DR. RICHARD L LINDROTH (Orcid ID : 0000-0003-4587-7255)

DR. ZACCHAEUS GREG COMPSON (Orcid ID : 0000-0003-2015-3015)

DR. REBECCA J. BEST (Orcid ID : 0000-0003-2103-064X)

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Title: Plastic responses to hot temperatures homogenize riparian leaf litter, speed decomposition, and reduce detritivores

Authors: Joann R. Jeplawy[1,2], Hillary F. Cooper[1,3,4], Jane Marks[3,5], Richard L. Lindroth[6], Morgan I. Andrews[1], Zacchaeus G. Compson[7], Catherine Gehring[3,4], Kevin R. Hultine[8], Kevin Grady[9], Thomas G. Whitham[3,4], Gerard J. Allan[3,4], Rebecca J. Best[1,10]

[1] School of Earth and Sustainability, Northern Arizona University, Flagstaff, AZ 86011, USA
[2] Tetra Tech, Inc., Denver, CO 80202, USA
[3] Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA
[4] Center for Adaptable Western Landscapes, Northern Arizona University, Flagstaff, AZ 86011, USA
[5] Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ 86011, USA

[6] Department of Entomology, University of Wisconsin-Madison, Madison, WI 53706

[7] Department of Biological Sciences, Advanced Environmental Research Institute, University of North Texas, Denton, TX, 76203, USA

[8] Department of Research, Conservation and Collections, Desert Botanical Garden, Phoenix, AZ, 85008, USA

[9] Department of Forestry, Northern Arizona University, Flagstaff, AZ 86011, USA

[10] Corresponding author. E-mail: rebecca.best@nau.edu

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ABSTRACT

Efforts to maintain the function of critical ecosystems under climate change often begin with foundation species. In the southwestern US, cottonwood trees support diverse communities in riparian ecosystems that are threatened by rising temperatures. Genetic variation within cottonwoods shapes communities and ecosystems, but these effects may be modified by phenotypic plasticity, where genotype traits change in response to environmental conditions. Here, we investigated plasticity in Fremont cottonwood (*Populus fremontii*) leaf litter traits as well as the consequences of plasticity for riparian ecosystems. We used three common gardens each planted with genotypes from six genetically divergent populations spanning a 12^{o}C temperature gradient, and a decomposition experiment in a common stream environment. We found that leaf litter area, specific leaf area, and carbon to nitrogen ratio (C:N) were determined by interactions between genetics and growing environment, as was the subsequent rate of litter decomposition. Most of the genetic variation in leaf litter traits appeared among rather than within source populations with distinct climate histories. Source populations from hotter climates generally produced litter that decomposed more quickly, but plasticity varied the magnitude of this effect. We also found that hotter growing conditions reduced the variation in litter traits produced across genotypes, homogenizing the litter inputs to riparian ecosystems. All genotypes in the hottest garden produced comparatively small leaves that decomposed quickly and supported lower abundances of aquatic invertebrates, whereas the same genotypes in the coldest garden produced litter with distinct morphologies and decomposition rates. Our results suggest that plastic responses to climate stress may constrict the expression of genetic variation in predictable ways that impact communities and ecosystems. Understanding these interactions between genetic and environmental variation is critical to our ability to plan for the role of foundation species when managing and restoring riparian ecosystems in a warming world.

Keywords: climate change, common gardens, decomposition, ecosystem function, foundation species, genotypes, phenotypic plasticity, riparian, stream ecology, subsidy, traits

INTRODUCTION

Predicting ecosystem-level responses to a rapidly changing climate is a major challenge for scientists and resource managers. Not only do species vary in their ability to tolerate change

(Hoffmann and Sgró 2011), but there is also intraspecific variation in the environmental tolerance of individuals and populations (Joshi et al. 2001, Kelly et al. 2012, Des Roches et al. 2018). Populations of widely distributed species that have experienced different environmental stresses and/or geographic isolation are expected to show substantial genotypic and phenotypic divergence (O'Neill et al. 2008, Ikeda et al. 2017). For example, multiple species of cottonwood trees (*Populus* spp.) native to riparian habitats of the American Southwest exhibit intraspecific variation in phytochemical, morphological, and phenological traits across their distributions (Grady et al. 2013, Evans et al. 2016, Cooper et al. 2019). Variation in these traits impacts not only the performance of the tree, but also the assembly of associated communities from microbes to insects (Marks et al. 2009, Whitham et al. 2012, Lamit et al. 2015), making genetic variation in habitat-forming foundation species a useful predictor of community and ecosystem processes (Schweitzer et al. 2004, LeRoy et al. 2007, Fischer et al. 2014). Thus, if we seek to understand ecosystem-level responses to climate change, we must first understand the responses of important foundation species and their traits.

Trait variation and diversity in riparian tree species such as cottonwoods may have particularly far-reaching effects because these trees shape and link both terrestrial and aquatic ecosystems. In forested stream reaches, riparian leaf litter drives nutrient cycling and dominates energy inputs (Fisher and Likens 1973). With a single cottonwood species producing over 90% of this input in some southwestern watersheds (Driebe and Whitham 2000), intraspecific variation in leaf litter quality can have important consequences for aquatic communities. Previous studies of genotypic variation in *Populus* litter from a single common garden have shown genetic effects on aquatic decomposition, macroinvertebrate communities, and transfer of carbon and nitrogen to higher trophic levels (LeRoy et al. 2007, Compson et al. 2016, 2018). For example, some genotypes produce litter with higher tannin concentrations, which decomposes more slowly (LeRoy et al. 2007, Compson et al. 2015). This slower decomposition facilitates the flow of energy to aquatic invertebrates rather than microbes (Marks 2019), leading to increased nitrogen assimilation and invertebrate growth rates in detritivores feeding on more recalcitrant *Populus* litter (Compson et al. 2018). Because of these different pathways for litter decomposition, local genetic diversity in litter characteristics can support diverse invertebrate communities or sustain the same invertebrates throughout their larval development (LeRoy and Marks 2006, Marks 2019). In turn, the abundance and diversity of invertebrates affects ecosystem functions such as the transfer of energy to higher trophic levels (Covich et al. 1999).

Although clear genetic differences among populations and genotypes have been demonstrated under uniform environmental conditions (Schweitzer et al. 2004, LeRoy et al. 2007, Whitham et al. 2012, Fischer et al. 2014), to understand whether these effects and their ecological consequences will persist under climate change we need to incorporate joint genetic and environmental effects (Madritch et al. 2006, Pregitzer et al. 2013, Cooper et al. 2019). Phenotypic plasticity, or the modification of trait expression by environmental cues (Scheiner and Goodnight 1984), allows organisms to respond to climate change more quickly than via evolutionary adaptation (Etterson and Shaw 2001, Davis et al. 2005, Franks et al. 2014). However, just like the traits themselves, plasticity in traits is often not uniform across a species range. Instead, populations that have experienced more regular heat stress throughout their evolutionary history are predicted to have higher temperature-related plasticity (Hendry 2016, Chevin and Hoffmann 2017). For example, Fremont cottonwood (*Populus fremontii* S. Watson) populations from hotter environments have higher plasticity in phenology than those from colder environments (Cooper et al. 2019). This variation in the magnitude of plasticity, also known as interactions between genetics (G) and environment (E) or GxE, may be common in species that span steep climate gradients. Predicting the prevalence and consequences of these interactions is key to predicting the community and ecosystem effects of such species (Patsiou et al. 2020).

To investigate whether genetic differences in leaf traits and their consequences for riparian ecosystems will persist or be altered under changing environmental conditions, we used a system of three common gardens containing the same genotypes of Fremont cottonwood and spanning a steep climate gradient. Both the source populations and the garden locations span over 12^{o}C difference in mean annual temperature, representing the full climatic range of this species (Fig. 1). This reciprocal transplant design allows us to both isolate genetic effects within a garden and assess the potential effects of climate change by using latitudinal and elevational variation in temperature as a proxy for future warming (Franks et al. 2014). We collected leaf litter from all three gardens and transplanted it to a common stream environment to quantify the effects of plasticity in litter characteristics on decomposition and colonization by a common pool of aquatic invertebrates. We tested three hypotheses: 1) Cottonwood leaf litter traits from divergent genotypes with different selection histories will be strongly impacted by genetic and environmental effects and by GxE interactions. 2) The magnitude of climate-induced trait plasticity will be higher in populations that have evolved with more exposure to heat stress. 3) Variation in litter traits will shape variation in community assembly and decomposition rates. Thus, if litter traits are shaped by GxE interactions, then decomposition rates and invertebrate community composition will also be shaped by GxE interactions.

METHODS

Study system and common gardens

Populus fremontii is native to the southwestern US and northern Mexico, but has been reduced to less than 3% of its historical range by habitat destruction and is already experiencing mortality due to heat and drought associated with climate change (Noss et al. 1995, Lower Colorado River Multi-Species Conservation Program 2004). To study environmental and genetic drivers of trait variation in this species, we used three common gardens established in 2014 across an elevational and latitudinal gradient. Mean annual temperatures (MAT) at the gardens are approximately 11, 17, and 23°C (located at approximately 1580, 990, and 50 m elevation, respectively) and all gardens receive regular watering throughout the growing season via flood or drip irrigation (Cooper et al. 2019, Hultine et al. 2020a). Each of the three gardens were planted with multiple genotypes from each of 16 populations collected throughout Arizona, with each genotype representing a single parent tree supplying replicate cuttings (clonal replicates) to all gardens.

For this study, we chose six populations with contrasting climatic origins along an elevation gradient (Fig. 1, see Appendix S1: Table S1 for population details). These six populations also cover the range of genomic variation found across all populations (based on >9000 RAD-seq loci, Cooper et al. unpub. data). Within each population we randomly selected four genotypes and three to four replicate trees for each genotype in each of the three gardens. Leaf litter was collected using whole-tree mesh nets, which catch natural leaf fall while avoiding colonization by decomposer communities from the local soil (LeRoy et al. 2007). Nets were set up before leaves changed color in fall of 2017 and litter was collected after all leaves had fallen from the tree. Litter was dry upon collection and stored at room temperature.

Litter traits

We measured leaf litter surface area, dry weight, specific leaf area (SLA), and carbon to nitrogen ratio (C:N) using 3-12 leaves (mean 11.2) from each tree. After weighing the dry-collected litter, we briefly immersed each in water to make them pliable, and then measured leaf area using a Leaf Scanner (model CI-203CA, CID Bioscience, Camas, WA, USA) or a flatbed scanner followed by image analysis in ImageJ (https://imagej.nih.gov/ij/). Leaf area was divided by dry weight to calculate SLA in mm^2/mg. For C:N, dry litter was ground using a Retsch Mixer Mill MM 200 (Retsch Inc., Newton, PA, USA) and analyzed at UW-Madison using combustion gas chromatography. To better understand variance in litter C:N, we also analyzed soil samples from the areas of each garden where litter was collected. Soil was collected in spring 2017 using an Oakfield soil sampler with a 4 cm diameter and 10 cm depth. Samples were transported in a cooler and within 24 hrs were homogenized, sieved through 2 mm mesh, and oven-dried for 48 h at 70 °C. Soil was analyzed for C:N at Northern Arizona University. For both litter and soil samples we used a Thermo Flash EA1112 elemental analyzer (Thermo Finnigan, Milan, Italy).

Field decomposition experiment

To measure genetic and environmental effects on the rate of litter decomposition and the community of invertebrates colonizing leaf litter, we used a total of 310 litter packs each holding 4 g of litter and placed in a natural stream environment. We used five replicates for each genotype grown in each garden (except three genotypes from the hot garden where lower litter availability reduced n to 1). For each pack we included litter from all replicate trees for that genotype grown in that garden. Because replicate trees varied in their litter production, we used the relative contribution by weight of each tree to each litter pack to calculate weighted averages of each litter trait. Packs were assembled using plastic mesh bags with 6 mm mesh size and attached in random groups of 12 packs to 1.2 m lengths of steel rebar.

Litter packs were placed in Oak Creek, a second order perennial stream near the center of the populations' range (Fig. 1) on March 11, 2018. The approximate mean annual air temperature at the site is 13.5°C, which is intermediate to the garden sites, and the average water temperature during the study period was 9.3°C. We ran the experiment in early spring to include a high diversity and abundance of shredders, which are important contributors to decomposition (Compson et al. 2015). After 26-28 days, samples were collected in a cooler and processed within 24 hours of collection. All invertebrates retained in a 250-µm mesh sieve were rinsed thoroughly with DI water and stored in 70% ethanol for identification to taxonomic order using a dissecting microscope (Leica S9, Germany). Because community identification required many hours per sample, we selected a subset of 227 litter packs representing all genotypes from four populations spanning the climate range, grown in each garden (KKH-OPI, PSA-SON, SCT-MEX, and LBW-BIL). Remaining leaf material from all 310 litter packs (7 to 35% of the initial mass) was rinsed and placed in a drying oven at 65°C for 24 hours, then weighed and ground. Samples were combusted at 550°C in a muffle furnace for 24 hours to determine ash-free dry mass (AFDM). AFDM of initial litter was estimated by regressing AFDM on dry mass for five handling packs, which were assembled and transported with the rest of the litter packs but were not placed in the creek. The slope from this regression was used to estimate AFDM for each pack from its dry mass. Decomposition was measured using the equation $L_f = L_i e^{-kt}$, where L_i is the AFDM of initial litter, L_f is the AFDM of remaining litter at time t, and k is the instantaneous decomposition rate constant (Benfield et al. 2017).

Statistical analysis

We used a linear mixed model (LMM) to test for the effects of genetics, growing environment, and their interaction (GxE) on each leaf trait and on decomposition rate. Ideally we would model all effects as random effects (Dingemanse and Dochtermann 2013, Arnold et al. 2019) to quantify the proportion of phenotypic variance attributable to G, E, and GxE (Scheiner and Goodnight 1984). However, with only three gardens, a random effect of environment would be very poorly estimated and is better modeled as a fixed effect with three levels (hot, mid, and cold). The remaining effects were coded as random effects, including population (six from throughout Arizona, Fig. 1), genotype (four nested within each population, 24 in total), population x environment, and genotype x environment. Both of the interaction terms are GxE interactions as both population and genotype are levels of genetic variation. Fortunately, models with only a single fixed effect can still be decomposed into the proportion of variance accounted for by that fixed effect vs. each random effect using R^2 metrics for mixed models (Nakagawa and Schielzeth 2013). Trait models used data from each tree, and decomposition models used data from each litter pack. Rebar group was also included as a random effect for the decomposition model. To compare the amount of variation in traits among populations and genotypes growing in each garden, we ran separate models for each garden with both population and genotype as random factors, and extracted the variance for both components. We also used LMMs to investigate the relationships between litter traits and decomposition, with random intercepts and slopes for each population.

Next, we tested whether the magnitude of trait plasticity depends on the climate stress of a population's home environment. For each trait, we calculated the mean value for each genotype in each garden, and quantified a genotype's plasticity as the difference between the max and min of these garden means (Cooper et al. 2019). We then tested whether plasticity values for each genotype could be predicted by the first axis (PC1) from a principal component analysis of seven temperature-related climate variables from Climate WNA (Wang et al. 2012), including mean annual temperature, temperature difference between warmest and coldest months, annual heat-to-moisture index, summer heat-to-moisture index, degree-days above 18^{o}C, extreme maximum temperature over a 30-year normal, and reference atmospheric evaporative demand. When regressing plasticity on the PC1 values for each population location, we accounted for the multiple genotypes within that population using a random effect.

Finally, we tested for G, E, and G x E effects on differences in aquatic invertebrate community assemblages in the litter packs using univariate and multivariate approaches. First, we calculated total invertebrate abundance and invertebrate diversity (Shannon's H'), evenness, and richness using order-level taxonomy for each litter pack. We then tested for G (population and genotype), E, and GxE effects on these metrics using the same LMM structure described for the leaf traits. Second, we used a distance-based redundancy analysis (dbRDA, Legendre and Anderson 1999) based on Bray-Curtis distances to test for G (population and genotype), E, and GxE effects on invertebrate community composition. To account for different amounts of remaining litter available, we included decomposition rate and rebar group as explanatory variables. We used indicator taxon analysis to determine if any invertebrate orders differentiated genotypes or growing environments.

We completed all analyses using R (R Core Team 2019). Mixed models were implemented using the *lmer* function in the *lme4* package (Bates et al. 2015). After checking residuals for normality and equal variance, we obtained p-values for fixed effects using Wald F tests with Kenward–Roger approximations for the denominator degrees of freedom using the *Anova* function in the *car* package (Fox and Weisberg 2011). Contrasts among levels of the fixed garden effect were tested using the *difflsmeans* function and the significance of random effects was tested using likelihood ratio tests in the *ranova* function, both in the *lmerTest* package (Kuznetsova et al. 2017). The dbRDA was implemented using the *capscale* function in the *vegan* package (Oksanen et al. 2016) and the indicator species analysis using the *indval* function in the *labdsv* package (Roberts 2013).

RESULTS

Leaf litter traits

In agreement with our first hypothesis, we found that leaf litter traits were shaped by genetic, environmental, and GxE effects, especially at the level of populations. Leaf area was strongly affected by growing environment (Fig. 2a), which explained over half of the total variance (Fig. 3a). Specifically, leaves grown in the hot garden were smaller than those grown in the mid or cold gardens ($p<0.001$ for both contrasts). However, the strength of this environmental response also differed by population (Fig. 2a, garden x population effect in Table 1). Within populations, neither genotype nor the genotype x garden interaction were significant.

For specific leaf area (SLA), populations again differed in the magnitude of plasticity (Fig. 2b, significant population x garden interaction in Table 1), overlaying effects of garden and population that again explained most of the variation (Fig. 3a). SLA values were lowest for leaves grown in the hot garden vs. the cooler gardens ($p<0.001$ for all pairwise garden contrasts), but higher for populations from hot origins vs. cold origins (Fig. 2b). Higher SLA corresponds to leaves that are thinner and often faster growing. As with leaf area, most genetic variation was at the population level, but the genotype x garden interaction was marginally significant (Table 1).

For leaf litter C:N, both levels of GxE interactions (population x garden and genotype x garden) were significant (Table 1), meaning that litter from different populations had different C:N ratios depending on the garden in which it was grown, as did litter from different genotypes within those populations. There was also a significant garden effect: C:N values were higher for leaves grown in the hot garden than either of the other two gardens ($p<0.004$, Fig. 2c). This may be partially explained by higher soil C:N in the hot garden (Appendix S1: Fig. S1). However, soil C:N was not the only driver of litter C:N because the mid and cold gardens also differed in their soil C:N (which was lowest in the mid elevation garden) but not in their litter C:N. There was no correlation between the soil C:N and leaf litter C:N sampled from corresponding plot locations within the gardens. When grown in the cold garden where traits were more variable, populations from colder climates generally produced leaves with a higher C:N ratio than those from hotter climates (Fig. 2c). Leaf chemistry was also related to leaf morphology, with high SLA (thinner) leaves having lower C:N values ($p<0.001$, $R^2=0.396$).

Predictability of variation in leaf traits

For our second hypothesis, we expected that populations sourced from hotter and drier locations would exhibit higher climate-related plasticity. Combining seven temperature-related climate variables in a PCA produced a PC1 axis that explained 73% of the variation, where positive values of the axis correspond to higher mean annual temperature, annual and summer heat-to-moisture index, degree-days above 18°C, extreme maximum temperature over a 30-year normal, and reference atmospheric evaporative demand (Appendix S1: Table S2). We found that populations from locations with higher heat stress had higher plasticity in C:N ($p=0.023$, $R^2m=53\%$). For leaf area and SLA, however, there was no relationship between PC1 and the plasticity scores ($p>0.1$, Appendix S1: Fig. S2).

Whereas population source climate predicted leaf trait plasticity in only one trait, growing environment had strong and predictable effects on both mean trait values and trait variation within a location. Trait variance across both genotypes and populations was always highest in the cold garden and usually lowest in the hot garden (Fig. 3b, Levene Test for equal variance across gardens $p<0.009$ for all leaf traits). Thus, growing environment itself had a large effect on trait predictability or diversity within and across populations.

Decomposition

Variation in leaf litter morphology and chemistry had predictable effects on rates of aquatic decomposition. Across all populations, decomposition declined with increasing leaf area and increasing C:N (lower nutrient content and/or more structural tissue, Fig. 4). Interestingly, the average decomposition rate and C:N were both higher in leaves from the hot garden, counter to the overall negative relationship. This may be due to the very small size of these leaves (rather than their C:N) driving faster decomposition.

Parallel to these underlying traits, aquatic decomposition rates were strongly affected by an interaction between population and garden (Fig. 2d, Table 1), as well as a significant garden effect. Leaves grown in the hot garden decomposed more quickly on average than those from other gardens ($p<0.017$). Consistent with our findings for leaf traits, litter from the cold garden had by far the greatest variation in decomposition rates among and within populations (Fig. 3b). Finally, litter produced by populations from colder origins decomposed more slowly than litter from hotter populations (Fig. 2d). Accounting for garden as a covariate, a population's average decomposition rate increased with the mean annual temperature at its origin (p=0.01).

Aquatic invertebrate community assembly

Whereas GxE interactions significantly affected all litter traits, invertebrate communities were shaped by additive effects of garden and population. We found 30-40% fewer invertebrates on litter sourced from the hot garden (Fig. 5a, Table 1), and this total abundance was not related to the amount of litter remaining in the packs at the end of the experiment (Appendix S1: Fig. S3). We identified 13 different taxonomic orders of invertebrates (Appendix S1: Table S3), with lower diversity on litter from the mid elevation garden (Fig. 5b). We also found that multivariate community composition differed among litter packs from the three gardens (p=0.001, Fig. 5c), and among litter packs from different populations (p=0.004), and was related to decomposition rate (p=0.007). There was no interaction between garden and population (p=0.14). Testing the nine invertebrate orders found in at least 5% of the litter packs for their value as indicators, we found that litter from the mid-elevation garden had a higher relative abundance of Diptera (true flies, p=0.001), whereas litter from the cold garden was colonized by higher relative abundances of Trichoptera (caddisflies, p=0.004) and Hygrophila (snails, p=0.007).

DISCUSSION

Phenotypic plasticity is predicted to play an important role in the survival of plant species under climate change (Matesanz et al. 2010, Wang et al. 2010, Reed et al. 2011, Franks et al. 2014), but we know much less about the consequences of plasticity for species interactions and ecosystem processes (Crutsinger 2016, Turcotte and Levine 2016). Here, we found that leaf litter traits were strongly affected by GxE interactions, which translated into GxE effects on decomposition. Although these interactions complicate our understanding of ecosystem-level responses to a changing climate, some important and novel predictions arise from this work. These include effects of population source climate on both average decomposition rates and the magnitude of plasticity in some traits, and effects of growing environment on the diversity of litter trait values and the composition of aquatic detritivores.

Environmental and genetic determinants of leaf traits

Whereas hotter growing conditions produced leaves that were smaller and thicker (lower SLA values), trees from hotter populations tended to make leaves that were smaller and thinner (at least in the hot and cold gardens, Fig. 2). For leaf size, these effects of current growing environment (garden) and home environment (source population) were in the same direction, and agree with detailed physiological research at the mid-elevation garden showing that smaller leaves contribute to increased midday thermal regulation (Hultine et al. 2020b). Smaller leaf size in hotter populations is also consistent with global interspecific variation, as plant species from hot and dry environments tend to have smaller leaves (Wright et al. 2017). Interestingly, our finding that hotter populations made smaller leaves than colder populations in all gardens is different from some previous work on Fremont cottonwood. Using several lower elevation populations in a garden with similar temperature to our hot garden but higher growth rates (possibly due to higher rates of watering reducing temperature stress), Grady et al. (2013) found no difference in leaf size among populations. This may be due to the smaller elevational range of populations studied and/or the fact that higher climate stress can reveal trait variation among populations that is not evident under less stressful conditions (Akman et al. 2021).

For SLA, the direction of plastic response to hotter climate contrasts with the direction of genetic responses (i.e., population adaptations to hotter climates), as one recent study on sedges also found (Walker et al. 2019). The low SLA (thicker leaves) produced in the hot garden is consistent with traits of species found in hot and dry conditions (Givnish 1987, Boyero et al. 2017), and could be related to moisture retention. Alternatively, if leaves continue to accumulate carbon and mass throughout the season, lower SLA could also be a consequence of the 1 to 2.5 months longer growing season in the hot southern garden than the cold northern garden (Cooper et al. 2019). In contrast, within a garden the populations from hot climates produced the highest SLA (thinnest leaves). Higher SLA is an adaptation to faster growth and lower leaf life span with lower investment in structural defenses (Cornelissen et al. 1999, Wright et al. 2004), and could reflect the potential for higher growth in hot climates as long as plants have sufficient water available to cope with extreme temperatures. This pattern of variation in SLA among gardens and populations has also remained consistent as the trees have continued to age, with leaves collected in 2019 and 2020 showing the same effects and relative SLA values across populations and gardens (Best et al. unpub. data). Further research to determine whether contrasting SLA patterns across populations vs. environments are due to water availability or growing season length could help strengthen predictions about the role of plasticity in altering the traits of local vs. foreign genotypes under warming conditions.

In addition to effects of population and garden, interactions between the two contributed to all leaf traits, and especially C:N (Table 1, Fig. 3a). This is consistent with one of the few other multi-common garden studies on tree leaf chemistry, which also found genotype by garden interactions in *Populus angustifolia* leaf tannins, possibly related to variation in soil characteristics (Pregitzer et al. 2013). Importantly, most of the interaction between genetics and growing environment in our study was at the level of population rather than genotype. This result suggests that variation in the magnitude of plasticity across the range of Fremont cottonwood reflects population differences in selection pressures, rather than random genotype differences. Differences in regional environments are clearly linked to ecotype formation in this species, with three different ecotypes identified across its range in the US (Ikeda et al. 2017), and significant differences in local climate across elevation and latitude gradients have resulted in local adaptation within ecotypes (Grady et al. 2011, 2015).

Trait determinants of litter decomposition

The morphological and chemical composition of leaf litter is a major determinant of decomposition, with slow-decomposing litter often having high C:N and high lignin, making it less digestible for detritivores (Cornwell et al. 2008). Our results are consistent with these predictions: after accounting for garden effects, litter with higher C:N decomposed more slowly (Fig. 4b). In this case C:N was itself likely influenced by both climate and soils. High C:N of litter in the hot garden corresponded to high soil C:N in that garden, but there was no relationship between soil and litter C:N within gardens or across the mid and cold gardens, where soil C:N was less variable and litter C:N was much more variable (Appendix S1: Fig. S1). Because soil nutrients can impact the production of multiple defensive compounds with effects on decomposition (Jackrel and Morton 2018), the interaction between climate change and soil fertility as environmental drivers of plasticity is an important area for further research.

Besides C:N, we also found that leaf area can play an important role in speeding or slowing decomposition. (Fig. 4a). Variation in leaf size is associated with structural modifications of leaves, with larger leaves generally investing disproportionately more mass into the mid-rib compared to small leaves (Niinemets et al. 2007). This greater investment in structural tissue could slow decomposition rates and explain why the much smaller leaves produced in the hot garden by all populations decomposed more quickly despite their high C:N. This also implicates climate differences across the gardens as the major driver of faster decomposition rates for litter from the hot garden, rather than low soil fertility. In fact, if the hotter temperatures at low elevation were coupled with higher soil fertility (lower C:N), then our results would predict that these small and more palatable leaves would have decomposed even more quickly.

Predicting genetic effects: trees from hotter and drier climates make litter that decomposes more quickly

Interactions between source populations and growing environment mean that the same genotypes will not produce litter with consistent traits across a range of environmental conditions. To address this, we need to predict not only mean differences among genotypes, but also differences in their plasticity, or sensitivity to growing conditions. One option is to test whether we can expect higher plasticity in populations from more stressful or more predictably variable past conditions (Hendry 2016, Chevin and Hoffmann 2017). Previous work in this system has found that plasticity in phenological traits is higher for populations from warmer and drier climates (Cooper et al. 2019). Here, we found that this pattern held for C:N but not the other litter traits measured in this study (Appendix S1: Fig. S2).

Perhaps more importantly, despite GxE interactions in all traits and in decomposition itself, we still found that through a combination of leaf area, SLA (thickness), and C:N, populations from warmer climates tended to make litter that decomposed more quickly than litter from colder populations regardless of growing environment (Fig. 2d). This has serious implications for restoration because it suggests that preferentially planting hot-adapted trees to increase future survival (Grady et al. 2011, Butterfield et al. 2017) could impact a major ecosystem process in riparian ecosystems. Faster decomposition can facilitate rapid uptake of carbon by microorganisms, reducing carbon assimilation by invertebrates (Compson et al. 2018, Siders et al. 2018, Marks 2019). Genotypes from hot origins should thus promote faster cycling of energy into aquatic systems and lower abundance of aquatic invertebrates, which could translate into reduced support of predators like fish and birds. This faster decomposition could be particularly problematic if climate stress also leads to lower total leaf production (Hultine et al. 2020a). Cottonwood litter productivity varies among genotypes and has major impacts on aquatic ecosystems (Rudman et al. 2015); the combination of less litter and less persistent litter would support substantially less biodiversity at higher trophic levels.

Predicting environmental effects: reduced trait variation and invertebrate communities

Growing environment had a dominant effect on both mean leaf trait values and aquatic invertebrate abundance, consistent with previous common garden studies on terrestrial arthropod communities colonizing plants (Johnson and Agrawal 2005, Barbour et al. 2019). In addition to mean leaf trait values, we also found environmental effects on trait variance. Depending on the trait and its selection history, higher climate stress can either amplify or compress trait variation among populations (Akman et al. 2021). This has ecosystem consequences because the diversity in the traits of locally produced and available litter can affect both decomposition and invertebrate communities (LeRoy and Marks 2006, Raffard et al. 2019). Our study did not manipulate litter diversity within an individual litter pack, but we did find that the trait diversity of litter produced in the hot garden was constricted across populations (in all traits) and genotypes (especially in leaf area). This means that litter was more homogeneous in this garden than that produced by the same populations and genotypes grown in colder conditions (Fig. 3b). Invertebrates feeding on the consistently faster-decomposing litter grown in the hot garden were also consistently lower in abundance (Fig. 5), which is consistent with less available energy for invertebrates in highly labile litter (Marks 2019).

For the multivariate community composition of aquatic detritivores, we found effects of both garden and source population. Compositional differences across growing conditions were partly due to dominance of Diptera larvae in the lower diversity communities associated with litter from the mid-elevation garden. Finer taxonomic identifications within this group would of course reveal substantial unquantified diversity, but within rather than across deep evolutionary lineages. These different patterns of phylogenetic diversity could correspond to different levels of functional diversity in some (but certainly not all (Poff et al. 2006)) invertebrate traits related to their habitat use and feeding modes For example, there are certainly multiple feeding modes within the Diptera in this system, but few if any species are likely to be as effective shredders as the larger Trichoptera (caddisflies), which were associated with the litter grown in the cool garden. Because the litter from this garden decomposed at a range of rates despite having more effective shredders, this again suggests an important role for leaf traits in determining both detritivore community composition and the rates at which those same communities can process litter. The prevalence of more Trichoptera on litter from the cold garden is also interesting given the association of these species with cold stream conditions (Hershey et al. 2010). It is possible for species sorting or local adaptation to cause an invertebrate community to prefer local litter characteristics (Jackrel and Wootton 2014), so that invertebrates in a colder location could prefer litter typical of colder locations. However, there was no evidence that Trichoptera were associated with litter from colder populations, only the colder garden.

As a riparian foundation species, Fremont cottonwood and its extended phenotypic effects on dependent communities can be wide-reaching (Whitham et al. 2012). Our study is the first to integrate genetic effects of source populations representing the breadth of a species' climatic range with simulated climate change to examine the consequences of warming temperatures for the transfer of energy in riparian ecosystems. We found that both selecting warm-adapted source populations for riparian restoration and future increases in growing temperatures regardless of source identity should result in more homogenously labile inputs from terrestrial to aquatic systems, and lower abundances of invertebrates at the base of aquatic food webs. Our results highlight that future rates of litter decomposition by microbes and invertebrates will depend not only on increasing water temperatures (Boyero et al. 2011, Follstad Shah et al. 2017), but also changes in litter quality resulting from changes in growing temperatures.

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

Additional supporting information may be found online at: [link to be added in production]

OPEN RESEARCH

Data (Jeplawy et al. 2021) are available in the Dryad digital repository: https://doi.org/10.5061/dryad.31zcrjdkh.

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Table 1. Results from linear mixed model (LMM) analyses of genetic, environmental, and GxE interaction effects on leaf litter traits, decomposition rates, and aquatic invertebrate community abundance and diversity. Significant p-values (<0.05) shown in bold. See Fig. 3 for relative explanatory power of all effects. All models returning random effect p-values of 1.0 were also run without those effects and conclusions were the same. Total abundance was log-transformed for analysis.

	Fixed		***Random***			
	Garden		***Population***	***Genotype***	***Population x Garden***	***Genotype x Garden***
Response	*F(df)*	*p-value*	*p-value*	*p-value*	*p-value*	*p-value*
Litter						
Leaf Area	$F_{(2, 9.99)} = 53.7$	**<0.001**	0.24	1.0	**0.004**	0.502
SLA	$F_{(2, 9.99)} = 87.4$	**<0.001**	**0.007**	1.0	**<0.001**	*0.054*
C:N	$F_{(2, 9.99)} = 9.8$	**0.004**	0.87	1.0	**<0.001**	**0.026**
Decomposition	$F_{(2, 10.05)} = 4.7$	**0.036**	0.26	0.061	**0.026**	1.0
Inverts						
Shannon's H'	$F_{(2, 6.78)} = 5.9$	**0.033**	1.0	1.0	1.0	1.0
Richness	$F_{(2, 6.63)} = 5.1$	**0.046**	1.0	1.0	1.0	1.0
Evenness	$F_{(2, 6.69)} = 7.8$	**0.018**	0.69	1.0	1.0	1.0
Abundance	$F_{(2, 7.11)} = 10.2$	**0.008**	0.63	1.0	0.070	1.0

FIGURE CAPTIONS

Fig. 1. Locations of Fremont cottonwood common gardens, source populations, and litter pack experiment location in Oak Creek. Mean annual temperature (MAT) data in the basemap are from WorldClim 2 (Fick and Hijmans 2017). Populations are colored on a relative scale of increasing MAT from blue to red (for population elevations, MAT values, and locations see Appendix S1: Table S1).

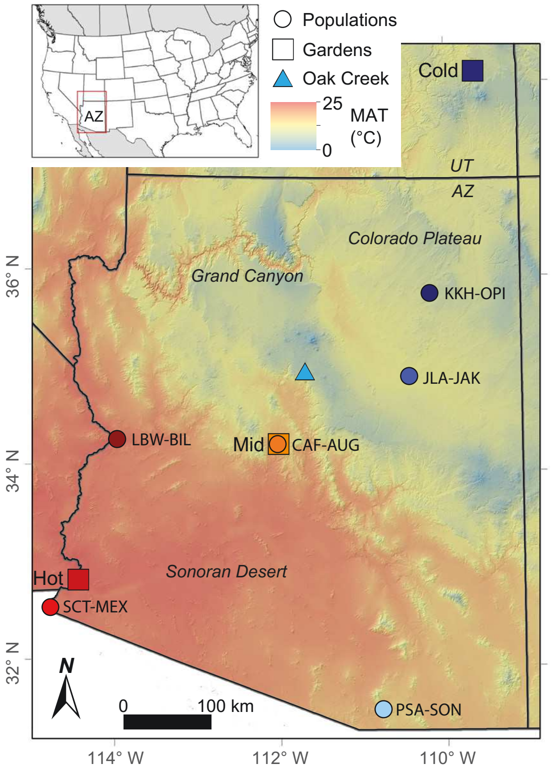
Fig. 2. Population means for (a) leaf area, (b) specific leaf area, (c) C:N, and (d) aquatic decomposition rates across the three common gardens. Each line represents the average of trees from four genotypes in that population; error bars are +/- 1 Standard Error.

Fig. 3. Variance in leaf traits explained by environmental, genetic, and GxE effects. a) Proportion of variance explained by each factor in the linear mixed model (LMM) for that trait, with variance for garden (the only fixed effect) estimated by $R^2_{m(arginal)}$. b) Variance in genetic factors within each garden, shown as a proportion of the maximum value for that trait.

Fig. 4: Average genotype decomposition rate predicted by leaf area, C:N, and growing environment. (a) For leaf area, the effect on decomposition was garden-specific (interaction $p=0.009$). (b) For C:N, effects were additive between C:N ($p=0.0002$) and garden ($p<0.0001$). $R^2_{m(arginal)}$ is the proportion of variance due to all fixed effects in the linear mixed model.

Fig. 5: Effects of growing conditions on (a) total abundance (# of individuals per litter pack), (b) diversity, and (c) composition of aquatic invertebrate communities colonizing leaf litter. In (a) and (b), * indicates a significant difference according to linear mixed models; error bars are +/- 1 Standard Error. In (c), each point represents the average invertebrate community (assessed using distance-based redundancy analysis, db-RDA) associated with leaf litter from one garden. See Appendix S1: Fig. S4 for a leaf-pack-level plot. Ellipses and error bars approximate 95% confidence intervals for the means (error bars are +/- 2 Standard Errors). Arrows indicate relative differences between the different taxonomic orders of invertebrates, and significant indicator species are highlighted with illustrations.

Figure 1



AZ
Populations
Gardens
Oak Creek
25
0
MAT (°C)
Cold
UT
AZ
Colorado Plateau
Grand Canyon
KKH-OPI
JLA-JAK
LBW-BIL
Mid
CAF-AUG
Hot
Sonoran Desert
SCT-MEX
N
0
100 km
PSA-SON
36° N
34° N
32° N
114° W
112° W
110° W

Figure 2

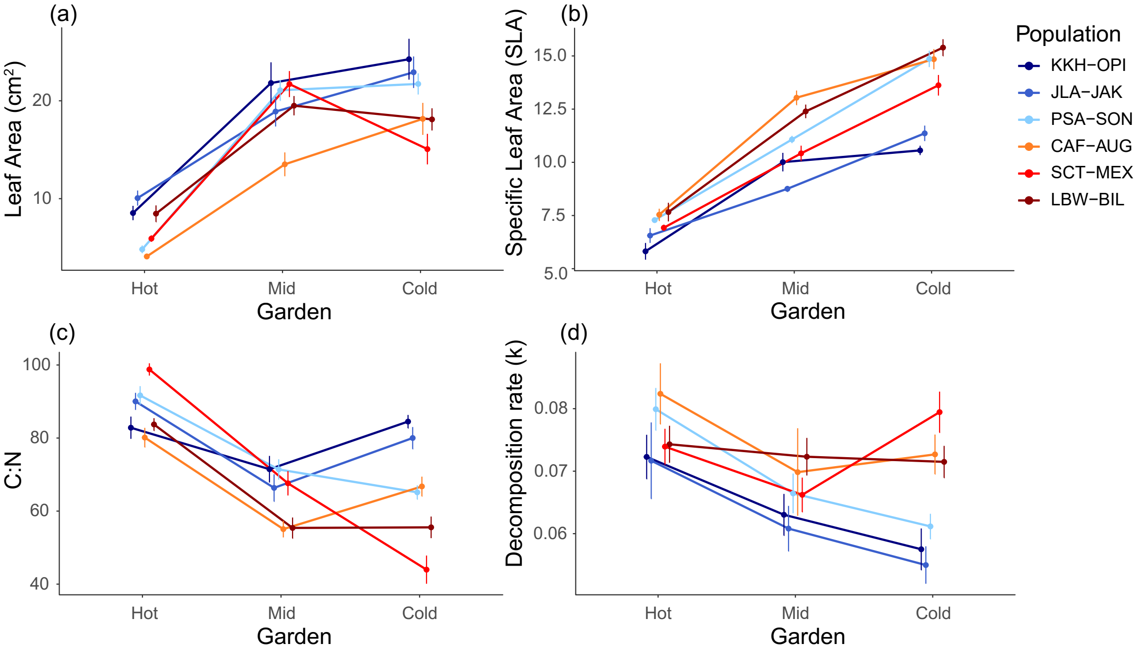

(a)
Leaf Area (cm^2)
10
20
Hot
Mid
Cold
Garden
(b)
Specific Leaf Area (SLA)
5.0
7.5
10.0
12.5
15.0
Hot
Mid
Cold
Garden
Population
KKH−OPI
JLA−JAK
PSA−SON
CAF−AUG
SCT−MEX
LBW−BIL
(c)
C:N
40
60
80
100
Hot
Mid
Cold
Garden
(d)
Decomposition rate (k)
0.06
0.07
0.08
Hot
Mid
Cold
Garden

Figure 3

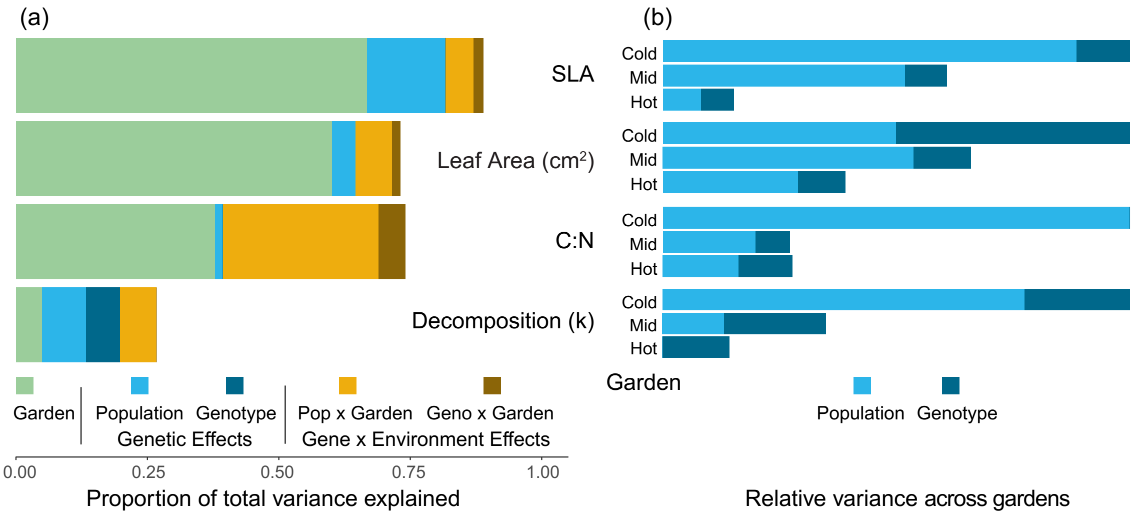

(a)
SLA
Leaf Area (cm²)
C:N
Decomposition (k)
Garden
Population
Genotype
Pop x Garden
Geno x Garden
Genetic Effects
Gene x Environment Effects
0.00
0.25
0.50
0.75
1.00
Proportion of total variance explained
(b)
Cold
Mid
Hot
Garden
Population
Genotype
Relative variance across gardens

Figure 4

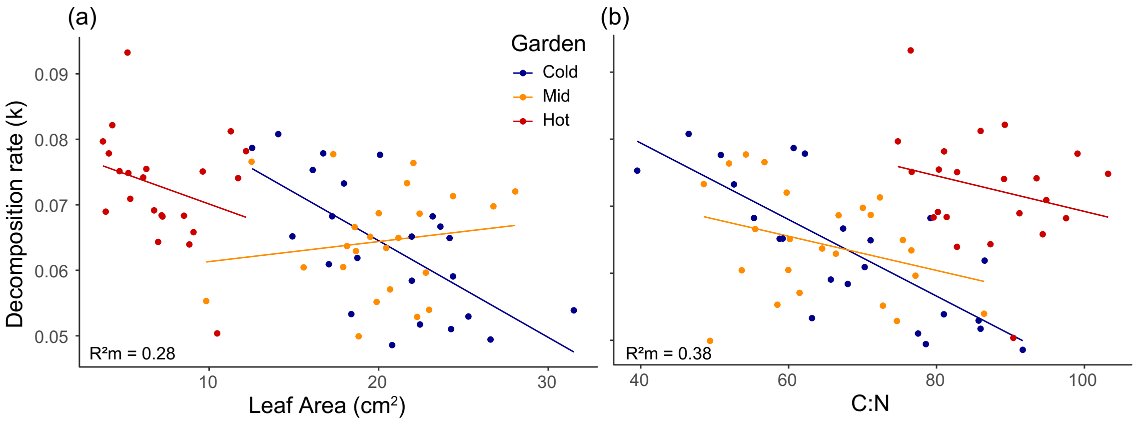
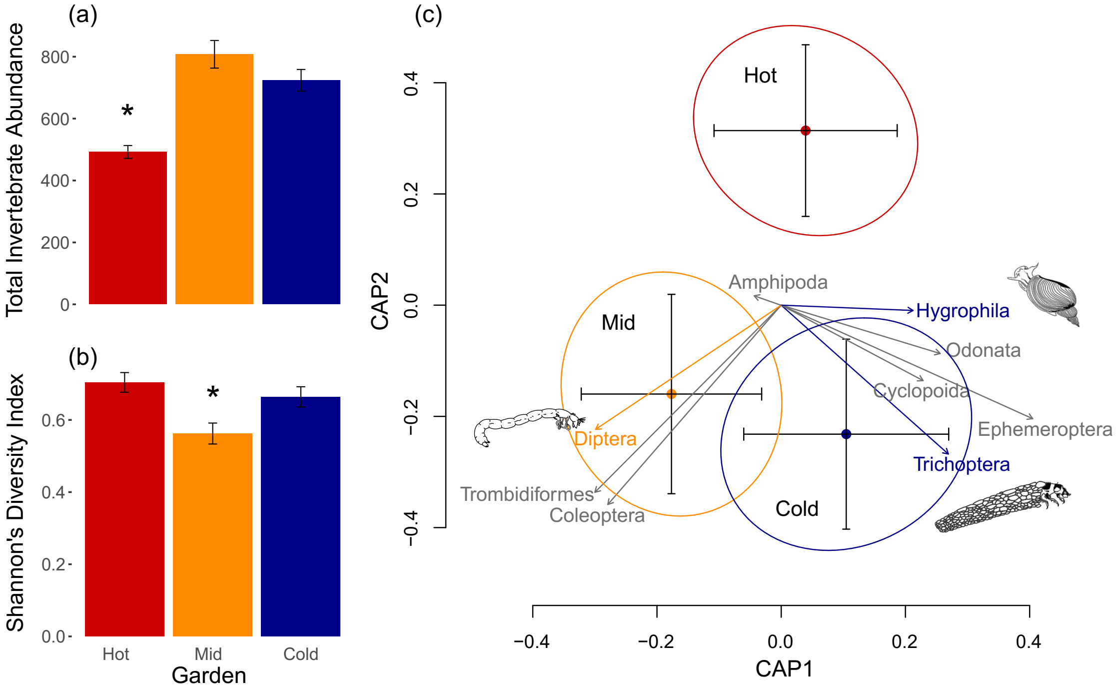

(a)
(b)
Decomposition rate (k)
0.09
0.08
0.07
0.06
0.05
Garden
Cold
Mid
Hot
R²m = 0.28
10
20
30
Leaf Area (cm²)
R²m = 0.38
40
60
80
100
C:N

Figure 5


(a)
Total Invertebrate Abundance
800
600
400
200
0
*
(b)
Shannon's Diversity Index
0.6
0.4
0.2
0.0
*
Hot
Mid
Cold
Garden
(c)
CAP2
0.4
0.2
0.0
−0.2
−0.4
Hot
Mid
Cold
Amphipoda
Hygrophila
Odonata
Cyclopoida
Ephemeroptera
Trichoptera
Diptera
Trombidiformes
Coleoptera
−0.4
−0.2
0.0
0.2
0.4
CAP1