Plasticity drives geographic variation and trait coordination in blue oak drought physiology

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Abstract

Two decades of widespread drought-induced forest mortality events on every forested continent have raised the specter of future unpredictable, rapid ecosystem changes in 21st century forests. Yet our ability to predict drought stress, much less drought-induced mortality across the landscape remains limited. This uncertainty stems at least in part from an incomplete understanding of within-species variation in hydraulic physiology, which reflects the interaction of genetic differentiation among populations (ecotypic variation) and phenotypic plasticity in response to growth environment. We examined among-population genetic differentiation in a number of morphological and hydraulic traits in California blue oak (*Quercus douglasii*) using a 30 year old common garden. We then compared this genetic trait differentiation and trait-trait integration to wild phenotypes in the field from the original source populations.
We found remarkably limited among-population genetic differentiation in all traits in the common garden, but considerable site-to-site variation in the field. However, it was difficult to explain trait variation in the field using site climate variables, suggesting that gridded climate data does not capture the drivers of plasticity in drought physiology in this species. Trait-trait relationships were also considerably stronger in the field than in the garden, particularly links between leaf morphology, leaf hydraulic efficiency and stem hydraulic efficiency. Indeed, while twelve of 45 potential trait-trait relationships showed significant wild phenotypic correlations, only four relationships showed both genetic and phenotypic correlations, and five relationships showed significantly different genetic and phenotypic correlations. Collectively, our results demonstrate limited ecotypic variation in drought-related physiology but considerable geographic variation in physiology and phenotypic integration in the wild, both driven largely by plasticity.

Introduction:

In the 21st century, trees living in a hotter, more variable and often drier world will need to acclimate or adapt to avoid local extirpation, or shift their geographic ranges through multi-generational migration. Recent drought- or heat-induced forest mortality events highlight the vulnerability of even highly drought-adapted forests to climate change (Allen *et al.* 2010; Brodribb *et al.* 2020; Hammond *et al.* 2022). Mass tree die-offs also illustrate the potential for extremely rapid ecosystem changes in a warming world, which have profound ecological consequences and impacts on human society (Anderegg *et al.* 2012). Unfortunately, despite multiple decades of concerted effort to understand the causes of drought-induced forest mortality, we still struggle to predict when and where trees will die off during drought (Trugman *et al.* 2021).

Part of the large uncertainty about drought vulnerability is a poor understanding of physiological variation within species (Trugman *et al.* 2021). Within-species variation can be substantial (Martinez-Vilalta *et al.* 2009; Mclean *et al.* 2014; Anderegg *et al.* 2021), can decrease climate vulnerability in some populations (Laforest-Lapointe *et al.* 2014; Garcia-Forner *et al.* 2016), and can differ between co-occurring species (Anderegg & HilleRisLambers 2016). Drought resistance is the complex result of numerous plant traits, all of which potentially vary across populations within a species. A key drought tolerance trait, namely xylem resistance to embolism, often shows limited among-population variation in conifers (Lamy *et al.* 2013) and angiosperms (Skelton *et al.* 2019). But morphological characteristics, for example high leaf mass per area (LMA) and high leaf dry matter content (LDMC) may indirectly allow plants to maintain function under increasingly negative water potentials during drought (Lamont *et al.* 2002; Poorter *et al.* 2009; Bartlett *et al.* 2012). Meanwhile, shifting allocation to different tissues, for example decreasing leaf area to sapwood area ratio (A_L:A_S), and increasing tissue-specific hydraulic efficiency can help plants avoid drought stress by minimizing the water potential drop required to maintain transpirational flux (Gleason *et al.* 2013; Mencuccini *et al.* 2019). Across species, coordinated physiological strategies or trait syndromes lead to correlated variation across many of these traits (Reich *et al.* 2003; Chave *et al.* 2009; Mencuccini *et al.* 2015; Sanchez Martinez *et al.* 2020). However, within individual species, these broad evolutionary trait-trait correlations often break down (Anderegg *et al.* 2018; Messier *et al.* 2018; Rosas *et al.* 2019). Consequently, both the total amount of within-species variation in drought resistance-related traits and the key physiologic axes that drive spatial variation in drought resistance remain poorly understood.

Possibly more important than the total amount of within-species variation are the drivers of this variation. Intraspecific variation can arise from two distinct processes with drastically different implications for near-term climate responses. First, spatio-temporal variation in environmental selection on heritable fitness-related phenotypes can lead to genetic differentiation among populations and local adaptation of functional traits (traits that mediate plant performance in a given environment) (Alberto *et al.* 2013). Substantial geographic variation in drought physiology due to local adaptation would imply that certain populations or genotypes (and not others) are drought resistant and that gene-flow (assisted or natural) is necessary for other populations to manifest improved drought resistance (Hoffmann *et al.* 2021). Local adaptation is widespread in plants, particularly species with large population sizes (Leimu & Fischer 2008; Savolainen *et al.* 2013). Indeed, provenance trials or common gardens (where multiple populations of a species are planted in a common environment) almost always detect genetic differentiation among populations in trees (Alberto *et al.* 2013; Ramírez-Valiente *et al.* 2022) and landscape genetic/genomic approaches often reveal evidence for local adaptation (Savolainen *et al.* 2013; Capblancq *et al.* 2020; Gugger *et al.* 2021; Dauphin *et al.* 2022). However, 'home site advantage' (a hallmark of local adaptation) has proven rarer than expected (see meta-analyses Leimu & Fischer 2008; Oduor *et al.* 2016), though it is harder to test for, as it requires reciprocal transplant experiments and lifetime fitness estimates.

Alternatively, adaptive trait plasticity, or the ability of each genotype to manifest a broad range of phenotypes depending on environmental cues, can generate geographic variation in water stress-related traits independent of genetic variation. If plasticity is not itself locally adapted (i.e., all populations or genotypes have the same amount of plasticity), all populations of a species could manifest drought resistant traits given the right environmental cues. As sessile organisms that experience a range of environments over their lifetime and even in different parts of the same organism (e.g., light availability in different parts of the canopy), plants show marked plasticity in many traits (Poorter *et al.* 2009; Palacio-López *et al.* 2015; Keenan & Niinemets 2016). Indeed, substantial plastic responses to drought and cold stress have been observed in multiple tree species (Gimeno *et al.* 2009; Gárate-Escamilla *et al.* 2019). However, the prevalence of active adaptive plasticity (as opposed to passive plasticity that results from reduced growth or other stresses under environmental limitation) remains the subject of long running debate (van Kleunen & Fischer 2005; Palacio-López *et al.* 2015).

Blue oak (*Quercus douglasii* Hook & Arn) is a culturally and ecologically important tree species and the dominant species in many of the oak savannas in California, USA. Blue oak experienced substantial and spatially widespread mortality during a major drought from 2012-2016, particularly in the southern portion of its geographic range (Brown *et al.* 2018; McLaughlin *et al.* 2020). This mortality highlights the potential vulnerability of blue oak in a changing climate, necessitating an improved understanding of blue oak drought tolerance in space and time to support proactive oak management. Blue oak grows across a wide latitude and huge range of water availability, and thus likely exhibits substantial within-species phenotypic variation. While blue oak exhibits minimal within-species variation in its xylem vulnerability to embolism (P50, or the water potential at which xylem suffers 50% embolism, a key drought tolerance metric, Skelton *et al.* 2019), drought avoidance traits such as hydraulic efficiency and allocation to transpiring leaf area as well as additional traits related to drought tolerance, such as leaf robustness (specific leaf area or SLA, leaf dry matter content or LDMC) are expected to vary considerably across blue oak populations.

We quantified the extent and drivers of geographic variation in drought-related traits within mature blue oak trees. We asked 1) how much do drought-related traits vary across the landscape, 2) how is drought resistance coordinated across different traits and tissues, and 3) does spatial variation and trait coordination arise from local adaptation or plasticity? We sought to disentangle the relative roles of local adaptation versus plasticity by measuring drought-related traits in a common garden experiment compared to the traits of the source populations in the wild. In the garden, trait differences between populations are indicative of between-population genetic differentiation/local adaptation (assuming limited maternal effects). Meanwhile, differences between the traits measured in the common garden and those measured in the wild source populations are due to plasticity.

Methods:

Blue oak (*Quercus douglasii* Hook & Arn.) is a deciduous species, which is endemic to California but widespread and abundant throughout the state in low elevation woodlands around the California Central Valley (Fig. S1). We measured morphological and hydraulic traits of leaves and stems from seven populations of blue oak in the wild and in a ~30 year old, reproductively mature common garden. These populations were selected to span the geographic range and range of moisture availability of *Q. douglasii* (Fig. S1, Table S1), using only populations whose original acorn source (for the common garden) had been accurately relocated, and whose source populations were accessible based on current land tenure. Climate data for the source populations, both 1951-1980 climate normal and 2018 water year meteorology, were extracted from the California state-wide Basin Characterization Model (Flint *et al.* 2013).

Common garden sampling

To investigate the amount of among-population genetic trait differentiation, we sampled an existing provenance trial/common garden planted at the Hopland Research and Extension Center (CA, USA). This trial was planted in 1992 with acorns collected from 26 *Q. douglasii* populations across California and planted in a randomized block design (J. McBride, pers. comm.; see also McBride *et al.* 1997). We subsampled seven populations, capturing as much of *Q. douglasii'*s aridity range as possible. For each of the seven populations, we sampled five to six individuals for hydraulic traits, leaf traits and branch wood density. Between April and mid-June of 2018, we collected >1 m long branches from the sunlit, south-facing portion of the canopy in the early morning (before 9am local time), relaxed the xylem by repeatedly recutting the stem underwater, and then placed the branches in large plastic bags for immediate transport back to the lab. One to two individuals from each of the seven sampled populations were collected from the garden at each sampling point (once or twice weekly) to control for temporal variation in hydraulic traits. Three small terminal twigs and subtending leaves were collected at the same time for the measurement of morphological traits. Tree diameter at 50cm and total tree height was also surveyed for every common garden tree in the winter of 2017 and used to calculate the total stem volume of the largest stem (assuming the stem was a cylinder) as a metric of total growth rate since planting.

Wild population sampling

We collected branches for trait measurement from six to eight mature trees from the acorn source populations used in the garden. Large branches (typically >1.5m long and >4cm basal diameter) from the south-facing canopy were collected in the same manner as in the common garden. Tree cores were also collected from the sampled trees for calculation of radial growth rates.

Morphological Traits

We selected three terminal branches from the south-facing sun-exposed canopy for morphological measurements (Table 1), cut at the prior year bud scar and including all current year stem and leaf tissue. Branches were rehydrated for >12 hrs using the 'partial rehydration' method (Pérez-Harguindeguy *et al.* 2013). We then measured specific leaf area (SLA, cm^2 wet leaf area per g^{-1} leaf dry mass), leaf dry matter content (LDMC, g leaf dry mass per g^{-1} leaf wet mass), median leaf size (cm^2 fresh leaf area), leaf dry mass to stem dry mass ratio (M_L:M_S), and leaf area to sapwood area ratio (A_L:A_S, cm^2 leaf area per mm^2 stem area underneath bark) on these current year terminal twigs using calipers, balances, and ImageJ image analysis software. We calculated mean leaf size as the average area per leaf for each terminal branch. We also measured wood density (WD, g dry mass per cm^3 wet volume) on one to five branch disks 2-5cm in diameter cut from the basal end of branches collected for hydraulic sampling. Bark was removed from branch disks and wet volume was measured via water displacement on a balance.

For all analyses using individual or population average traits, we also included leaf and stem P50 values (the xylem tension causing 50% embolism) from Skelton *et al.* (2019), which were measured on branches collected at the same time and using the same methods as branches collected for hydraulic efficiency measurements reported here. However, P50 measurements had few or no replicates per individual and were thus not suitable for branch-level analyses.

Hydraulic traits

Due to extremely long vessel lengths in oaks (often >1 m in branches of *Q. douglasii*, based on pressurized branches recut at the basal end until air bubbles were seen at the distal end; RPS and LDLA *pers obs*), classic hydraulic methods using stem segments were impossible without considerable open vessel artifacts. Instead, we performed hydraulic measurements on terminal branches of 1-2 mm basal diameter using the vacuum chamber method (Kolb *et al.* 1996). We targeted current year growth when possible (similar to branch sampling for morphology), but included up to three years of growth when the current year was <2 cm long and stem diameter was not sufficiently large to fit in hydraulic tubing. For each terminal branch, all subtending leaves were cut under water at the petiole with a razor blade, and the entire stem was inserted into a vacuum chamber. Flow from a scale, through the branch and out the cut petioles was induced by subjecting the stem to a ~60 kPa vacuum. Nevertheless, any stem that was suspected of having an open vessel (i.e. any stem that had a high apparent conductance) was checked for open vessels by attaching to pressurized nitrogen for ~10 minutes and checking under water for air bubbles from the stem or petioles. The leaf area of all subtending leaves was measured via flatbed scanner and ImageJ (Schneider *et al.* 2012), basal stem diameter at 4 radii averaged, and the length of the stem and all branches measured with digital calipers.

Raw stem conductance was standardized two different ways. First, raw conductance was standardized per unit leaf area, here termed k_{stem}, indicating leaf area-specific stem conductance (i.e. not standardized by path length, so including the effects of differential stem growth in long versus short stems, Table 1). Raw conductance was also divided by stem cross-sectional area and multiplied by total stem length (including length of branches if stem was branched) to produce sapwood area specific conductivity, or K_s.

Leaf hydraulic conductance was also measured on terminal branches (cut from the same >1 m long branch as stem conductance) using the 'rehydration kinetics' (RK) method (Brodribb & Holbrook 2003). Because leaves often had very small and irregular petioles, we measured multiple leaves attached to a terminal twig. Leaf conductance was an order of magnitude lower than stem conductance, meaning the effect of the stem in the conductance observed via the RK measurements was negligible. Total leaf area for each sample was calculated via flatbed scanner and ImageJ for each sample, and leaf-area specific leaf conductance, k_{leaf} was calculated. Only measurements from leaves with an initial water potential < -0.2 MPa and > -2 MPa were analyzed to avoid large measurement errors in samples with small pressure gradients or potential embolism.

Growth rate:

We calculated growth rates for the common garden individuals based on a winter of 2017survey of tree diameter at 50 cm and stem height. We calculated total stem volume growth since planting, assuming the stem was a cylinder with the diameter of the basal diameter and a height of tree height, using only the largest stem of multi-stemmed individuals. Growth rates were calculated for the wild trees from tree cores, which were collected via increment borer at 1.3 m height, mounted, sanded, and 5 years worth of rings identified using a dissecting microscope. The length of the 2013-2018 5-year growth period was measured via digital calipers and radial growth was converted to Basal Area Increment (BAI) based on tree DBH. Tree BAI is a function of tree size (Figure S2), so BAI was standardized for tree size by calculating the percent of size-specific maximum Basal Area Increment (BAI) over the 2013-2018 period. Size-specific maximum BAI (the fastest rate a tree of a given DBH was observed to grow) was calculated for each tree's DBH based on the 90th quantile regression of BAI versus tree DBH for all study trees (n=32) plus tree core data from 29 trees spanning five additional sites across California to expand the range of sampled tree sizes (total DBH range 7.8cm-104cm, Figure S2). The observed BAI was then divided by the maximum BAI for each tree to produce '% max BAI'. Tree cores were collected in Oct of 2018, but could not be collected from one site due to loss of site access (n=6 sites rather than 7).

Variance decomposition analysis:

We performed variances decompositions, separately in the garden and the wild, on all branch-level trait measurements to quantify trait variation within canopy (among branches), among individuals within populations, and among populations. We fit linear mixed-effects models separately for the garden or the wild traits, with a fixed intercept term, a random intercept for population and a random intercept for individual nested within population. We employed the lmer() function from the *lme4* (v 1.1-28) and *lmerTest* (v 3.1-3) packages. We then extracted the random effect variance parameters, and calculated the proportion of total trait variance that was attributed to among-population differences (population random effect), individual differences within populations (individual random effect) or variation within individual tree canopies (residual variance). We also calculated the coefficient of variation (CV = trait mean / trait standard deviation) for each trait in the garden and in the wild. Finally, to compare the total trait variation in the garden versus in the wild while accounting for unequal sample sizes, we bootstrapped variance estimates, randomly sampling with replacement each dataset 1000 times with sample number set to the minimum sample size of the two datasets (wild versus garden) for each trait. We then compared the median bootstrapped trait variance for the wild versus garden.

Among-population trait differentiation and climatic variation

We tested for significant among-population trait differences by averaging trait values per individual and then performing one-way ANOVAs separately in the garden and in the wild, and calculated the omega-squared (ω^2) as an estimate of the proportion of variance explained by among-population differences. Replicate was never a statistically significant factor in the garden, and was excluded from the final ANOVAs (fitted using the aov() function in the *stats* package, v 4.1.2). We then used AICc (Akiake's Information Criterion corrected for small sample sizes, AICc() function from the *MuMIn* package, v 1.43.17) to select the best single climatic predictors of among-population differences for each trait. First, we determined whether a random intercept for population was required to account for non-independence among individuals in a population by fitting an 'over the top' fixed effects structure (Zuur *et al.* 2009), including mean annual precipitation, mean annual potential evapotranspiration and mean minimum temperature) and using likelihood ratio test to determine whether the population random effect was needed (using the gls() and lme() functions from the *nlme* package, version 3.1-155). We then used AICc to select the best climate predictor for each trait using linear models (lm in the *stats* package) or linear mixed models with a population random intercept (lmer in the *lme4* package) and assessed significance of the best predictor using t-tests, using Satterthwaite's degrees of freedom from the *lmerTest* package (Kuznetsova *et al.* 2016). For the common garden, potential predictors included only 30 year climate normals of mean annual precipitation (PPT_{30yr}), mean annual potential evapotranspiration (PET_{30ry}), mean annual actual evapotranspiration (AET_{30yr}), mean annual climatic water deficit (CWD_{30yr}=PET_{30yr}-AET_{30yr}), and mean annual minimum temperature ($Tmin_{30yr}$). For wild traits, we also included growth year (2017-2018) weather information as well: wet season (Nov-May) minimum temperature ($Tmin_{gy}$), maximum temperature ($Tmax_{gy}$), precipitation (PPT_{gy}), potential evapotranspiration (PET_{gy}), actual evapotranspiration (AET_{gy}) and climatic water deficit (CWD_{gy}), as well as the anomaly of the 2018 water year from the site 30 year normal (PPT_{anom}, PET_{anom}, AET_{anom}, CWD_{anom}). We visually examined quantile-quantile plots and other patterns in the residuals to identify outliers and ensure model assumptions were met.

Trait-trait coordination

To examine the magnitude of phenotypic (genetic plus plastic variation in the wild) and genetic (variation in the garden) trait correlations, we calculated Pearson's correlation coefficients for all pairs of individual-averaged traits in the wild and in the common garden. We visualized the correlation structure using the corrplot() function in the *corrplot* package (v 0.92). We then used a similar procedure to the bootstrapped variance comparisons to test for significant differences between genetic and phenotypic trait correlations, randomly sampling individuals with replacement from the entire wild and entire common garden datasets to produce two populations of equal size to the smallest of the garden or wild complete pairwise observations, resampling 1000 times per trait combination. We then calculated the difference between the trait-trait correlations in each bootstrapped pair of garden and wild datasets and determined the two-tailed probability that the distribution of differences did not include 0 (e.g., alpha < 0.05 if either the 2.5th percentile of differences was greater than zero or the 97.5th percentile of differences is less than zero, alpha < 0.1 if the 5th and 95th percentile range did not include zero, and alpha < 0.2 if the 10th to 90th percentile range did not include zero).

All code and data for analyses and figure generation can be found at https://github.com/leanderegg/BlueOakGarden.git, and all data are also available on Dryad at [insert Dryad link upon acceptance].

Results

Genetic variation among populations was low in all morphological, allocation and hydraulic traits in the common garden (Fig 1a). However, all traits except for stem sapwood area-specific hydraulic conductivity (K_s) and leaf and stem vulnerability to embolism ($P50_{leaf}$, $P50_{stem}$) showed substantial among-population variation in the wild. Among-population variation in the wild was consistently 25%-30% of total trait variation in most traits, with SLA and LDMC showing even larger among-population variation (46% and 40%, respectively, Fig 1b). Meanwhile, branch-to-branch variation within tree canopies consistently made up the majority of trait variation in the common garden, constituting >50% of total variation in all traits except WD (42% of total) and over 75% of total variation in k_{leaf}, k_{stem}, and K_s (Fig. 1a). In the wild, within-tree variation was typically less than 50% of total variation, except in M_L:M_S and the three hydraulic traits (Fig 1b).

When traits were averaged to the individual, 40-60% of the total tree-to-tree variation in almost all traits was between populations in the wild (Fig 2a) and population differences were significant in 8 of 11 traits (all but K_s, $P50_{leaf}$, and $P50_{stem}$) plus growth (ANOVAs $p < 0.05$, Table S2). Meanwhile, typically <30% of tree-to-tree variation was between populations in the garden, and population differences were only significant in 2 of 10 traits (SLA and leaf size) plus growth in the garden (Table S2). Leaf size was the one notable trait that showed significant and similar among-population differentiation in both the wild and garden.

However, despite the consistent among-population variation in wild traits, climate predictors (historical climate normals, meteorology of the water year of sampling, or the sampling year anomaly from historical climate) very rarely explained differences among populations (Fig. 2b). Based on AICc of linear or linear mixed models (when there was support for a site random intercept, see Table S2), univariate climate predictors were only statistically significant for four wild traits (Fig 2b) with WD decreasing with AET_{anom}, $P50_{stem}$ decreasing (growing more negative) with AET_{30yr}, and M_L:M_S decreasing and k_{stem} increasing with $Tmin_{gy}$ (Figs S3,S4). (Fig 2b, Table S2). Meanwhile, in the garden three traits and growth were significantly associated with source population climate (Table S2). In the garden, increasing PPT_{30yr} was significantly associated with decreasing wood density and increasing leaf size, while increasing PET_{30yr} was significantly associated with increasing SLA and decreasing growth (Fig S3,S4).

While the among-population variance in the garden was always a small fraction of the among-site variation in the wild, this did not generally result in decreased total trait variance the garden (Figure 3). Bootstrapped estimates of the variance in individual averaged traits (i.e., among individual variance) generally showed larger median variance estimates in wild traits than the common garden, but ratio of the garden variance to wild variance was only significantly less than one (alpha <0.05) for SLA, LDMC, and WD. Meanwhile, M_L:M_S and k_{leaf} had similar variances in the wild and the garden despite significant among-population differentiation on the landscape and not in the garden, and A_L:A_S and k_{stem} had only marginally higher wild variances. K_s, $P_{50[stem]}$ and $P_{50[leaf]}$ had similar variances in the wild compared to the garden and no significant among-population differentiation in either location (Table S2), while growth could not be compared because of differing metrics (% of max basal area increment vs 30 yr stem volume). Ultimately, population-average trait values were entirely uncorrelated in the garden and in the wild except for M_L:M_S (Figure S2), even for the traits with similar amounts of total variation in the two settings.

Trait coordination

Trait-trait coordination was much stronger in the wild than in the common garden, suggesting phenotypic correlations are not generally driven by genetic correlations or constraints but rather by coordinated plasticity. Only six of 55 possible trait-trait correlations were significant in both the garden and the wild (Fig. 4), almost all of which are unsurprising (e.g., A_L:A_S ~ M_L:M_S, SLA ~ LDMC) or mathematically related (K_s ~ k_{stem} or K_s~A_L:A_S because K_s was calculated as k_{stem} * A_L:A_S * branch length). The main notable correlations consistent across the garden and the wild trees were positive relationships between average leaf size and leaf vs stem allocation on both an area basis (A_L:A_S) and a mass basis (M_L:M_S). Moreover, average leaf size was much more strongly associated with variation in A_L:A_S than number of leaves per branch in both the garden and the wild (Fig. S3), suggesting that leaf expansion may be a key regulator of leaf-to-stem allocation.

Beyond these correlations, only three additional trait correlations were significant in the garden, while 10 additional trait correlations were significant in the wild (Fig 4). The change in trait-trait correlations from garden to wild was statistically significant ($\alpha < 0.05$) in four trait pairs and marginally significant ($\alpha < 0.1$) in two more pairs (based on 1000 bootstrapped correlation comparisons, Fig 5). The most striking change in trait coordination occurred amongst k_{leaf}, k_{stem} and A_L:A_S. Whereas there was only weak coordination between k_{stem}, k_{leaf} and A_L:A_S in the garden, there was a strong positive correlation between leaf area-specific branch and leaf conductance in the wild (significantly different in the wild vs garden, $p < 0.05$, Fig 5) as well as strong negative relationships between both leaf and stem conductance and A_L:A_S. This plastic increase in hydraulic integration in wild trees appears to be driven by leaf size, which is strongly negatively correlated with k_{leaf} and k_{stem} in the wild (change in correlation is statistically significant for k_{stem}). Across the landscape, trees with smaller leaves had lower A_L:A_S, but consequently greater k_{leaf} and k_{stem}.

Trait-Growth relationships

In the garden, traits were generally not strongly predictive of population average growth (30 year height). Contrary to expectations, LDMC was positively and k_{stem} negatively correlated with growth rates. Leaf size was the only trait correlated with growth in the expected direction, with populations with larger leaves having higher average growth rates (Fig. S4). In the wild, no traits were correlated with radial growth rates (calculated as the percent of maximum size-specific Basal Area Increment), with the exception of K_s (Fig. S5), though growth was only measured in six of the seven populations due to lost access at one site after initial trait sampling. K_s was negatively correlated with growth, contrary to expectations.

Discussion

We found very little among-population genetic differentiation but consistent among-population variation across the landscape in morphological and hydraulic traits of a widespread oak species. This landscape-scale plasticity could not be easily explained using gridded climate or annual meteorological data, but drove trait-trait coordination – particularly of leaf and stem hydraulic traits – that was otherwise lacking in the common garden.

Traits in the common garden: little local adaptation

In a relatively mesic common garden (978 mm of mean annual precipitation, greater than all but two of the sampled populations, Table S1), we found very little evidence for genetically based trait variation among populations. Populations showed significantly different growth rates (height attained at 30 years) in the garden, but only SLA and leaf size showed significant among-population variation (Figure 2). Among individual trees in the common garden, there was remarkably little trait coordination to suggest strong genetic correlations among traits, even though many of these traits are correlated across species (Mencuccini *et al.* 2019; Sanchez Martinez *et al.* 2020). Moreover, this lack of coordination was not necessarily an artifact of limited total trait variation in the common garden, as only three of 11 possible traits showed significantly smaller variance in the garden than in the wild (Fig. 3). Thus, the trait variation manifested in the garden was not merely the wild trait variance less among-site plasticity, and neither the lack of trait coordination (Fig 4) nor the lack of correlation between wild and garden trait values (Fig. S5) was likely driven by restricted garden trait variance.

At the same time, the only traits that showed expected relationships with growth rates in the common garden were leaf to stem allocation traits (M_L:M_S and potentially A_L:A_S), with leafier populations showing faster growth, and leaf size, with larger leaved populations showing faster growth. We conclude that changes to allometry were the primary drivers of functional differences among populations in the common garden in line with classic predictions about the drivers of growth rate variation (Lambers & Poorter 1992), and that this variation in allocation was linked in part to genetically determined variation in leaf size (Fig. S3). Meanwhile, leaf dry matter content (LDMC) and leaf-specific stem conductance (k_s) were significantly correlated with growth rates, but in a direction contrary to expectations. For LDMC, we interpret this as a consequence rather than a cause of growth rate variation (faster growing trees had accumulated more photosynthate in their leaves by the sampling period and thus had higher LDMC), and for k_s, rather than high conductivity promoting growth (Hajek *et al.* 2014) slower growth in high k_s populations appears to be a consequence of high hydraulic efficiency in the two most arid populations that grew slowly in the garden.

Traits in the wild

In contrast to the common garden results, all traits except K_s and $P50_{stem,\ leaf}$ showed substantial among-population trait differentiation across *Quercus douglasii'*s geographic range. While all traits exhibited large branch-to-branch variation within a canopy (in both the garden and the wild), among-population trait differences were as large or larger than differences among trees in the wild (Fig 1b, 2a). Thus, it appears that spatial variation in drought-related physiology is substantial in blue oak, and is primarily driven by trait plasticity.

Surprisingly, this site-to-site trait variability was not strongly related to available site climate data. Neither 30 year site climate normals nor meteorological data from the water year of sample collection, nor the climate anomaly of the sampled year compared to climate normals predicted among-site trait variation. For the four traits that were significantly predicted by site climate, winter minimum temperatures ($Tmin_{gy}$) was the best predictor for two traits (M_L:M_S and k_{stem}) and a water balance metrics (some actual evapotranspiration metric, AET_{anom} and AET_{30yr}) was only a significant predictor for two traits (WD and k_{leaf}, respectively). We hypothesize that this discrepancy is the result of *Quercus douglasii*'s deep rooting strategy, which combined with the substantial geologic and edaphic variation among the sampled sites to largely decouple the actual water availability (the 'weather underground', sensu (McLaughlin *et al.* 2020)) from above-ground climate.

Strikingly, the plasticity-driven trait variation across California resulted in strong trait-trait coordination on the landscape, particularly among hydraulic efficiency and allocation traits. Leaf and branch morphology and P50 were largely uncoupled from other traits in both the wild and the common garden (Fig 4). However, k_{leaf} and k_{stem} significantly changed their correlation strength from uncorrelated in the garden to positively correlated in the wild, and both traits showed a strong correlation with both leaf size and A_L:A_S in the wild. Collectively, this resulted in strong integration across a leaf and stem 'hydraulic module', wherein trees with small leaves had small A_L:A_S ratios and high leaf area-specific leaf and stem hydraulic conductance. We found no evidence for a tradeoff between safety and efficiency in either leaves or stems (Fig S6).

We also found very little evidence for trait-growth relationships in the wild, despite much larger among-population trait differentiation. The only significant relationship was a decrease in growth with increasing K_s, which may be consistent with increasing drought avoidance in the driest populations (Fig S5). This lack of wild trait-growth relationship is perhaps not surprising, given that both traits and environmental conditions and resources differ among populations, making it difficult to disentangle cause versus effect.

Leaf area-driven hydraulic coordination

In theory, the coordination or integration of plant traits across tissues should optimize whole-plant function (Reich 2014). However, perhaps partly as a result of traits rarely being measured simultaneously for multiple tissues, this coordination is not universally observed among tissues (Vleminckx *et al.* 2021) or types of traits (Sanchez Martinez *et al.* 2020), and the actual mechanisms of this coordination (e.g., coordinated evolution, developmental constraints, etc.) remain elusive. The leaf and stem hydraulic integration that we found across wild populations suggests that, within individual species, plastically determined leaf size, presumably coordinated by leaf expansion, may be a key mechanism coordinating hydraulic efficiency across tissues.

We found little evidence for genetic correlations among hydraulic traits in a common environment (Fig 4a), suggesting that hydraulic variation within species was not due to genetic linkage or coordinated microevolution. However, strong hydraulic integration between the leaf area-specific hydraulic conductance of leaves and stems across wild populations indicates coordinated trait plasticity. This coordination seems to be mediated by allocation to leaf area (A_L:A_S), which was largely driven by the average size of leaves (rather than leaf number, Figure S3). Average leaf size had a larger coefficient of variation than stem diameter (0.41 versus 0.31, respectively), and had a stronger negative correlation with both k_{leaf} ($\rho = -0.43$) and k_{stem} ($\rho = -0.54$) than A_L:A_S itself did with either trait ($\rho = -0.39$ and $\rho = -0.30$ for k_{leaf} and k_{stem} respectively). Further supporting the importance of plasticity, average leaf size was uncorrelated with either k_{leaf} or k_{stem} in the garden, and the increase in the correlation from garden to wild was strong for both traits and statistically significant for k_{stem} ($p < 0.05$). Meanwhile, the more commonly measured sapwood-specific branch conductivity (K_s), which is standardized for branch xylem conductive area and path length, was highly variable but not differentiated among populations (Fig 1) and unrelated to either leaf size or k_{leaf} in the wild. This may partly be due to the difficulty of measuring path length for our K_s estimates, because in order to avoid open vessels in this long-vesseled oak species we had to measure the conductance of whole terminal branches cut at the petioles (rather than branch segments) and estimate the path length from the total branch length, even though leaf attachment to the branch occurred along much of its length. Thus, k_{stem} (conductance of the whole branch per unit leaf area) was likely a more accurate measurement of hydraulic efficiency than K_s (conductivity per sapwood area for a 1cm stem length) in this study.

Ultimately, it appears that whole-branch conductance of terminal branches and leaf conductance were coordinated in the wild by plastic changes in leaf size, presumably regulated by environmental cues governing spring leaf expansion, rather than changes in the xylem efficiency itself. K_s, while highly variable, did not differ among populations either in the garden or the wild (Fig 1) and therefore could not drive this pattern. A developmentally fixed hydraulic architecture (in both leaves and stems) that then gets allocated to supply a variable amount of leaf area based on leaf expansion presents a parsimonious mechanism for regulating whole-tissue hydraulic resistance, as regulation of transpirational area may be much easier to regulate in response to environmental cues through turgor driven leaf expansion than anatomical changes to xylem efficiency. Moreover, the negative relationship between leaf size and k_{leaf}/k_{stem} documented here contrasts with the lack of relationship between k_{leaf} and leaf size among species and suggests a developmental constraint rather than adaptive mechanism.

Management implications

Our results from mature trees would indicate that genetically informed management or restoration of blue oaks may not require strong consideration of the aridity of the source materials, as mature tree drought resilience appears to be determined by canalized thresholds of xylem vulnerability to drought (Skelton *et al.* 2019) and largely plastic adjustments to drought avoidance-related traits (e.g. k_{branch} and k_{leaf}). While we could not predict trait variation across the landscape based on site climate (Fig 2b), the substantial among-population variation in leaf-to-stem allocation and hydraulic efficiency are presumably adaptive and therefore constitute plastic adjustments to drought exposure by increasing plant hydraulic efficiency. This decreases the minimum leaf water potential required to attain a given rate of transpiration (Whitehead & Jarvis 1981; Mencuccini *et al.* 2019; Trugman *et al.* 2019) and is quite consistent with within-species adjustments to promote drought avoidance in numerous other systems (Mencuccini & Grace 1995; Martinez-Vilalta *et al.* 2009; Anderegg & HilleRisLambers 2016; Rosas *et al.* 2019; Anderegg *et al.* 2021).

Our findings of limited local adaptation are also consistent with the relatively small amount of local adaptation found in blue oak growth rates (Fig 1) and phenology (Papper & Ackerly 2021), and the relatively high rates of gene flow in blue oak (Papper 2021). While other California oak species have been found to show strong genetic structure across their range (Sork *et al.* 2013; Gugger *et al.* 2021), evidence suggests that blue oak population differentiation across its broad geographic distribution is more limited. Given the strong potential for plastic adjustments to plant hydraulics documented here, this might suggest that most populations can (and may) manifest more drought avoidant phenotypes in a warmer and drier future climate, regardless of their climate history.

Two important caveats to our finding of limited drought-related local adaptation are 1) that we only studied reproductively mature trees and 2) that we only studied traits in a relatively mesic garden. Local adaptation at the earliest life stages may be most relevant for restoration, and limited local adaptation in adult phenotypes does not guarantee limited local adaptation in juvenile phenotypes. Moreover, we were only able to perform trait measurements in a relatively wet common garden. If the expression of genetic differences depends on the environment – e.g., if there are strong GxE interactions for drought-related phenotypes – then our results could differ entirely in a drier common garden location. It remains possible that genotypes from drier populations have larger potential for plasticity (as documented in a *Eucalyptus* species, Mclean *et al.* 2014), which could imply that the same source populations planted in a dry location could show substantial among-population variation due to the dry-adapted populations manifesting more plasticity than wet-adapted populations.

Conclusion

In a study of range-wide trait variation in blue oak (*Quercus douglasii*), we found little evidence for local adaptation in any of numerous morphological or hydraulic traits but substantial realized trait variation across the landscape. Our results suggest that this landscape-scale trait variation involved plastic trait adjustments, and that this plasticity drove among-tissue trait coordination. Thus, plastic adjustments, likely during the process of leaf development and expansion, drive the coordinated manifestation of drought avoidant phenotypes with high hydraulic efficiency in leaves and stems and increased carbon investment in stems relative to leaves. However, these phenotypes could not be predicted by site climate and were poorly linked to growth rates, indicating that our understanding of blue oak drought exposure and integrated performance remains limited.

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756 **Table 1:** Trait definitions and abbreviations as employed by this study.

Trait	Definition
SLA	Specific leaf area (cm^2 g^{-1})
LDMC	Leaf dry matter content (g dry mass per g fresh mass)
WD	Wood density
M_L:M_S	Terminal branch leaf dry mass to stem dry mass ratio (g/g)
A_L:A_S	Terminal branch leaf area to sapwood area ratio (cm^2 mm^{-2})
Leaf size	Average area of a single leaf based on all leaves on a terminal branch (cm^2)
k_{leaf}	Leaf conductance per unit leaf area (mmol m^{-2} s^{-1} MPa^{-1})
k_{stem}	Leaf area-specific stem conductance of full current year terminal branch (mmol cm^{-2} s^{-1} kPa^{-1})
K_s	Sapwood area-specific stem conductivity per branch length (k[stem] * Al:As * length, mmol cm s^{-1} kPa^{-1})
$P50_{leaf,\ stem}$	Leaf and stem P50 measured with optical technique from Skelton et al. 2019
Growth	**Garden**: stem volume attained at 30 yrs, based on basal diameter and height of largest stem assuming cylindrical stem. **Wild**: percent of size-specific maximum basal area increment (based on rangewide 90th percentile BAI at a given DBH)

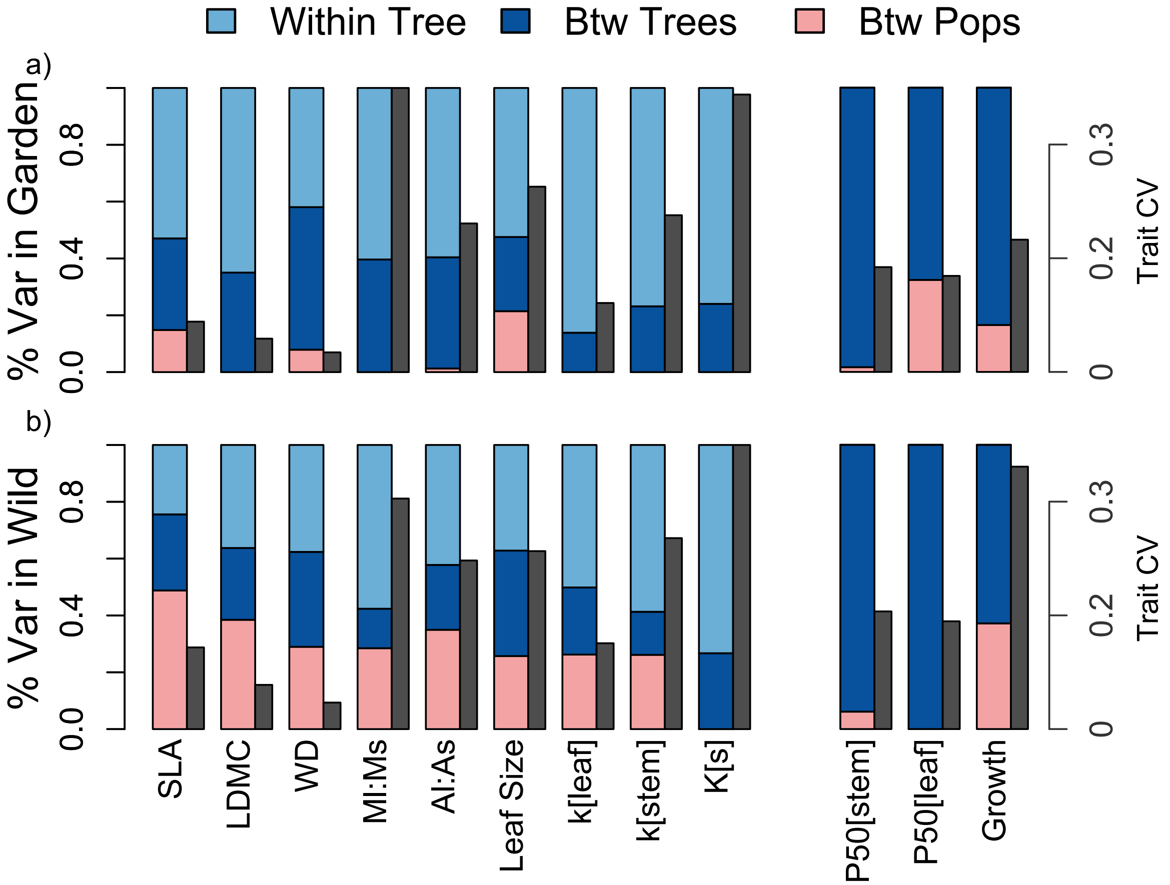

Figure 1: *Variance decomposition of all branch-level measurements in the common garden (a) and wild source populations (b). Grey bars beside the colored bars show the magnitude of the trait coefficient of variation. $P50_{stem}$, $P50_{leaf}$ and Growth do not have replicates within tree, so only contain between tree and between population variance components.*

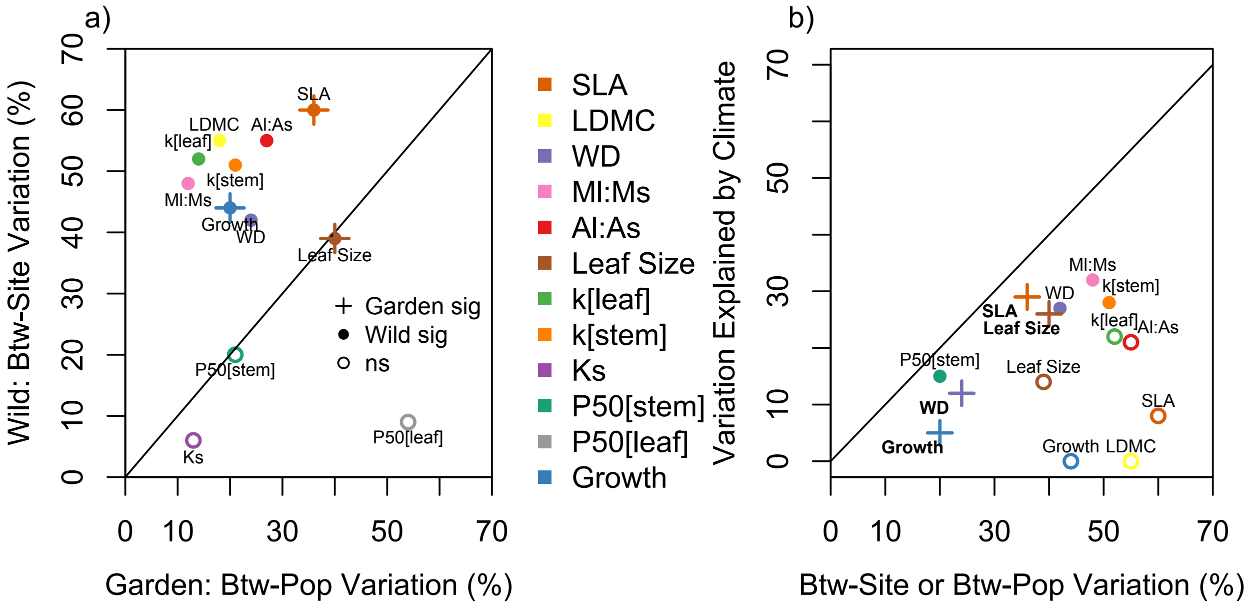

Figure 2: *(a) % of the total tree-to-tree variation attributable to population in the garden versus attributable to sites in the wild. Traits with significant between-site variation (ANOVA p <0.05) in the wild are shown as filled points, while traits with significant between population variation in the garden are shown with crosses. (b) The among-population and among-site variation that could be explained with climate variables. Y-axis shows* R^2 *of best climate predictor based on AICc, filled points indicate predictors that are statistically significant for wild traits, open points show traits with significant among-population differentiation but non-significant climate predictors, and crosses with bold text show garden traits with significant climate predictors (Table S2). Black line shows 1:1 relationship.*

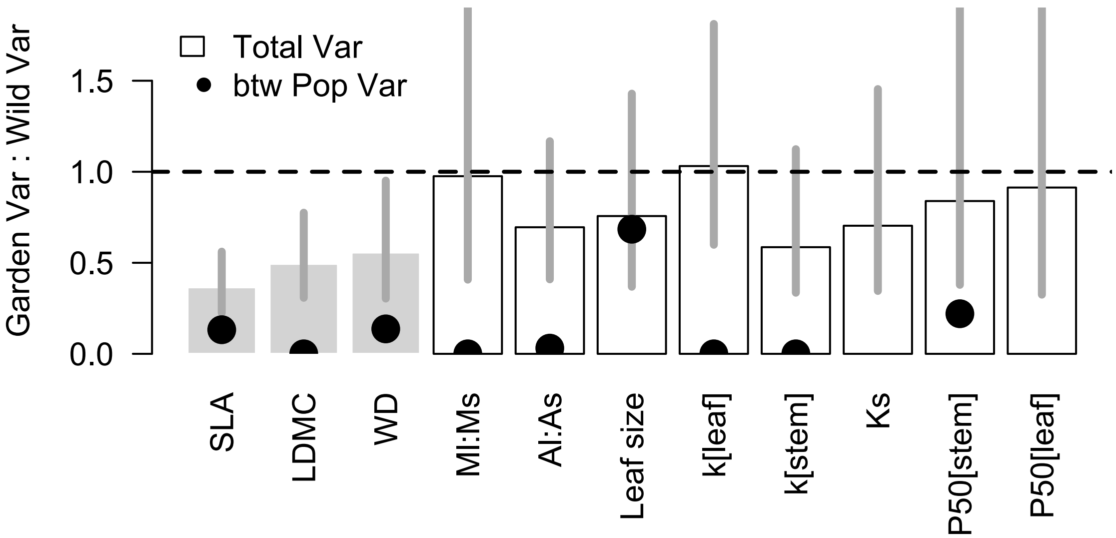

Figure 3: *Ratio of trait variance in the common garden compared to the wild (values <1 indicating more trait variance in the wild). Bars show the ratio of total trait variance (median of 1000 bootstrapped variance estimates, lines show 5^{th} – 95^{th} percentile of ratio), gray bars indicate significantly lower variance in the garden. Points show the ratio of the between-population variance component alone (Ks and $P50_{leaf}$ had 0 estimated between-population variance in the wild and thus no points).*

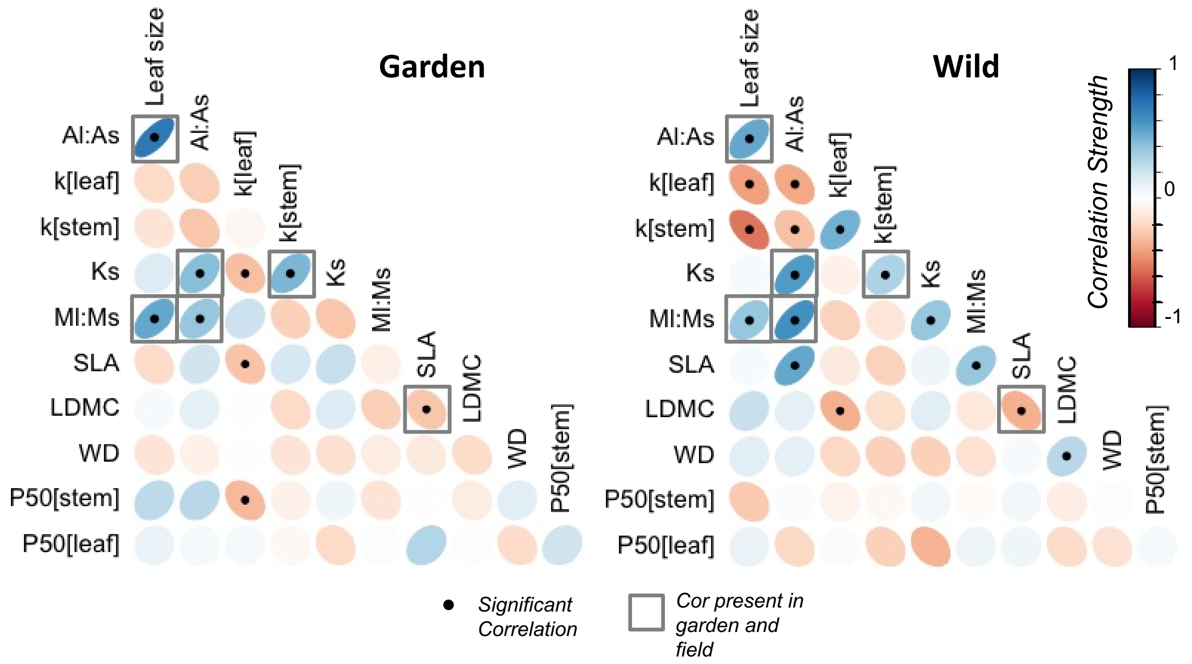

Figure 4: *Tree level trait-trait correlations in the garden (a) and in the wild (b). Ellipses and color show direction and strength of the correlation, points show statistically significant relationships, and grey boxes show relationships that are significant in both the garden and the wild.*

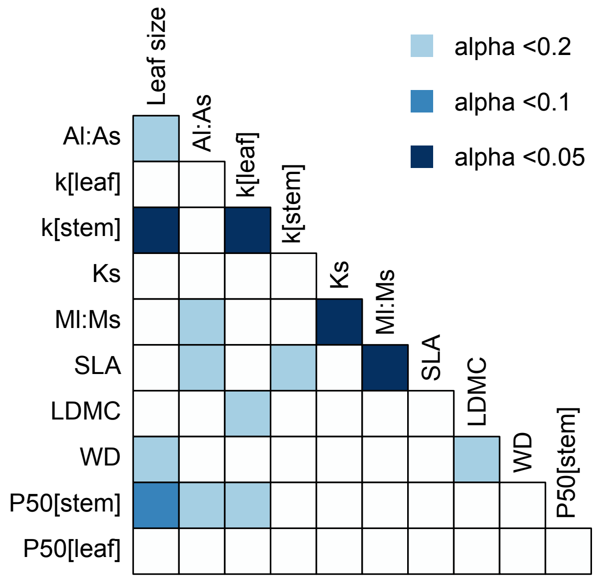

Figure 5: *Multiple trait correlations were significantly different in the wild versus the garden (based on 1000 bootstrapped comparisons of correlations), particularly k[stem] and k[leaf] (significant correlation between leaf and stem hydraulic efficiency in whole terminal branch tissues in the field but not the garden) and in relationships relating to leaf size (again suggesting something interesting is going on with the drivers of plasticity in leaf expansion/development that leads to phenotypic integration in the wild).*