002; Madritch & Lindroth, 2011; Winder et al., 2013). Chemical variation in *P. fremontii* and other cottonwood species also has well-documented implications for community structure and ecosystem processes (Whitham et al., 2006). For example, condensed tannin levels in cottonwood affect beaver preference, which can ultimately lead to changes in cottonwood stand compositions (Bailey et al., 2004; Whitham et al., 2006). Condensed tannin levels in cottonwood leaf litter also influence soil microbial communities (Schweitzer et al., 2006) and nitrogen mineralization (Schweitzer et al., 2004). Both condensed tannins and carbon to nitrogen ratios affect aquatic macroinvertebrate communities and leaf litter decomposition (Compson et al., 2013; Jeplawy et al., 2021; LeRoy et al., 2006). Finally, the phytochemical composition of cottonwood leaves drives foliar arthropod community composition (Bangert et al., 2006; Wimp et al., 2007) and affects avian foraging (Bailey et al., 2006).

We found that the effects of growing climate and simulated herbivore damage on Fremont cottonwood chemistry were highly variable across provenance zones and genotypes within this species. Importantly, our evidence that cooler-adapted trees may switch from induced to constitutive defense strategies under warming conditions may have important implications for riparian ecosystems of the southwestern US. These systems are increasingly confronted with above-average temperatures, drought events, and likely also insect outbreaks (Archer & Predick, 2008; Gonzalez et al., 2018). If these combined threats cause trees to produce higher levels of some defenses and lower levels of others, associated communities will likely experience structural and functional changes. Predicting changes in chemistry could provide an efficient way to predict higher-level community and ecosystem consequences of climate change. Results of this work thus help to both reveal fundamental constraints on plastic responses to multiple stressors, and plan for the restoration and conservation of tree genotypes that can sustain riparian ecosystems.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data on leaf chemistry and provenance climate data are available in the Dryad Digital Repository: https://orcid.org/10.5061/dryad.rn8pk0pd3.

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