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Local climatic heterogeneity predicts differences in

phenotypic plasticity across populations of a

widely-distributed California oak species

A thesis submitted in partial satisfaction

of the requirements for the degree Master of Science

in Biology

by

Brandon William Selbie MacDonald

2017

ABSTRACT OF THE THESIS

Local climatic heterogeneity predicts

differences in phenotypic plasticity across populations of a

widely-distributed California oak species

by

Brandon William Selbie MacDonald

Master of Science in Biology

University of California, Los Angeles, 2017

Professor Victoria Sork, Chair

In variable environments, phenotypic plasticity-- the ability of a genotype to produce different phenotypes in different environments -- may play a critical role in survival of an organism. It has been proposed that populations living in more climatically variable environments may evolve greater phenotypic plasticity than populations in more stable environments, which may be particularly beneficial for sessile long-lived organisms, such as trees, which once established will live in one location for a long time. We test this hypothesis by examining leaf traits in *Quercus lobata*, a wide-spread California oak, which were planted into two common gardens. Common gardens were established with 6000 seedlings grown from acorns harvested from trees across the species range. We measure leaf traits that are likely to demonstrate plasticity, and are

known to be associated with plant response to climate. In support of our hypothesis, we find that leaf thickness, leaf lobedness, and trichome density show clines in plasticity in their response to the environments of the two gardens that are correlated with two measures of environmental heterogeneity—temperature seasonality and precipitation seasonality. Seedlings from climates which are more seasonal in temperature and precipitation tend to display higher levels of plasticity in the common gardens. We also find geographic structure in patterns of plasticity and identify leaf lobedness as the most plastic leaf trait in the common gardens. More plastic maternal families tend to display lower levels of fitness in the common gardens suggesting a cost associated with plasticity. We conclude that there is local adaptation for plasticity in some leaf traits, and that there is a fitness cost to that plasticity outside of the native environment.

The thesis of Brandon William Selbie MacDonald is approved.

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Introduction

Phenotypic plasticity, which is the ability of a genotype to produce different phenotypes in response to variation in the environment, is a key mechanism allowing organisms to persist in heterogeneous environments (West-Eberhard, 1989; Schlichting 1998; Fordyce 2006). Plastic responses to the environment are trait specific and vary among maternal families and populations (Sultan et al. 2000; McLean et al. 2014; Ramirez-Valiente 2010; Gratani et al. 2003; Aspelmeier & Leuschner 2004). For species with populations that occupy dissimilar habitats, selection will favor the evolution of locally adaption that maximizes the fitness of individuals to their local environment (Stebbins, 1970; Savolainen, 2007). However, high gene flow among populations may prevent or reduce local adaptation by making ecotypes more similar, and plasticity may instead be favored to allow survival across complex landscapes (Schoener 1993; Kawecki 2004; Lasky 2014). In addition, in temporally variable environments, plasticity may be more likely to evolve in some traits, rather than local adaptation for organisms experiencing dissimilar sets of environmental conditions across seasons or years (Moran 1992; Alpert & Simms 2002; Sultan & Spencer 2002; Kawecki 2004; Lasky 2014).

Phenotypic plasticity may have trade-offs due to the cost of maintaining the mechanisms necessary to respond to different conditions (Gienapp et al. 2008). For example, plastic genotypes are typically less able to develop extreme phenotypes (Gienapp et al. 2008). Indeed, different studies have shown an adaptive benefit to both high and low plasticity (Schmitt et al. 1999; Ghalambor et al. 2007; Pratt & Mooney 2013). Further, phenotypic plasticity can be a

maladaptive byproduct of environmental influences (Kawecki 2004), so an adaptive benefit to plasticity needs to be demonstrated.

As sessile organisms, plants have the ability to display an amazing diversity of morphologies and physiologies in response to their environment (Valladares, 2000; Pigliucci, 2001), and leaves are the most plastic plant organ. Leaf traits which were likely to display plasticity were chosen. Evidence of plasticity in all of the discussed leaf traits has been found in previous studies. The expectation is that all traits will show some degree of plasticity in the common garden experiment. Evidence for plasticity has been found in leaf lobedness (Albarrán-Lara et al. 2015; Mathiasen et al. 2016). Lobedness is responsive to temperature, and moisture availability (Niinemets, 2001). More deeply lobed leaves allow for wind to more easily carry away heat and water vapor, so increasing lobedness could be a response to wetter, warmer environments (Semchenko & Zobel 2007). Evidence for plasticity in leaf area (Albarrán-Lara et al. 2015; Picotte et al. 2007; Mathiasen et al. 2016; Gratani et al. 2003; Ramirez-Valiente et al. 2010; McLean et al. 2014), leaf dry mass (Albarrán-Lara et al. 2015; Mathiasen et al. 2016; Gratani et al. 2003), leaf length to width ratio (Albarrán-Lara et al. 2015; Picotte et al. 2007; Mathiasen et al. 2016) and leaf mass per area (the one sided area of a leaf divided by its dry mass) in response to both light a moisture availability has been found by many authors (Niinemets, 2001; Mathiasen et al. 2016; Gratani et al. 2003; Ramirez-Valiente et al. 2010; Santiso et al. 2015; McLean et al. 2014). Leaf thickness is also commonly found to be plastic (Albarrán-Lara et al. 2015; McLean et al. 2014) in response to light, temperature, and water availability (Perez et al. 2013). Wide, thin leaves are indicative of high levels of moisture availability, as wide thin

leaves are more effective at capturing light, but the higher amount of surface area makes them more susceptible to desiccation. Conversely, narrow thick leaves are better suited to dry conditions as they are not as subject to water loss (Niinemets, 2001). Trichome density has been found to be plastic in response to temperature as well as photoperiod (Gianfagna et al. 1992; Picotte et al. 2007). Trichomes create a thicker boundary layer of air around the leaves (Ning et al. 2016). This means that leaves with large numbers of trichomes will have less air movement at the surface of the leaf, which will slow down the process of desiccation, and make the plant more suited for drought conditions.

Provenance studies have long been used in forestry to help select optimal seed sources for tree planting (Illingworth 1978; Wright, 2014). Having multiple common gardens allows for the opportunity to investigate phenotypic plasticity and population level differences in that plasticity. Because genetically similar individuals are planted in multiple environments, the response of the genotype to the different environments can be measured (Illingworth 1978; Wright, 2014). The Illingworth test of lodgepole pine established in 1969 in British Columbia with 140 populations planted across 62 sites is an example of the effectiveness of provenance studies in constructing environmental response functions, finding large differences between sites (Illingworth 1978; Rehfeldt et al. 1999; Wang et al. 2010).

An additional motivation for this study is to assess whether phenotypic plasticity allows long-lived plants to survive under conditions of rapid climate change. Because phenotypic plasticity allows for rapid responses, climates climate change is expected to increase the fitness of

plasticity (Anderson et al. 2012; Franks et al. 2013). By enabling survivorship in the short term, plasticity could also facilitate genetic adaptation in the long term (West-Eberhard 2005; Ghalambor et al. 2007; Nicotra et al. 2010). Migration and evolutionary adaption is slow in long-lived, slowly dispersing plants, such as oaks and many other tree species, rendering these mechanisms ineffective as short-term responses to rapid climate change (Thomas 2010; Aitken et al. 2008; Sork 2016; Sawyer & Keeler-Wolf 1995), so plastic responses will be important in the short term in order to rapidly respond to changing climates.

Valley oak, *Quercus lobata* Née, provides an excellent species to assess the extent to which leaf traits might show adaptive phenotypic plasticity. It is distributed across a range of environments in scattered patches in the Central Valley, and in the surrounding foothills, Sierra Nevada Mountain valleys, Coastal ranges, and Transverse ranges with a latitudinal range of 34-40° (Grivet et al. 2006). Valley oak is a species of concern for conservationists as its habitat has become increasingly fragmented, and populations have declined sharply over the last 300 years due to habitat loss, and is experiencing limited recruitment in some areas (Albarran-Lara et al. 2015).

The overall goal of this study is to test the hypothesis that heterogeneous environments select for plasticity across maternal families. Using data on leaf traits and growth response of seedlings derived from species-wide populations of *Quercus lobata*, this project addresses three questions. First, which leaf traits show greater amounts of phenotypic plasticity across maternal families? Second, do we see evidence that maternal families from locals of greater climatic

variability exhibit greater plasticity than families from more stable environments? Such evidence would suggest that there may be local adaptation for plasticity in valley oaks. Because differences in plasticity among trees may be a reflection of neutral spatial genetic structure, which has been shown in *Quercus lobata* (Grivet et al. 2006; Gugger et al. 2013; Sork et al. 2010), we test an alternative hypothesis that geography is associated with phenotypic plasticity. Finally, does plasticity across maternal families associate with fitness in the common gardens? On one hand, if phenotypic plasticity is beneficial to plant performance, levels of plasticity may enhance growth in novel environments such as the common gardens. On the other hand, phenotypic plasticity has a cost that could lead to a trade-off with growth (Gienapp et al. 2008; Kawecki 2004). Comparison of families grown in a common environment allows us to assess whether populations are genetically differentiated for plasticity with negative effects on growth. Findings of this study will demonstrate the extent to which phenotypic plasticity may be advantageous in variable environments and provide some resilience for future climate change.

Methods

Study System

Valley oak (*Quercus lobata* Née) is an ecologically important winter-deciduous tree, which is endemic to California and is dominant or co-dominant in oak savannas (Griffin and Critchfield, 1972). The species is distributed in scattered patches in the Central Valley, and in the surrounding foothills, Sierra Nevada Mountain valleys, Coastal ranges, and Transverse ranges with a latitudinal range of 34-40° (Ogden, 1980). It is restricted to deep loamy soils but inhabits

diverse climatic and geographical zones (Griffin & Critchfield, 1972). It is generally found below an elevation of 600 m, but some populations occur up to elevations of 1700 m in Southern California (Pavlik et al. 1995). Valley oak is a species of concern for conservationists as populations have declined sharply over the last 300 years due to habitat loss, and is experiencing limited recruitment in some areas (Tyler et al. 2006).

California valley oak is a wind-pollinated species whose acorns are dispersed by acorn woodpeckers, scrub jays and rodents (Thompson et al 2014. Koenig et al. 2009; Sork 2015). There is considerable genetic structure within the species due to restricted of gene flow allowing to local adaptation (Grivet et al. 2005; Sork et al. 2002), although connectivity is maintained by long-distance pollen dispersal (Austerlitz et al. 2004). Climate niche modeling was done in order to predict future climate niches of valley oak (Sork et al. 2010; Gugger et al. 2013). It was estimated that in some parts of the species range, climate niches could move by 60-100km by the end of the century. They concluded that gene flow through pollen and seed dispersal was unlikely to be sufficient for some populations in order to track suitable sites potentially leading to valley oak extirpation in some regions.

Study Sites (Common Gardens)

This experiment is comprised of two common gardens grown at two sites, administered through the US Forest Service: the Chico Seed Orchard at Chico, California and the Institute of Forest Genetics at Placerville, CA (Delfino-Mix et al. 2015). At an elevation of 60m, Chico is the garden in the warmer, drier climate, while the site near Placerville (elevation 569m) is situated

in a cooler, wetter climate. According to the Climate WNA (2016) mean annual temperature in Chico is 16.6 °C. Placerville has a mean annual temperature of 14.8 °C. The average annual precipitation is only 68.1 cm in Chico compared to Placerville with gets almost 150% more rainfall with 95.8 cm annually. While both sites undergo similarly dry summers, Placerville experiences significantly wetter winters, however the trees in the Chico site are being more heavily irrigated by overhead sprinklers as opposed to Placerville which is more conservatively watered with drip irrigation. Differences in soils types, and pathogens compound to obvious differences between the two sites especially in terms of the size of trees, so the large environmental effect on phenotypic variation is clear.

Sampling and Experimental Design

In 2012, approximately 11,000 acorns were collected from 95 localities throughout the species range of *Q. lobata* (Delfino-Mix et al. 2015). Seeds were submerged in a 10 percent bleach solution for one minute to remove molds and other contaminants. Floating acorns were removed. The acorns were germinated under a 50 percent shade cloth. In November of 2012, the acorns were planted in containers (6.4 cm diameter, 25.0 cm depth, 656 ml volume) filled with Sunshine #4 aggregate plus soil mix. The acorns were placed in the soil sideways. After removing mutant plants, in the winter of 2013-2014, the one year-old plants were transplanted into larger containers (10.0 cm wide, 36.0 cm high, volume 2.83 liters). In the winter of 2014-2015, the two-year old plants were outplanted into two common gardens (Delfino-Mix et al. 2015). The resulting experimental design was comprised of 95 provenances, up to 8 families per provenance, and 5 seedlings per family in each garden. One progeny from each family was

planted in each block. All provenances are represented in both common gardens, resulting in

640 families and 3500 seedlings in each common garden. Mortality in the common gardens

brought the total number of trees to 5,488 at the time of sampling. Because some families

lacked a sufficient number of seedlings for planting, a few families are only represented in one

garden, or are only represented by a single individual in one of the two gardens.

Phenotypic measurements

In the fall of 2016 and through 2017, we measured a range of traits for individual young trees,

including those which are likely to exhibit plasticity. Trait measurements have been selected to

assess plasticity. Every tree was sampled from both common gardens, totaling 5,488 trees. We

sampled the most recently matured sun leaves which were ~10cm from the branch tip. We

picked leaves from different sides of the tree, between waist and shoulder height from the

ground. This usually meant we were picking leaves from the top half of the tree. Leaves could

not easily be sampled from the tops of the tallest trees in the Chico common garden. We

estimate that we were unable to reach the tops of ~1 in 10 trees. One leaf sample per

individual was analyzed for trichome density, two were analyzed for leaf thickness and 4-5

leaves were analyzed per individual tree for leaf area, dry mass, leaf lobedness, leaf length to

width ratio.

Leaf area was measured by laying out fully hydrated leaves and a ruler for scale on a scanner.

They were scanned and upload to a computer to be analyzed with ImageJ software. Leaf

perimeter^2 was divided by leaf area to produce a measure of leaf lobedness (Fig 1). After

scanned images were taken, leaves were put in a leaf press until dry and then weighed (Perez et al. 2013). Specific leaf area (SLA) is the one-sided area of a fresh leaf divided by its dried mass (Cornelissen et al. 2003).

Leaf thickness was measured with digital calipers. Because thickness varies across the surface of the leaf, leaves were all measured at the midpoint between the perimeter and midrib, midway between the base and the tip. Secondary veins were avoided. Further, indentation of the leaf surface was avoided by recording measurement without squeezing the calipers. These measurement practices are recommended by Perez et al. (2013).

Trichome density was estimated by viewing the abaxial side of the leaf under a microscope at 1500x magnification (Fig 1). This method has also been used by Gianfagna et al. (1992) and Picotte et al. (2007). Trichomes in the field of view were counted for the first 1000 individuals. Data from these 1000 individuals was used to define 6 categories of trichome density. The remaining data was collected by estimating the trichome density category.

We measured height and estimate the number of leaves at the end of the 4th year growing season, which is associated with fitness. Number of leaves was estimated and classified into one of seven categories; 1-100 leaves, 100-200, 200-400, 400-800, 800-1600, 1600-3200, or more than 3200 leaves. Because these oaks have not yet matured to a point at which they are producing acorns, growth is the best estimation of their fitness. The plant's fitness will be used to determine if the plasticity of its leaf traits is associated with plant fitness in a novel

environment.

Statistical Analysis

To test the first question, a statistical analysis was done in R (R Core Team, 2016). Interaction plots were generated and *lme4* (Bates et al. 2015) was used in addition to perform a linear mixed effects test of the environmental effect, genotypic effect and interactions between the environmental and genotypic effects on trait variation. As fixed effects, the environmental effect of garden was put into the model. As random intercept effects block nested within garden, provenance, family nested within provenance, and the garden by provenance interaction were put into the model. Visual inspection of the residual plots did not reveal any obvious deviations from the assumptions of constant variance, or normality. *lmerTest* (Kuznetsova et al. 2016) was used to do a likelihood ratio test to obtain p-values for random effects, and no obvious deviations from the assumptions of the likelihood ratio test including normal distributions of restricted and unrestricted estimators, were observed.

To measure plasticity, we utilized the Relative Distance Plasticity Index (RDPI) (Valladares, 2006), which has the advantages of not assuming a particular distribution of the data. RDPI is the quantification of a maternal family's plasticity. It is on a scale from 0 (no plasticity) to 1 (maximal plasticity). In order to calculate RDPI one measures the phenotypes of two individuals from same family grown in two environments. The difference between the trait values of an individual (i) in the Placerville (p) garden and an individual in the Chico garden (c) from the same family (f) is calculated. Then, divide this difference by the sum of those two trait values to

get a 'relative distance' measure. Finally, take the average relative distance of all possible pairs

of individuals from the same family. It is calculated as follows where n is the total number of

distances.

$$RDPI = \sum((i_{fp} - i_{fc}) / (i_{fp} + i_{fc}))/n$$

RDPI provides a distribution of relative distance measures which can be subject to hypothesis

testing. In this way the first question can be tested; which traits and which maternal families

show the most plasticity across the common gardens? By using all possible pairs of individuals

from the same family across the two gardens, a large sample of RDPI values is collected leading

to a high level of statistical power when comparing differences in plasticity between maternal

families, or between traits (Valladares, 2006). RDPI values for maternal families were removed

if the family was only represented by one individual in one of the two gardens. Plasticity of

trichome density cannot be compared to plasticity of other leaf traits however, because

trichome density was measured as a categorical variable, while all other measures are

continuous. Bootstrapping methods were used to produce 95% confidence intervals which

tested for significant differences between plasticity of traits. The *ggplot2* package (Wickham,

2009) was used to create density plots of RDPI values for different traits.

To address the second question of whether or not environmental heterogeneity at the site of

maternal origin or geography can predict plasticity across maternal families, a regression

analysis and MANOVA were done. Regression analysis was done to determine variables which

could predict plasticity in leaf traits. Four different groups of variables were used; geographic

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variables, measures of average temperature and precipitation, measures of seasonality, and measures of between year variation in climate (table 1). Models were made separately for geographic variables and climate variables because geography is often correlated with climate.

Climate seasonality, including temperature seasonality and precipitation seasonality, are measured using variables from Bioclim, an open online climate database with a spatial resolution of ~ $1km^2$ (O'Donnel et al. 2012). Precipitation and temperature seasonality are coefficients of variation of monthly temperature and precipitation over the course of the year (O'Donnel et al. 2012). Seasonality therefore, in this paper refers to within year variation in climate. Maximum temperature of warmest month and spring precipitation measures are also taken from Bioclim. In order to measure between year variation in climate we took the standard deviation of mean warmest month temperature, spring mean maximum temperature, spring mean minimum temperature and spring precipitation over a 30-year period. This data was collected from Climate WNA (Wang et al. 2016).

A MANOVA was then done with trichome plasticity, leaf thickness plasticity and leaf lobedness plasticity as dependent variables. Geography and variables measuring within-year variation in climate were used as predictors. Pillai trace values measures contribution to a model (Pillai, 1955). They are a statistic ranging from 0 (small contribution to the model) to 1 (larger contribution to the model). To make maps showing geographic variation in plasticity we used two packages in R including *ggmaps* (Kahle and H. Wickham, 2013), *ggplot2* (Wickham, 2009).

To examine the third question, a MANOVA analysis tested the association between plasticity in leaf traits and plant fitness as measured by whole-plant growth traits. There is a latitudinal gradient in growing season as well as many of the leaf morphology traits which are considered in this study. A longer growing season leads to more growth in the common gardens, so in order to test weather plasticity in leaf traits were associated with fitness, growing season had to first be controlled for, before the MANOVA was done. Dependent variables in the model included RDPI measures of plasticity for all 5 leaf traits.

Results

Phenotypic plasticity in leaf traits

As predicted, we found evidence of plasticity in all traits (Fig. 2). Confidence intervals of relative distance plasticity index measures for all traits did not include zero, suggesting that some degree of plasticity was found in all traits (Fig 2). Leaf lobedness was the most plastic leaf trait lobedness (median = 0.172, 95% CI [0.168, 0.176]), followed by leaf thickness (median = 0.125, 95% CI [0.121, 0.128]). RDPI measures for maternal families did not show significant correlation between traits. A Pearson's correlation test indicated that maternal family which displayed a relatively high amount of plasticity in one trait did not do so across the board in all leaf traits. Overall, valley oak plants growing in the Chico common garden tend to have leaves with more trichomes and a higher length-to-width ratio (Table 2, Fig 3), while plants in the Placerville common garden have leaves with a larger specific leaf area (Table 2, Fig 3). These are confirmed by significant gardens effects in the two-way ANOVA results (Table 2). Significant block effects further demonstrate environmental effects on leaf traits (Table 2).

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Phenotypic plasticity and environmental heterogeneity

Norms of reaction plots illustrate that provenances vary in their environmental response (Fig. 3). Two-way ANOVA results confirm that there is differentiation between provenances, and between families within provenances in terms of their expressed leaf traits in the common gardens (Table 2). Significant garden x provenance interaction effects for all traits confirm what is observable in the norms of reaction plots; provenances vary in their environmental response (Table 2).

Geography and measures of within-year climatic variations were commonly the best predictors of plasticity across the leaf traits. There were strong latitudinal and longitudinal gradients found, especially in plasticity of both trichome density (Fig 4, Table 5). Trichomes density tended to be more plastic in the north and in the west (Fig 4a). Latitude and longitude were also strong predictors of plasticity when measures of plasticity were tested together in the MANOVA analysis (Table 5). There was also an elevational gradient in trichome plasticity, decreasing in plasticity as elevation increases (Table 5). Maternal families from the north also tended to have fewer trichomes overall in the common gardens (Fig 5 & 6).

As was predicted, measures of within-year variation in climate (temperature and precipitation seasonality) were commonly found to be significant predictors of plasticity (Table 6). Temperature seasonality was positively associated with plasticity in leaf thickness, leaf lobedness and leaf length-to-width ratio, and precipitation seasonality was positively associated

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with leaf length-width ratio (Table 6). Temperature seasonality was the only significant non-geographical predictor of plasticity when measures of plasticity were tested together in the MANOVA analysis (Table 7). Measures of between-year variation in climate were also found to be positively associated with plasticity in leaf traits (Table 6). Maternal families which come from more variable environments tended to be more plastic in the common gardens (Table 6).

Phenotypic plasticity and fitness

We found higher levels of plasticity in trichome density and leaf lobedness to have a significant negative association with fitness as measured by height and number of leaves in the common gardens (Table 9). Pillai trace statistics suggest that trichome density and leaf lobedness also made the largest contributions to the MANOVA which tested the association between plasticity in leaf traits and growth in the common gardens. There was a much closer association between plasticity and plant height as compared to plasticity and number of leaves, such that family which were more plastic in trichome density and leaf lobedness tended to have trees with were shorter, but did not necessarily have fewer leaves than trees from other families.

Discussion

This study finds evidence of the association between environmental heterogeneity and phenotypic plasticity in leaf traits. In fact, our experiment found that temperature seasonality in the site of maternal origin predicted plasticity in the most plastic traits (Table 6), especially leaf lobedness and leaf thickness. The association between environmental heterogeneity has been found in other species, but for year-to-year variation rather than season variation. For example,

Gianoli and González-Teuber (2005) found interannual variation in precipitation to be predictive of plasticity in leaf traits of *Convolvulus chilensi*s, and Molina-Montenegro and Gianoli (2010) found rainfall variation during the growth season was positively associated with plasticity in water shortage, photosynthetic performance and flowering time in *Taraxacum officinal*e. Nonetheless, as we discuss below, phenotypic plasticity in *Quercus lobata* may have evolved in response to climatic heterogeneity.

Relative Plasticity of Leaf Traits

Leaf lobedness was revealed to be the most plastic trait, followed by leaf thickness, while specific leaf area and leaf length-width ratio were found to be the least plastic (Fig 2). While the RDPI measures of plasticity of trichome density could not be compared to plasticity of other traits (Fig 2), the effect of the garden accounted for a large portion of the variation in trichome density relative to the effects of the genotype as indicated by estimates of provenance and family in Table 2. This suggests that trichome density is a trait which is not genetically fixed and very responsive to its environment.

Leaf lobedness and leaf thickness were significantly more plastic than SLA and leaf length-width ratio (Fig. 2). The estimates of the garden effect on leaf thickness was lager that the genotypic effects of provenance and family, suggesting that variation in these traits are highly affected by their environment, and not just genetically determined (Table 2). Leaf lobedness however had a relatively small estimate of its environmental effect compared to the genotypic effects (Table 2), despite the fact that the trait revealed itself to be highly plastic as measured by RDPI (Fig 2).

This is likely because of strong interaction effects (Table 2, Fig 3). Maternal families were highly responsive to their environment, but their responses varied in direction (Fig 3), resulting in a small overall environmental effect.

SLA was found to have a higher estimate of its provenance effect compared to its garden effect (Table 2). Unlike other leaf traits, variation in SLA is more determined by the plant's site of origin than by the environment in which it is grown. Finding such little plasticity in SLA and leaf length-width ratio was somewhat surprising given that other studies have found them to be plastic traits (Albarrán-Lara et al. 2015; Mathiasen et al. 2016; Gratani et al. 2003). It is possible that although SLA and leaf length-width ratio didn't express high degrees of plasticity between the environments in which we grew the plants in, they might have displayed more plasticity if different environments had been compared. It has been demonstrated that plants can show non-linear responses to environmental clines (Wang et al. 2006; Valladares, 2006). The environments in which plants were grown in our study may have fallen onto regions of a larger environmental response curve with a shallow slope. Had different environments been considered, greater signatures of plastic response might have emerged.

Plasticity Along Clines of Environmental Heterogeneity and Geography

We found plasticity to vary across maternal families along geographic clines and along clines of environmental heterogeneity. Significant garden x provenance interaction terms (Table 2, Fig. 3) demonstrate that maternal families differ in their environmental response between the two gardens, enabling us to investigate patterns in this intraspecific differentiation.

Geography was a strong predictor of plasticity in trichome density (Table 5). This is in line with previous research which has shown that valley oak has genetic structure within the species across its landscape (Grivet et al. 2005; Sork et al. 2002). Maternal families from the north, tended to be more plastic that families from the south (Fig 4a). It was also found that maternal families in the north tended to have fewer trichomes overall (Fig 5a & 6a). One possible explanation for this pattern is that perhaps there are diminishing returns to adding more trichomes to the leaf surface. Maternal families from the south tended to have many trichomes, and perhaps their trichomes are so dense that there is not much benefit to adding more trichomes to the leaf surface through plastic responses. Another possible explanation could have to do with the idea proposed by Gienapp et al. (2008) that plastic genotypes are typically less able to develop extreme phenotypes. Perhaps maternal families from the south are producing extreme phenotypes in terms of their trichome density, and this could not be achieved if trichome density was more plastic.

Further, it was demonstrated that there were broad geographic patterns to plasticity (Table 7). More plastic maternal families tended to be found in northern and western parts of the species range (Fig. 4) as well as at higher elevations (Table 7). It is interesting to note, that different geographical patterns in plasticity were found between different leaf traits. All of the analyzed leaf traits have implications for a plants water retention ability, and are responsive to temperature and moisture availability (Niinemets, 2001; Semchenko & Zobel 2007; Mathiasen et al. 2016; Gratani et al. 2003; McLean et al. 2014; Gianfagna et al. 1992; Picotte et al. 2007),

so it is possible that in different parts of the species range, valley oaks are responding to climactic ques in different ways.

Measures of within-year climate variability, or seasonality, were also found to be highly predictive of plasticity (Table 6). This association with climate heterogeneity and plasticity lends support for the hypothesis that variable environments lead to the evolution of plasticity (Moran 1992; Alpert & Simms 2002; Sultan & Spencer 2002; Kawecki 2004; Lasky 2014). Interestingly, we also found strong associations with plasticity and measures of between-year variation in climate (Table 6) similar to other studies (Gianoli & González-Teuber, 2005; Molina-Montenegro & Gianoli, 2010). If variation in climate within the year is selecting for plasticity across maternal families, this might suggest that an ability to plastically change leaf traits over the course of one growing season might have been under selection. Further investigation into plasticity within an individual over the course of a growing season is warranted.

The identification of clinal patters in plasticity is a finding which has not been achieved by many studies. There have been studies which have demonstrated intraspecific differentiation in plasticity in *Quercus suber* (Ramírez-Valiente et al. 2010), *Betula pendula* (Meier & Leuschner 2008) and *Populus davidiana* (Zhang et al. 2004), but these studies only test a few populations, and therefore they had a limited ability to identify clinal patters, such as the patterns we found across geographical and seasonal clines. McLean et al. (2014) did however determine that plasticity in leaf traits of a Eucalyptus varied across a precipitation gradient. Further, Li et al

(2000) found that provenances from drier climates tended to have high plasticity in SLA and leaf Nitrogen content in seedlings of *Eucalyptus camaldulensis* and *Eucalyptus microtheca*.

A Cost to Plasticity

We did not find evidence to suggest that plasticity observed in the common gardens was adaptive. Both leaf lobedness and trichome density plasticity were negatively associated with height and number of leaves in the common gardens (Table 8). This supports the hypothesis that there is a cost to maintaining the mechanisms necessary to carry out plastic changes (Gienapp et al. 2008), and this cost might outweigh any benefit incurred by plastic responses to the environment. Other studies have found mixed benefits to both high and low plasticity (Schmitt et al. 1999; Ghalambor et al. 2007; Pratt & Mooney 2013). The negative association between plasticity and growth was largely accounted for by a negative relationship between height and both leaf lobedness and trichome density plasticity.

Local adaptation of plasticity might be expected to result in lower levels of fitness outside of the site of maternal origin. We have demonstrated that the plastic responses of maternal families vary, in terms of the traits in which plants display plasticity, and it has been demonstrated that plasticity can be triggered by a variety of environmental cues (Sultan et al. 2000; McLean et al. 2014; Aspelmeier & Leuschner 2004). For example, the plasticity of a particular genotype may only be beneficial for the plant when the conditions become colder, warmer, wetter or drier than the condition experienced in the common gardens. Therefore, plasticity which may be adaptive in the native environment, may be maladaptive in a novel one.

Further, plasticity could be affected by a covariate that simultaneously decreases fitness and increases plasticity. Another possibility is that plants could be coming from environments which are more heterogeneous than that of the common garden, and therefore, their capacity for plastic may not be beneficial in the common garden. Further research could deepen our understanding of the cost benefit of plasticity in valley oaks.

Conclusions

Valley oak shows evidence in support of the hypotheses that environmental heterogeneity leads to the evolution of phenotypic plasticity. We found that that leaf traits show significant genetic differentiation among maternal families, a significant interaction between genetic and garden effects, and that plasticity varies along clines of seasonality, especially in terms of temperature. Collectively these findings suggest that plasticity may be locally adapted. Families from the north, west, higher elevations tend to be more plastic overall. Leaf lobedness, which shapes water and heat retention in plants, was the most plastic leaf trait across the common gardens. Such findings indicate that some valley oak populations possess some degree of resiliency to changing climates, but they may also do so at a cost to growth rates. Future research could utilize evidence from the common gardens on growth rates to model impact of future climates on valley oak and could include specific experiments to assess the extent to which such resiliency will allow some populations to tolerate future climate change.
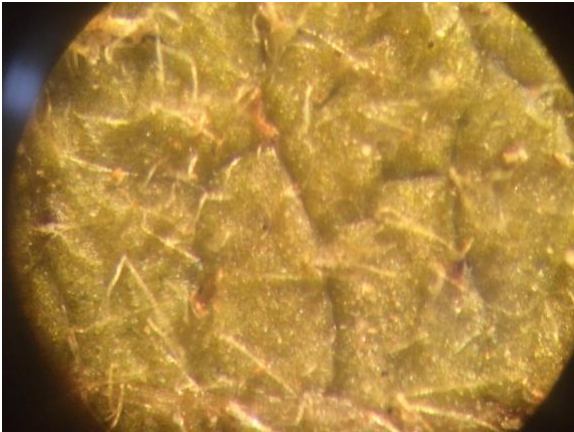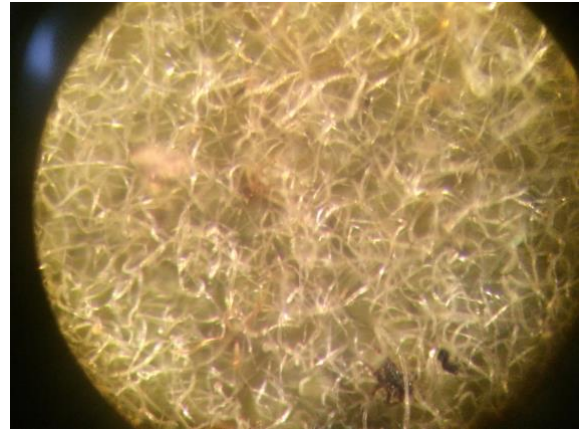
Figure 1. Microscope images demonstrating variation in leaf traits of *Quercus lobata*. As examples, we compare leaves with few trichomes (a) and dense trichomes (b), and leaves with high (c) and low (d) measures of lobedness.
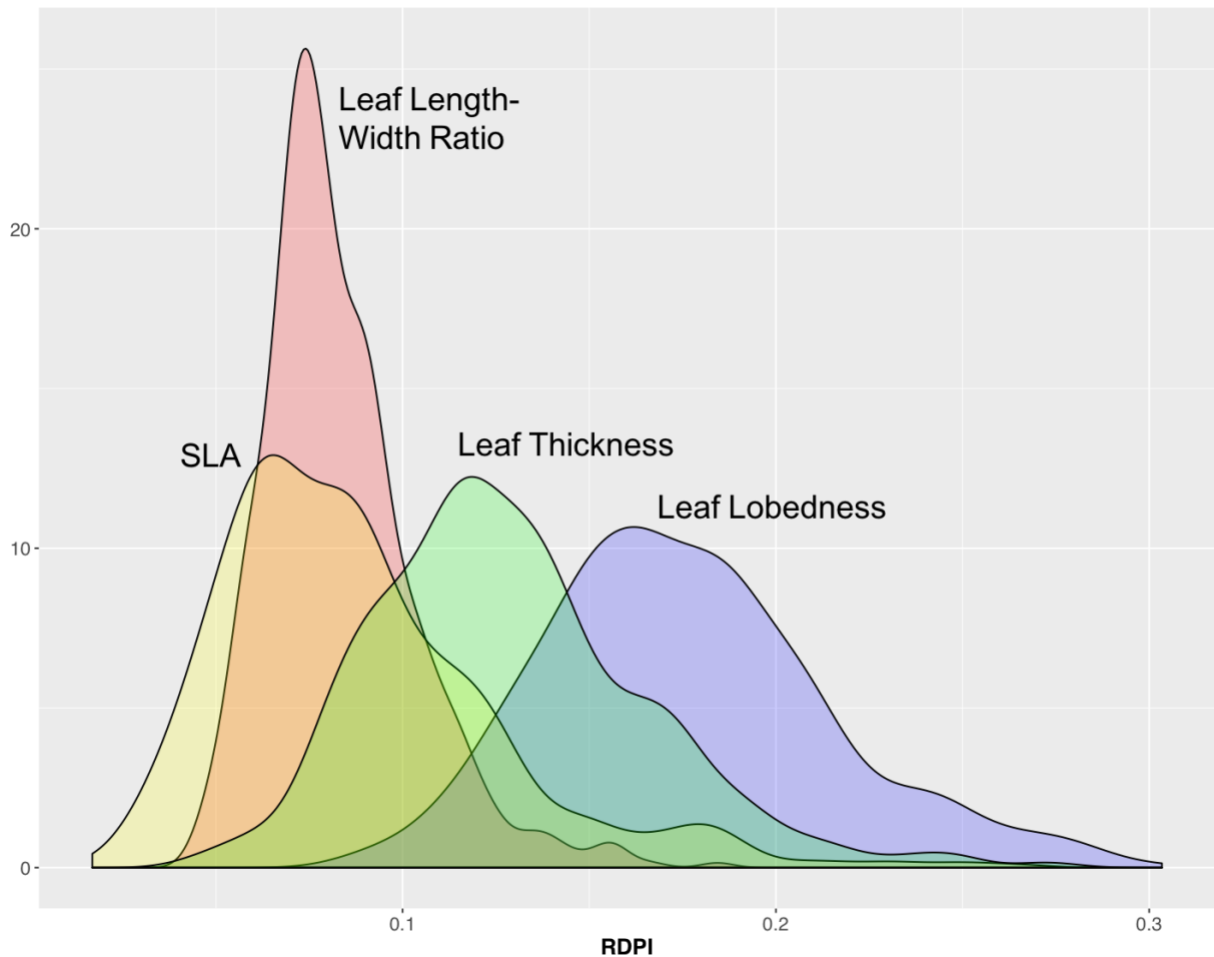
Figure 2. Frequency distributions of measures of Relative Distance Plasticity Index (RDPI) measures of maternal families for five different leaf traits. RDPI is on a scale from 0 to 1 so that 1 denotes maximal plasticity and 0 denotes no plasticity. Leaf thickness RDPI (median = 0.125, 95% CI [0.121, 0.128]), is significantly different from all others, as is lobedness (median = 0.172, 95% CI [0.168, 0.176]). Leaf length-width ratio RDPI (median = 0.079, 95% CI [0.078, 0.081]) and SLA (median = 0.081, 95% CI [0.078, 0.085]) are not significantly different from each other, but are significantly different from the other two leaf traits. Trichome density is not included, because it is a categorical measure, and so cannot be compared to continuous measures.
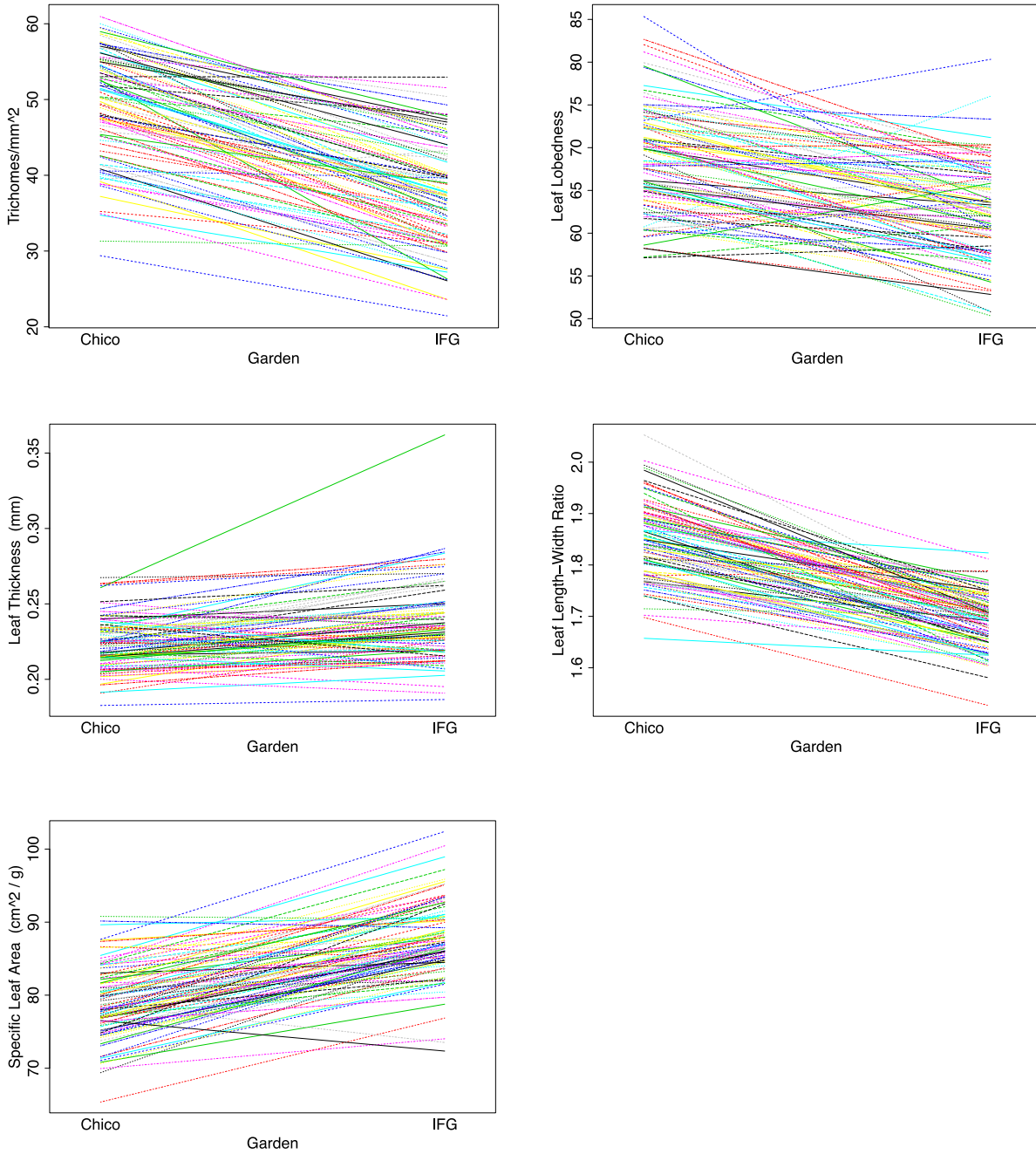
Figure 3. Interaction between provenance × garden for 95 populations of *Quercus lobata* grown across two common gardens in Placerville and Chico, California for five leaf traits.
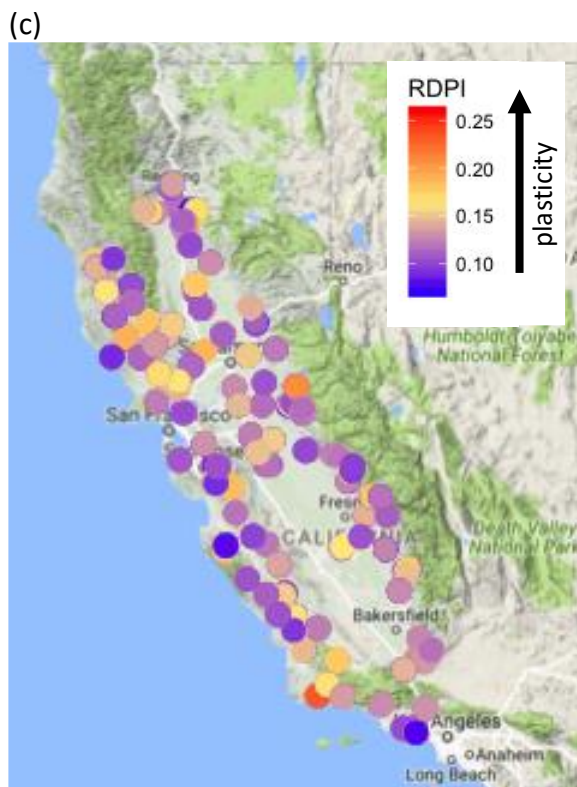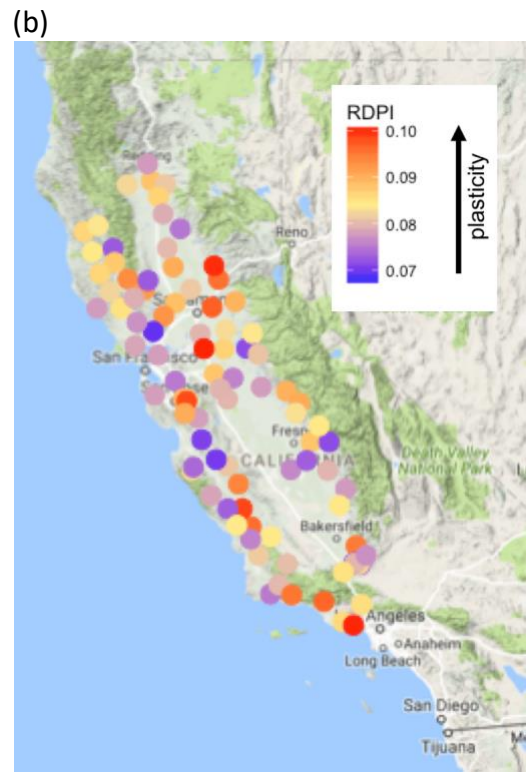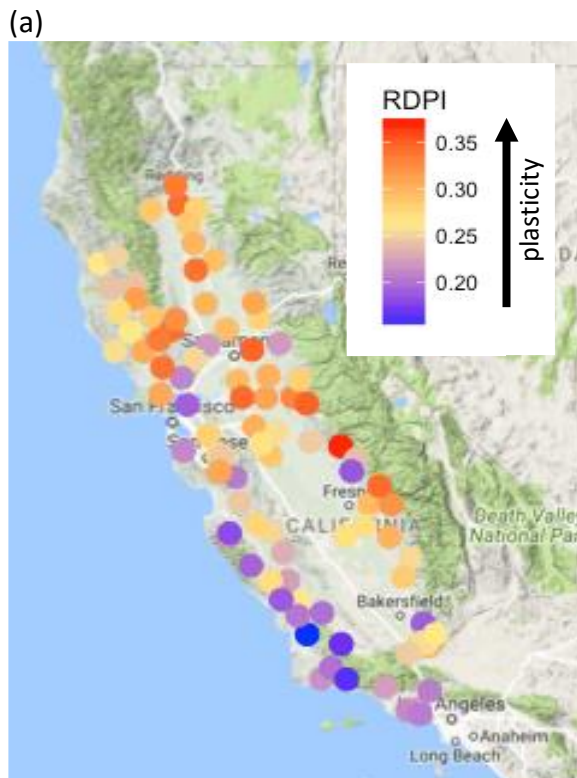
Figure 4. Maps showing geographical variation in plasticity of trichome density (a), leaf length-width ratio (b), and leaf lobedness (c).
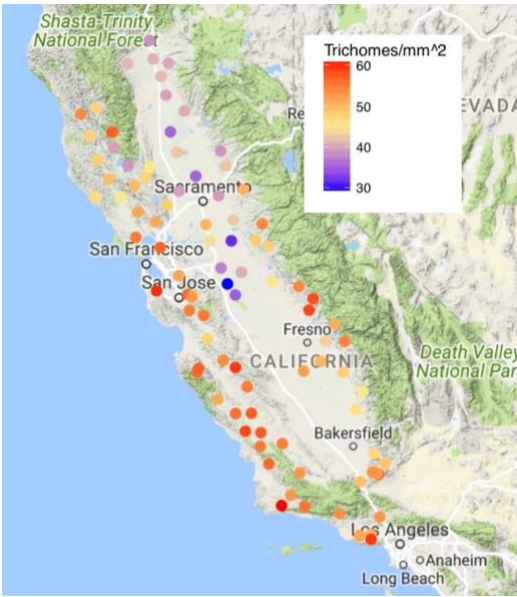
(a)
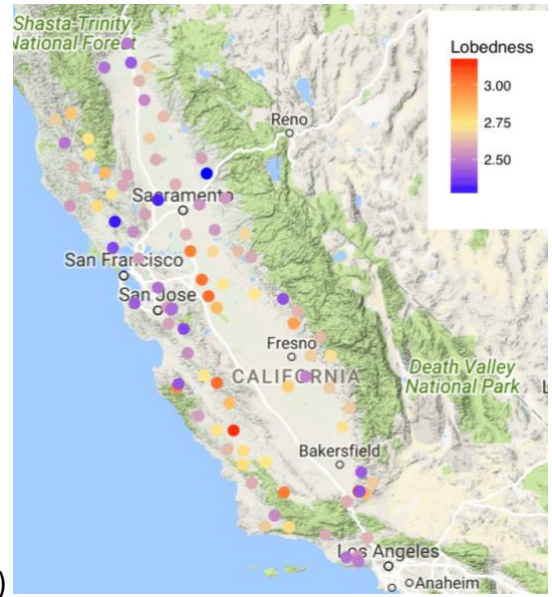
(b)
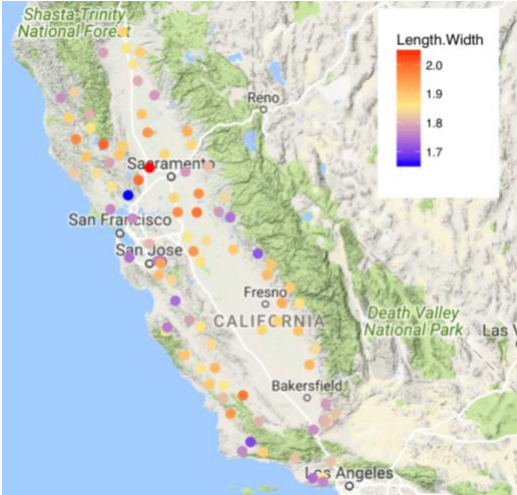
(c)
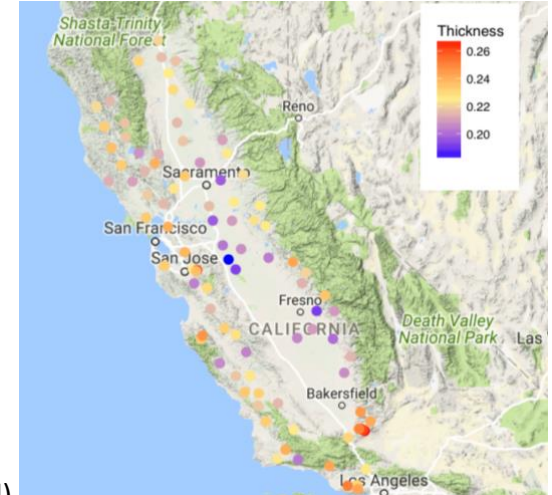
(d)
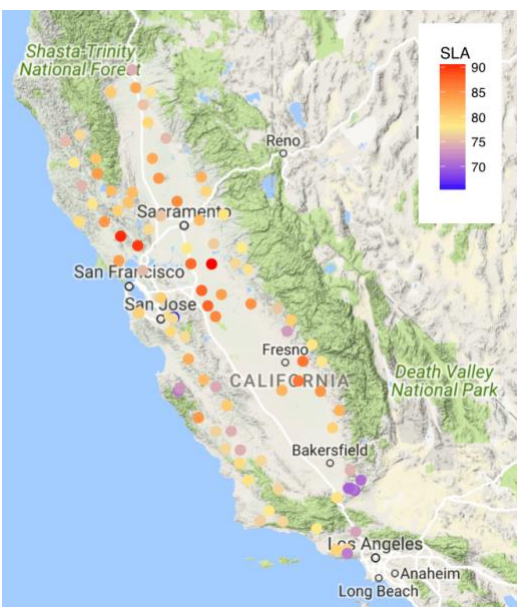
(e)

Figure 5. Maps showing variation in leaf trait values in the Chico common garden based on site of maternal origin.

(a)

(b)

(c)

(d)
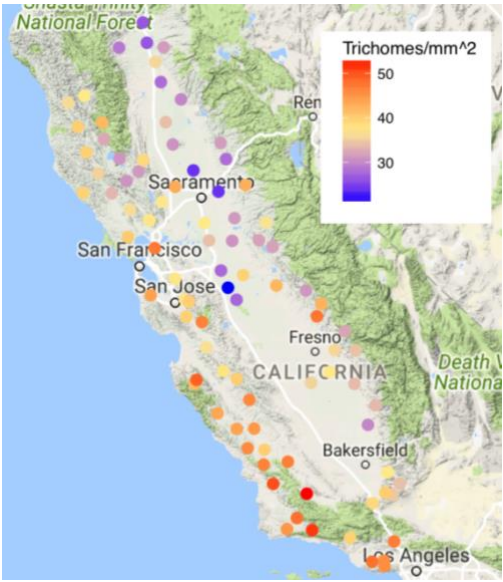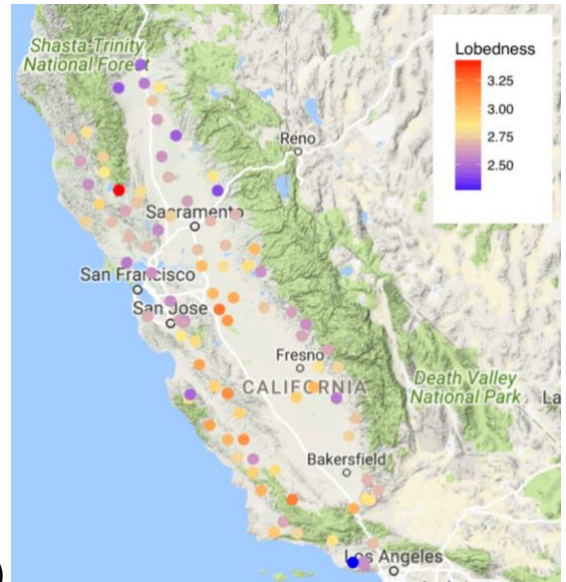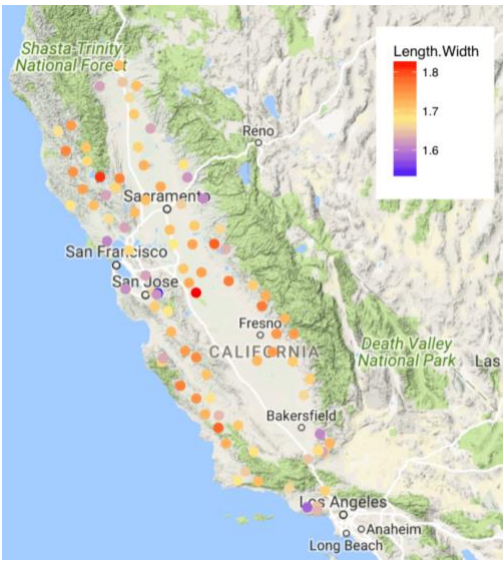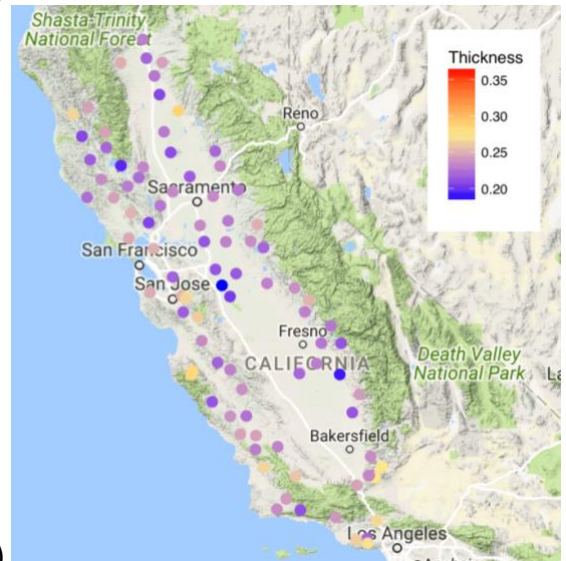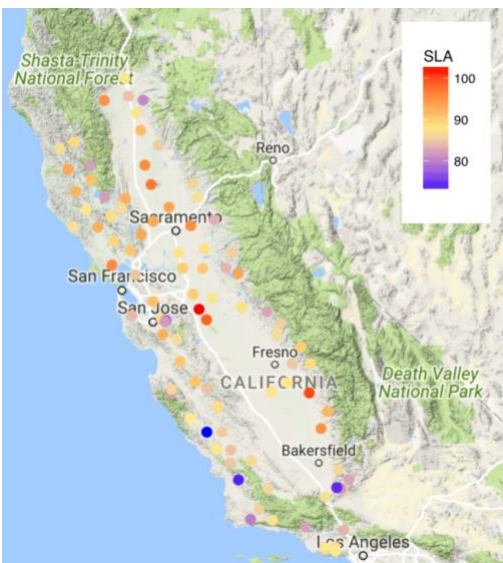
Figure 6. Maps showing variation in leaf trait values in the IFG common garden based on site of maternal origin.

(e)

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Table 1. Spatial and climate variables associated with the sampling locality of maternal tree, which are used as predictor variables in the AIC analysis testing association with the phenotypic plasticity index (Tables 3, 4, 5 and 6).

Geography Variables
Latitude
Latitude^2
Longitude
Longitude^2
Elevation
Elevation^2
Latitude * Latitude

Between-Year Variation in Climate
Variation in mean warmest month temperature
Variation in spring mean maximum temperature
Variation in spring mean minimum temperature
Variation in spring precipitation

Mean Annual Climate Variables
Maximum temperature of warmest month
Spring precipitation

Within-year Variation in Climate
Temperature seasonality
Precipitation seasonality

Table 2. Two-way ANOVA tests of the effects of common garden site, block within the common garden, provenance, family and the interaction of garden and provenance on five functional traits in the common gardens. Effects are illustrated graphically in Figure 3. These models test the traits values themselves as opposed to plasticity in the traits. ***P < 0.001; **P < 0.01; *P < 0.05; **+** P < 0.1.

Trichome Density

Fixed Effects	Df	Estimate	SE	P
Garden	1	-1.0569	0.1026	***
Random Effects		Variance	SD	
Block(Garden)	9	0.0142	0.1193	***
Provenance	94	0.3309	0.5753	***
Family(Provenance)	657	0.1038	0.3221	***
Garden * Provenance	94	0.0578	0.2404	+

Leaf Thickness

Fixed Effects	Df	Estimate	SE	P
Garden	1	0.0114	0.0145	
Random Effects		Variance	SD	
Block(Garden)	9	0.0003	0.0183	***
Provenance	94	0.0002	0.0144	***
Family(Provenance)	657	0.0003	0.0167	***
Garden * Provenance	94	0.0002	0.0152	***

Leaf Lobedness

Fixed Effects	Df	Estimate	SE	P
Garden	1	-7.684	2.207	**
Random Effects		Variance	SD	
Block(Garden)	9	8.45	2.91	***
Provenance	94	25.40	5.04	***
Family(Provenance)	657	47.51	6.89	***
Garden * Provenance	94	25.23	5.02	***

Table 2, continued

Leaf Length : Width Ratio

Fixed Effects	Df	Estimate	SE	P
Garden	1	-0.1787	0.0188	***
Random Effects		Variance	SD	
Block(Garden)	9	0.0006	0.0245	***
Provenance	94	0.0027	0.0517	***
Family(Provenance)	657	0.0052	0.0720	***
Garden * Provenance	94	0.0016	0.0400	***

Specific Leaf Area

Fixed Effects	Df	Estimate	SE	P
Garden	1	8.262	1.594	***
Random Effects		Variance	SD	
Block(Garden)	9	8.444	2.906	***
Provenance	94	16.145	4.018	***
Family(Provenance)	657	4.754	2.180	***
Garden * Provenance	94	11.984	3.462	***

Table 3. Summary of AIC results for models relating the relationship between measures of geography in the sites of maternal origin and plasticity in the common gardens. Models are presented in the order in which they were made. Model 1 includes all of the geography variables noted in Table 1 as predictors of plasticity for a given leaf trait. Each model in the table is a revision on the previous model, such that in order to make each model, the least significant variable was removed from the previous model. The best model, as determined by the AIC value is bolded and is represented in table 5. Model 8 includes no predictors. AIC values and Adjusted R^2 values are given. Δ AIC values indicate the change in the model's AIC value from the previous model.

	Trichome Density			Leaf Thickness			Leaf Lobedness			Leaf Length : Width			Specific Leaf Area		
	AIC	Δ AIC	R^2	AIC	Δ AIC	R^2	AIC	Δ AIC	R^2	AIC	Δ AIC	R^2	AIC	Δ AIC	R^2
Model 1	**-1281.33**	**0**	0.139	-2395.80	0	0.009	-2642.57	0	0.008	-3100.74	0	-0.000	-2350.28	0	-0.004
Model 2	**-1281.63**	**-0.29**	0.137	-2398.99	-3.19	0.010	-2642.24	0.34	0.004	-3101.57	-0.83	-0.001	-2352.03	-1.75	-0.003
Model 3	-1278.98	2.64	0.132	-2400.99	-2.00	0.012	-2642.82	-0.58	0.004	-3103.47	-1.91	0.001	-2353.60	-1.57	-0.002
Model 4				-2402.93	-1.94	0.014	-2644.44	-1.62	0.004	-3104.73	-1.26	0.001	-2354.95	-1.35	-0.002
Model 5				-2402.91	0.02	0.012	-2646.38	-1.94	0.005	-3103.50	1.23	-0.002	-2356.43	-1.48	-0.001
Model 6				-2398.88	4.03	0.004	-2648.33	-1.94	0.006	-3104.75	-1.25	-0.002	-2358.43	-2.00	0.001
Model 7							-2644.44	3.88	0.008	-3106.05	-1.30	-0.001	**-2358.98**	**-0.55**	**-0.000**
Model 8										-3107.95	-1.91	NA	**-2360.03**	**-1.04**	**NA**

Table 4. Summary of AIC results for models relating the relationship between measures of climate in the sites of maternal origin and plasticity in the common gardens. Models are presented in the order in which they were made. Model 1 includes all of the climatic variables noted in Table 1 as predictors of plasticity for a given leaf trait. Each model in the table is a revision on the previous model, such that in order to make each model, the least significant variable was removed from the previous model. The best model, as determined by the AIC value is bolded and is represented in Table 6. Model 9 includes no predictors. AIC values and Adjusted R^2 values are given. Δ AIC values indicate the change in the model's AIC value from the previous model.

	Trichome Density			Leaf Thickness			Leaf Lobedness			Leaf Length : Width			Specific Leaf Area		
	AIC	Δ AIC	Adj. R^2	AIC	Δ AIC	R^2	AIC	Δ AIC	R^2	AIC	Δ AIC	R^2	AIC	Δ AIC	R^2
Model 1	-1254.15	0	0.103	-2401.99	0	0.020	-2644.32	0	0.012	-3112.02	0	0.019	-2348.97	0	-0.005
Model 2	-1255.02	-0.87	0.103	-2403.46	-1.47	0.021	-2646.30	-1.98	0.014	-3113.88	-1.86	0.020	-2350.96	-1.99	-0.003
Model 3	-1255.70	-0.68	0.102	-2405.04	-1.58	0.021	-2647.45	-1.15	0.014	-3115.09	-1.21	0.021	-2352.72	-1.76	-0.002
Model 4	-1257.69	-1.99	0.104	-2405.46	-0.42	0.021	-2649.45	-2.00	0.016	**-3116.83**	**-1.74**	**0.022**	-2354.72	-2.00	-0.001
Model 5	-1258.42	-0.74	0.104	**-2407.08**	**-1.62**	**0.022**	-2649.91	-0.47	0.015	-3117.60	-0.77	0.022	-2356.58	-1.86	0.001
Model 6	-1258.28	0.14	0.102	**-2407.56**	**-0.48**	**0.021**	-2651.83	-1.92	0.016	-3117.04	0.56	0.019	-2358.011	-1.43	0.002
Model 7	-1258.19	0.09	0.100	**-2405.64**	**1.92**	**0.016**	-2650.96	0.87	0.013	-3116.82	0.21	0.017	-2357.85	0.17	-0.001
Model 8	-1253.04	5.15	0.092				-2648.45	2.52	0.008				**-2358.89**	**-1.04**	**-0.000**
Model 9													**-2360.03**	**-1.14**	**NA**

Table 5. Summary of test results produced by linear models of the effect of the relationship between measures of geography in the sites of maternal origin and plasticity in the common gardens. Black spaces indicate the predictor was removed from the model based on AIC criteria (Table 3). Positive estimates of the predictor are indicated by (+) and negative estimates are indicated by (−), and where these signs are bolded indicates that the variable was found in the best model based on AIC criteria. Predictor variables found in models which were within 2 AIC points of the best model are included and are not bolded.

	Trichome Density	Leaf Thickness	Leaf Lobedness	Leaf Length-Width	Specific Leaf Area
Geography Variables					
Latitude	**(−)**				
Latitidue^2	**(−)**				
Longitude	(−)				(+)
Longitude^2	(−)				
Elevation	**(−)**				
Elevation^2	**(+)**				
Latitude * Longitude	**(−)**				

Table 6. Summary of test results produced by linear models of the effect of climate variables on plasticity across two common gardens of five leaf traits using climate in the sites of maternal origin. Black spaces indicate the predictor was removed from the model based on AIC criteria (Table 4). Positive estimates of the predictor are indicated by (+) and negative estimates are indicated by (−), and where these signs are bolded indicates that the variable was found in the best model based on AIC criteria. Predictor variables found in models which were within 2 AIC points of the best model are included and are not bolded.

	Trichome Density	Leaf Thickness	Leaf Lobedness	Leaf Length-Width	Specific Leaf Area
Mean Annual Climate Variables					
Maximum temp. of warmest month		**(−)**			
Spring precipitation			**(−)**	**(+)**	
Within-year Variation in Climate					
Precipitation seasonality		**(−)**		**(+)**	
Temperature seasonality		(+)	(+)	**(+)**	
Among-Year Variation in Climate					
Variation in mean warmest month temp		**(−)**		**(+)**	
Variation in spring mean maximum temp					(+)
Variation in spring mean minimum temp			**(+)**		
Variation in spring precipitation			**(+)**	(−)	

Table 7: MANOVA test of the relationship between geography of the sites of maternal origin and plasticity of five leaf traits, using mean values of plasticity per maternal family grown in the common gardens. Degrees of freedom (Df), Pillai trace value, F values, and significance levels are provided. ***P < 0.001; **P < 0.01; *P < 0.05; **+** P < 0.1. Pillai trace values measures contribution to a model. They are a statistic ranging from 0 (small contribution to the model) to 1 (larger contribution to the model).

Factors	Df	Pillai	F	num Df	Den Df	Pr (>F)
latitude	1	0.0862	19.593	3	621	***
longitude	1	0.0546	12.004	3	621	***
elevation	1	0.0199	4.216	3	621	**
I(latitude^2)	1	0.0105	2.211	3	621	**+**
I(longitude^2)	1	0.0072	1.496	3	621	
I(elevation^2)	1	0.0137	2.894	3	621	*
Latitude : longitude	1	0.0027	0.570	3	621	
Residuals	625					

Table 8: MANOVA test of the relationship between geography of the sites of maternal origin and plasticity of five leaf traits, using mean values of plasticity per maternal family grown in the common gardens. Degrees of freedom (Df), Pillai trace value, F values, and significance levels are provided. ***P < 0.001. Pillai trace values measures contribution to a model. They are a statistic ranging from 0 (small contribution to the model) to 1 (larger contribution to the model).

Factors	Df	Pillai	F	num Df	Den Df	Pr (>F)
temperature seasonality	1	0.0934	21.573	3	628	***
precipitation seasonality	1	0.0068	1.432	3	628	
Residuals	630					

Table 9: MANOVA of the association between maternal family plasticity of leaf trichome density, leaf lobedness and leaf thickness, and two components of fitness: height and number of leaves. Degrees of freedom (Df), Pillai trace value, F values, and significance levels are provided. ***P < 0.001. Pillai trace values measures contribution to a model. They are a statistic ranging from 0 (small contribution to the model) to 1 (larger contribution to the model).

Factors	Df	Pillai	F	num Df	Den Df	Pr (>F)
Trichome Density Plasticity	1	0.0238	13.724	2	1126	***
Thickness Plasticity	1	0.0027	1.548	2	1126	
Leaf Lobedness Plasticity	1	0.0202	11.612	2	1126	***
Leaf Length:Width Plasticity	1	0.0003	0.146	2	1126	
SLA Plasticity	1	0.0010	0.589	2	1126	
Residuals	627					

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