VARIATION IN LEAF SHAPE IN A *QUERCUS LOBATA* COMMON GARDEN: TESTS FOR ADAPTATION TO CLIMATE AND PHYSIOLOGICAL CONSEQUENCES

HE-LO RAMIREZ, CHRISTOPHER T. IVEY
Department of Biological Sciences, California State University, Chico, CA 95929-0515
crivey@csuchico.edu

JESSICA W. WRIGHT
USDA Forest Service, Pacific Southwest Research Station, 1731 Research Park Drive, Davis, CA 95618

BRANDON W. S. MACDONALD, VICTORIA L. SORK
Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095-1438

ABSTRACT

Oak leaf morphology is highly variable. Leaf shape in oaks has been shown to covary with climate, and leaf dissection is negatively correlated with hydraulic resistance. Such patterns may reflect local adaptation of genotypes or plastic responses to local environments. We tested two hypotheses regarding variation in leaf shape in *Quercus lobata* Née, a widely distributed oak tree endemic to California, using subsamples of trees from a large provenance trial involving source populations throughout the species range. First, we tested the hypothesis that variation in leaf dissection (perimeter \(^2\)/area \(^1\)) and specific leaf area could be explained by adaptation to climate. If so, we predicted that the progeny of trees originating from contrasting climates would also contrast in leaf dissection or specific leaf area when grown in a common environment. Second, we tested the hypothesis that variation in leaf dissection is associated with photosynthetic rate. Because dissection affects hydraulic resistance and heat transfer, more dissected leaves are thought to experience lower water stress. If so, we predicted that individuals with more dissected leaves would maintain higher rates of photosynthesis than those with less dissected leaves, especially during hot and dry conditions. We found no association of leaf traits with maternal climate, but we observed a positive relationship between leaf dissection and photosynthetic rates. This result suggests variation in leaf shape may have functional consequences and influence how valley oaks cope with environmental stress in California’s Mediterranean climate.

Key Words: adaptation, climate, common garden, dissection, leaf shape, photosynthesis, *Quercus lobata*, water stress.

Leaves are the primary organs of carbon assimilation, water relations, and energy balance in plants, and thus leaf traits that affect fitness, such as morphology, may be under strong selection, with optimal leaf morphology depending on local environmental conditions (Givnish 1978; Wright et al. 2005; Ferris 2019). The shape of leaves can affect plant thermoregulation, vulnerability to drought, resistance to herbivory, and light interception, among other processes (Nicotra et al. 2011; Ferris 2019), any of which may have consequences for plant survival and reproduction. The potential for local adaptation in leaf traits should be especially pronounced in widely distributed species that experience substantial variation in local climatic conditions (Valladares et al. 2000; Royer 2012; Ramírez-Valiente et al. 2017a).

Oaks (genus *Quercus*) are well known for harboring substantial intraspecific variation in leaf morphology, and this variation may reflect different ecological strategies (Jensen 1990; Valladares et al. 2000). Previous studies, for example, have shown that specific leaf area and leaf shape of some oak species covary with climatic variables, including temperature and precipitation (Kolb et al. 1990; Valladares et al. 2000; MacDonald 2017) and elevation (Albarrán-Lara et al. 2015). Ramirez-Valiente et al. (2017b), for example, reported that genetically based variation in functional leaf traits among populations of *Q. oleoides* Schltdl. & Cham., including specific leaf area and lamina size, resulted from adaptation to precipitation regimes. In addition, Sisó et al. (2001) found that leaf dissection is negatively associated with hydraulic resistance in several North American *Quercus* species, indicating a functional consequence of leaf dissection that may drive adaptation. Leaf dissection appears to improve heat transfer (Gurevitch and Schuepp 1990), which likely is adaptive for plants exposed to high temperatures. Taken together, studies of oaks suggest that leaf morphological variation adaptively mediates responses to the environment (e.g., Abrams 1990; Cavender-Bares et al. 2004; Riordan et al. 2016).

In this study, we tested two hypotheses regarding variation in leaf morphology of *Quercus lobata* Née, California’s valley oak, in the context of a large common garden experiment (Delfino-Mix et al.
Leaf morphology in valley oak has been found to vary with elevation (Albarrán-Lara et al. 2015) and to differ genetically among populations (MacDonald 2017). In addition, the broad topographic and geographic distribution of valley oak, including the Central Valley, Sierra Nevada foothills, and Costal Ranges of California (Tyler et al. 2006) suggests that the substantial variation in climate across its range may have imposed selection on important morphological and physiological traits (MacDonald 2017; Browne et al. 2019). First, we tested the idea that variation in leaf morphology is explained by adaptation to the climate in which a population evolves. If so, we predicted that trees grown from acorns originating in contrasting climates would differ in leaf morphology even when grown in a common garden. Second, we tested the hypothesis that variation in leaf morphology is associated with photosynthetic rate. Higher photosynthetic rates are positively associated with individual fecundity (e.g., Arntz et al. 2000) and population growth (e.g., Westerband and Horvitz 2017) in many plants (reviewed in Ackerley et al. 2000). Sisoé et al. (2001) found that more dissected leaves of several Quercus species experienced reduced hydraulic resistance, which may allow individuals with dissected leaves to have improved water balance, especially during periods of drought stress. If leaf dissection ameliorates water stress, we predict that more dissected leaves would have higher carbon assimilation rates (a measure of photosynthesis), particularly during periods of water stress, given the demands of photosynthesis for water use.

METHODS

Study Species

Valley oak (Quercus lobata [Fagaceae]) is an iconic, keystone species within California, and it provides a useful study system because of its broad geographic range, as well as the availability of extensive background information. Valley oak populations harbor fine-scale genetic structure (Dutech et al. 2005), leading to the potential for local adaptation to environmental conditions. This structure is likely a consequence of relatively restricted effective distances of pollen-mediated and seed-mediated gene flow (Sork et al. 2002; Grivet et al. 2005; Grivet et al. 2009; Sork et al. 2015). In addition, genetic structure for putatively neutral loci (Sork et al. 2010; Gugger et al. 2013), as well as non-neutral loci (Sork et al. 2016) has been shown to be correlated with climate gradients, which supports the idea that this species has adapted to climate (see also Browne et al. 2019). Moreover, valley oak leaves appear to harbor substantial morphological variation, from genetic as well as environmental sources (MacDonald 2017). A range-wide field study of valley oaks reported geographic variation in morphological as well as physiological traits (R. Coria, K. D. Gaddis, J. M. Espelta, and V. L. Sork, unpublished data). Valley oak is currently threatened throughout its range (Tyler et al. 2006; Mclaughlin and Zavaleta 2012) due to extensive habitat loss (Whipple et al. 2011), and the species is predicted to experience a substantial reduction in available habitat within the next century due to climate change (Kueppers et al. 2005; Sork et al. 2010). In addition, valley oak is sensitive to water stress, especially as seedlings (Meyer 2002).

Experimental Design

This study was conducted using a large fully replicated provenance test established at two locations, in which acorns collected from maternal trees were grown in a common environment (for details of study see Delfino-Mix et al. 2015). In fall 2012, 20 acorns were collected from each of 672 mature trees at 95 localities (provenances) across the native range of valley oak. On 14 and 15 November 2012, up to 16 surface-sterilized acorns within a maternal family (total 10,326) were planted into containers and reared in a lath house under 50% shade cover. In late 2014 and early 2015, five saplings (maternal families) from each sampled mature tree were transplanted into large field plots using a randomized block design at each of two locations: (1) the Chico Seed Orchard (“Chico”) in Chico, CA and (2) the Institute of Forest Genetics (“Placerville”) in Placerville, CA (Fig. 1). The two sites are quite distinct climatically, but both fall within the range of climate variation across the sites from which acorns were
collected (Delfino-Mix et al. 2015). Chico is a warmer, drier climate (68 m elevation; Mean Annual Temperature [MAT] 16.4 °C; Mean Annual Precipitation [MAP] 64.1 cm), while Placerville has a cooler, wetter climate (838 m elevation; MAT 14.5°C; MAP 103.8 cm; Wang et al. 2016). Both tests were irrigated periodically during summers during our study, and competing vegetation was controlled with mowing and herbicide. See Delfino-Mix et al. (2015) for more information about sampling, cultivation, and design of the provenance trial.

**Sampling and traits**

To test for leaf morphological adaptation to climate, we identified a subset of 180 trees within the provenance test representing the extremes and median of multivariate maternal climatic conditions based on a principal component analysis of a 30-year (1971-2000) georeferenced baseline dataset of 23 annual climate variables (Wang et al. 2016) at the source locations for the 672 maternal lineages. Six maternal lines were selected from among each of the highest, lowest, and median scores for the first principal component of all climate variables with the stipulation that no more than two maternal lines were selected from one locality (Fig. 1). The first principal component explained 43.8% of the variance in the climate data and was most strongly associated with variables involving temperature and seasonality (strongest positive factor loadings included mean annual temperature [0.28], degree-days > 5°C [0.28], and number of frost-free days [0.25]; strongest negative factor loadings included degree-days below 18°C [-0.30], mm precipitation as snow [-0.27], and degree-days below 0°C [-0.25]). We haphazardly sampled five leaves from all progeny (n = 5) from each of the 18 focal maternal lineages within each of the two experimental sites (Chico and Placerville; because progeny mortality led to incomplete sampling, the total trees sampled = 141 and total leaves sampled = 707). We measured the area (mm²) and perimeter (mm) of each leaf from scanned images of fresh leaves using ImageJ (Schneider et al. 2012). Leaves were then dried to constant mass at 50 °C, a reference chamber CO2 concentration (400 ppm). For leaves that were too small or deeply lobed to completely fill the area of the 2 cm² chamber, the area of leaf tissue inside the chamber was calculated manually by tracing the edges of the leaf inside the chamber with ink, removing the leaf from the tree, and later scanning an image of the leaf using a digital scanner. We then used ImageJ (Schneider et al. 2012) to estimate the measured area of each leaf, and gas exchange estimates were adjusted based on these values using the Li-Cor recompute utility. In addition, we used ImageJ to measure the area (mm²) and perimeter (mm) of each leaf, which were then used to calculate leaf dissection as described above.

To test the association between leaf morphology and photosynthesis, we selected trees to subsample within the Chico site using leaf trait data collected by MacDonald (2017), which included all progeny from all 672 maternal lines within both experimental sites. MacDonald’s (2017) study tested the effects of maternal climate on plasticity (or variation) in leaf traits, whereas the current study examined mean differences in traits among climate extremes as described by the PCA scores (see above). During 2016, MacDonald (2017) measured morphological traits on five leaves from each of the 3360 trees within each of the two common garden locations. Using this larger dataset, we selected 24 of the 672 maternal lines within Chico that had mean values of leaf dissection that were high (mean [SD] = 3.553 [0.157], intermediate (2.628 [0.003]), or low (2.038 [0.056]) as reported by MacDonald (2017). Our objective with this approach was to sample trees representing a broad range of leaf dissection values across the experiment. By focusing on these lines, we assumed – and were able to test (see Results) – that variation in leaf morphology between years within a maternal line would be smaller than variation among lines.

Using a portable infra-red gas analyzer (Li-Cor 6400, LI-COR Biosciences, Lincoln, NE) we measured carbon assimilation (A, μmol CO2 · m⁻² · s⁻¹) on three leaves from each of a total of 28 progeny chosen among 17 of the 24 targeted maternal lines to maximize representation across expected leaf dissection values, based on measurements from 2016 (MacDonald 2017). Time constraints required for measurements with the instrument (e.g., internal equilibration required about 15 min for each leaf before measurements could be recorded) limited the number of trees we were able to sample. Measurements were collected across six days in 2018 (18, 19, 26, 29 June and 9, 13 July) in the morning between 0800 and 1200 h, prior to midday stomatal closure when photosynthetic rates fell to zero. The site was irrigated once during this period on 22 June 2018. Leaves were selected based on appearance (no apparent damage from herbivores). Internal chamber settings were as follows: photosynthetically active radiation (PAR) = 1500 μmol · s⁻¹; stomatal ratio = 1.0; flow = 500 μmol · s⁻¹; and reference chamber CO2 concentration = 400 ppm. For leaves that were too small or deeply lobed to completely fill the area of the 2 cm² chamber, the area of leaf tissue inside the chamber was calculated manually by tracing the edges of the leaf inside the chamber with ink, removing the leaf from the tree, and later scanning an image of the leaf using a digital scanner. We then used ImageJ (Schneider et al. 2012) to estimate the measured area of each leaf, and gas exchange estimates were adjusted based on these values using the Li-Cor recompute utility. In addition, we used ImageJ to measure the area (mm²) and perimeter (mm) of each leaf, which were then used to calculate leaf dissection as described above.

**Analysis**

Analyses were conducted using SAS version 9.3 (SAS Institute, Cary, NC). Specific leaf area and leaf dissection were each compared across climate categories (high, median, low) using mixed-model nested ANOVAs with the Kenward-Roger approximation for degrees of freedom. Climate category and locality (category) were included as fixed effects, and maternal family (category x locality) and individual tree (category x locality x family) were included as fixed effects.
random effects. The significance of random effects was tested using likelihood-ratio tests (Littel et al. 1996). To correct for heteroscedasticity, analyses were conducted using natural log-transformed values of leaf dissection, although means are reported below on the untransformed scale. Specific leaf area required no transformation to meet model assumptions. Separate statistical models were used for data collected from each site (Chico and Placerville). Significant differences in leaf traits among climate categories were considered consistent with the hypothesis that leaf shape evolves in response to local climate. For the Chico dataset focused on carbon assimilation and leaf morphology, variation in A (carbon assimilation) was regressed against leaf dissection using a mixed-model nested ANCOVA. Sampling date and leaf dissection were included as fixed effects, and individual tree was included as a random effect. The sampling date x leaf dissection interaction term did not significantly explain variation in A (P > 0.6), indicating that the effect of leaf dissection on A did not vary among sampling dates, so it was removed from the final model. Leaf dissection and A were both natural log-transformed prior to analysis to correct for heteroscedasticity. A significantly positive relationship between leaf dissection and A was considered consistent with the hypothesis that greater leaf dissection is associated with higher photosynthetic rates.

**RESULTS**

Leaf dissection and specific leaf area varied widely among sampled leaves (coefficient of variation [CV] for specific leaf area = 28.4 and 19.0 for Placerville and Chico, respectively; for leaf dissection, CV = 29.8 and 25.4 for Placerville and Chico, respectively). Nonetheless, neither trait varied significantly among categories of maternal multivariate climatic characteristics at either site (Table 1; Fig. 2).

The subsampling of trees for measuring A was successful at capturing variation in leaf dissection within Chico. The CV of maternal mean leaf dissection values from the full dataset measured in 2016 was 13.6 (MacDonald 2017), whereas the CV from our 2018 subsample of 18 maternal mean leaf dissection values was 19.6. In addition, maternal mean leaf dissection scores were positively correlated across the two datasets (r_s = 0.71, P = 0.0009, n = 18), validating our assumption that measurements of leaf dissection on trees in 2016 would predict measurements during 2018. Carbon assimilation increased significantly with leaf dissection among sampled trees (Table 2; Fig. 3; Slope = 0.86). In addition, estimates of A declined over the sampling period, possibly reflecting increasing air temperature and water limitation during the early summer sampling period (Table 2; Fig. 3).

**TABLE 1. MIXED-MODEL ANALYSES OF VARIANCE OF SPECIFIC LEAF AREA (mm^2 · g^-1) AND LEAF DISSECTION (mm · mm^-2) AMONG QUERCUS LOBATA LEAVES SAMPLED FROM 180 SAPLINGS (10 PROGENY FROM EACH OF 18 FAMILIES, ORIGINATING FROM 9 LOCALITIES) PLANTED IN TWO COMMON GARDENS. Sampled trees were selected to represent extremes and median of multivariate climatic conditions of maternal source trees (see Methods). F-tests of fixed effects and \( \chi^2 \) values from likelihood-ratio tests of random effects are shown.**

<table>
<thead>
<tr>
<th>Test site</th>
<th>Trait</th>
<th>Effect type</th>
<th>Source</th>
<th>F_nift, ddf or ( \chi^2 )</th>
<th>P-value</th>
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</thead>
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<td>Specific leaf area</td>
<td>Fixed</td>
<td>Maternal climate category</td>
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<td></td>
<td></td>
<td></td>
<td>Locality (category)</td>
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<td>0.3</td>
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<td>Family (category x locality)</td>
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<td>0.9</td>
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<tr>
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<td></td>
<td></td>
<td>Individual tree (category x locality x family)</td>
<td>163.9</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Placerville</td>
<td>Specific leaf area</td>
<td>Fixed</td>
<td>Maternal climate category</td>
<td>0.02_2, 65</td>
<td>0.9</td>
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<td></td>
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<td>Locality (category)</td>
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<td></td>
<td></td>
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<td>0.9</td>
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<td>Individual tree (category x locality x family)</td>
<td>78.7</td>
<td>&lt;0.0001</td>
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</tbody>
</table>

**TABLE 2. MIXED MODEL ANALYSIS OF COVARIANCE TESTING THE EFFECTS OF LEAF DISSECTION (MM · MM^-2) AND SAMPLING DAY ON CARBON ASSIMILATION (\( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)) IN QUERCUS LOBATA GROWING IN A COMMON GARDEN EXPERIMENT AT CHICO. Twenty-eight saplings (17 families) were subsampled to maximize variation in leaf dissection (see Methods). F-tests of fixed effects and \( \chi^2 \) value from a likelihood-ratio test of the random effect are shown.**

<table>
<thead>
<tr>
<th>Effect type</th>
<th>Source</th>
<th>F_nift, ddf or ( \chi^2 )</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
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<td>Leaf dissection</td>
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<td>0.03</td>
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<td></td>
<td>Sampling day</td>
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<tr>
<td>Random</td>
<td>Individual Tree</td>
<td>8.6</td>
<td>0.003</td>
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</table>
FIG. 2. Tukey’s box plots of specific leaf area and leaf dissection (perimeter · area⁻¹) among leaves collected from *Quercus lobata* grown in common gardens in Chico (A and B) and Placerville, California (C and D) as a function of multivariate climatic characteristics of the maternal seed source (see Methods). See Table 1 for results of statistical tests.

FIG. 3. Carbon assimilation as a function of leaf dissection (perimeter · area⁻¹ in mm · mm⁻²) in *Quercus lobata* sampled at the Chico common garden site. Sampling day was included in the model as a covariate. Carbon assimilation and dissection were log-transformed for analysis (see Methods). See Table 2 for results of statistical tests.
DISCUSSION

Oak leaves are well known to harbor tremendous variation in shape. We explored two hypotheses associated with that variation. First, we tested the hypothesis that variation in leaf shape among populations is a consequence of adaptation to prevailing climatic conditions. Previous studies have reported that leaf morphological traits, including leaf dissection, vary with climate and other site characteristics (Ogaya and Peñuelas 2007; Peppe et al. 2011; Royer 2012; Albarra´n-Lara et al. 2015; Riordan et al. 2016; MacDonald 2017). If this hypothesis were true, we would expect variation in leaf morphology among trees in the common garden to be associated with the climatic conditions of the maternal source trees, because of inherited leaf morphological variations from the maternal trees. We instead found that the wide variation in leaf morphology observed was not associated with variation in climate, thus failing to support this hypothesis (Fig. 2). This may indicate that leaf dissection is principally influenced by the environment. Trait plasticity in response to climate may itself be adaptive in variable environments and could facilitate species persistence in response to climate change in circumstances where adaptive evolution is slow (Hoffmann and Sgrò 2011; but see MacDonald 2017). On the other hand, phenotypic variation in leaf morphology may be genetically controlled, but not associated with adaptation to climate. MacDonald (2017), in a much larger study of leaf morphology within the common garden, reported significant variation among family lines for leaf dissection and specific leaf area, which suggests that variation is genetically based.

The extent to which leaf morphological variation in natural populations of Q. lobata is associated with climate is unclear, although the data herein may provide additional insight into this hypothesis. Albarra´n-Lara et al. (2015) examined phenotypic variation in Q. lobata leaves sampled from 127 adults distributed among three elevational transects and found substantial morphological variation, although climatic variation within transects was relatively small. Leaf thickness in the progeny of the sampled trees was positively correlated with maximum temperature of the site of maternal trees (Albarra´n-Lara et al. 2015). Other studies of oaks have reported that leaf morphology varies adaptively in response to climate (Abrams 1990; Cavender-Bares et al. 2004; Riordan et al. 2016; but see Royer et al. 2008). We suggest that study of phenotypic variation in field populations of valley oak across its range may provide additional insight into the validity of the hypothesis that leaf morphology is associated with climate.

Second, we tested the hypothesis that variation in leaf shape has a functional consequence for plant physiology. We found that more dissected leaves had higher photosynthetic rates (Fig. 3), which is consistent with this hypothesis. Carbon assimilation (A) measurements were collected during June and July, and A decreased over the period during which data were collected. California’s central valley, where Chico is located, has a very hot, dry season typically beginning in May; during the study no precipitation fell and temperatures routinely exceeded 35°C (University of California, Division of Agriculture and Natural Resources 2019). Even though the site was irrigated for one day during the time we collected A measurements (see Methods), the intensity of water stress experienced by the trees may have increased throughout this period. We avoided collecting A measurements for four days following the irrigation event to minimize its impact on our data. In any event, declines in A with increasing water stress are not uncommon (Chaves 1991; Osakabe et al. 2014), thus the temporal decline in A that we observed may have been a consequence of increased water stress experienced by trees.

The positive relationship between leaf dissection and A may be a consequence of water relations. Prior research, for example, has found variation in leaf dissection in oaks to be negatively associated with hydraulic resistance (Sisó et al. 2001). Similarly, Nicotra et al. (2008) found higher A and greater water loss in leaves of Pelargonium that were more dissected. In addition, other studies have suggested that a dissected morphology improves air exchange across leaf surfaces, leading to a more efficient transfer of heat (Gurevitch and Schuepp 1990). Thus, as early summer became increasingly hot, individual trees with more dissected leaves may have experienced reduced water stress, and consequently, these individuals may have been able to maintain higher photosynthetic rates under dry conditions than trees with less dissected leaves. Although we were not able to collect these data during the current study, this idea could be tested by concurrent collection of plant water potential and carbon assimilation measurements in trees with a range of leaf dissection values.

This study provides evidence that variation in leaf shape found among valley oak individuals within the common garden is associated with photosynthetic rate. In addition, our results show that factors other than maternal climate influence variation in the leaf traits we measured. Some of these factors may be environmental, as the traits we measured are known to hold substantial phenotypic plasticity; MacDonald (2017), for example, found leaf dissection to be the most plastic of five leaf traits measured. Studies of other oak taxa also report plasticity in leaf morphology that is associated with functional responses to environmental variation (Wu et al. 2016; Kusi and Karsai 2019). Within the Q. lobata common garden, genetically based variation in leaf morphology has also been reported (MacDonald 2017). Oaks are known to harbor variation in leaf traits that involve adaptations to climate (Cavender-Bares 2004; Ramírez-Valiente et al. 2017a; Mead et al. 2019). Variation in leaf shape within valley oaks, whether plastic or genetic, appears to play a
functional role in mitigating environmental stress and climatic variation. Our results suggest future studies exploring the functional consequences of variation in leaf shape would be productive.

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LITERATURE CITED


