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2016

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UNIVERSITY OF CALIFORNIA
RIVERSIDE

A Study on Variation in Leaf Physiognomy of City Trees in Relation to Temperature

A Thesis submitted in partial satisfaction
of the requirements for the degree of

Master of Science

in

Plant Biology

by

Lauren Marie Velasco

March 2017

Thesis Committee:

Dr. Darrel Jenerette, Chairperson

Dr. Louis Santiago

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The Thesis of Lauren Marie Velasco is approved:

Committee Chairperson

University of California, Riverside

Acknowledgments:

I would like to acknowledge Darrel Jenerette, my advisor and co-author in this work as well as both the National Science Foundation and the National Aeronautics and Space Association for their funding of this research.

Dedication:

I would like to dedicate this work to my grandparents, who taught me the value of hard work. My grandpa Carlos, who worked so hard all of his life to be the finest in his profession that he could be. My grandpa Tom, who never let the his inability to attend college stop him from becoming a success or furthering his education. My grandma Lupe, who was there to help to raise me and let me destroy her garden on a semi-regular basis. And my grandma Doris, who gave me her love of plants, rocks, and all things natural.

ABSTRACT OF THE THESIS

A Study on Variation in Leaf Physiognomy of City Trees in Relation to Temperature

by

Lauren Marie Velasco

Master of Science, Graduate Program in Plant Biology
University of California, Riverside, March 2017
Dr. Darrel Jenerette, Chairperson

Climate models are predicting that the world will become warmer and understanding how individual tree species cope with increased temperatures will be important for making predictions of species survival. City trees are valuable resources as they include trees from a wide variety of habitats under regular watering regimes with only temperatures changing. A tree's ability to acclimate to changing temperatures may be controlled by plasticity in leaf shape. We hypothesized trees species will acclimate to increased temperatures by increasing the dissection of their leaves which would be more prominent in species with wider natural distributions. In this study we focused on 7 species growing across three sites distributed along a coastal to inland temperature gradient in southern California, USA. Selected trees had the requirement of being found in vegetated areas with regular watering in at least two of the three sites. A minimum of three specimens from each species were selected at each site. From each specimen, three recently mature, sun-exposed leaves were collected from each tree, scanned and the Dissection Index calculated. Initial measurements indicate that of the species which

have been measured two, *Platanus racemosa* ($p = 0.0265$) and *Schinus terebinthifolius* ($p < 0.001$) show increasing levels of leaf dissection across the temperature gradient while one, *Jacaranda mimosifolia*, no difference was detected ($p > 0.05$) in part because of a high degree of variability across the gradient. The species with the highest increases in dissection, *P. racemosa*, originated in limited riparian environments while the species with lower dissection levels, *S. terebinthifolius*, came from a wider environmental distribution. These findings support a hypothesis of increasing dissection with increasing heat, but do not support the hypothesis that natural habitat distributions may be linked to plasticity. The high degree of variability in *J. mimosifolia*, which is considered invasive in tropical areas of the United States, may suggest that this species may survive by producing a wide range of individual capable of surviving in different habitats.

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Introduction: Currently climate change models are predicting that many areas of the planet are only likely to become hotter and drier in the coming decades (Cayan et al 2010, Chang et al 2013). How these factors will impact individual species as well as plant communities has been studied extensively, with many predictions indicating that individual plant species will be forced to shift their distributions to cooler areas (Chakraborty et al 2013, Feeley et al 2012, Feeley et al 2013). This typically means shifting distributions upward in elevation in order to survive. While these studies may look at larger scales, focusing on the community or the species as a whole, they fail to address the subject of how an individual plant may survive increasingly warm conditions.

Unlike most animal species, which are capable of free movement from one area to another, once an individual plant becomes rooted, it must remain in that position for the remainder of its life. A plant must therefore be able to acclimate to whatever conditions it experiences or it will die. This ability to acclimate becomes important when looking at the species as a whole. While some species, such as annuals, have rapid life cycles which allow species to shift their distributions within a matter of years, longer lived, slower growing species such as tree tend not reproduce rapidly and have their ability to shift distributions hindered. It is therefore important in these longer-lived species to understand how individuals may acclimate to increasing temperatures, since their long life spans mean a greater likelihood of exposure to catastrophic conditions that cut short the typical lifetime compromise the ability to reproduce. This makes the ability to acclimate within an

individual will be an especially important question to answer in the coming years. Studying the ability to acclimate within a species may help answer the question why some species are better able to survive to temperature change than others.

This research will focus on city trees across a temperature gradient in southern California (Figure 1). The use of city trees has already proven valuable in assessing the effects of climate change on the spread and impacts of disease within major urban tree species (Yang 2009). Widespread planting of cities trees in conjunction with constant irrigation from sprinklers and drip lines in Los Angeles and Riverside counties has created an ideal system in which to measure temperature responses. Across this gradient water levels are held relatively steady while temperature increases as one moves from the coast to further inland. This system allows us to study temperature responses in mature trees without having to create a common garden experiment. While a common garden experiments are absolutely essential to the scientific process, the amount of time it would take for trees from a number of different species to reach maturity makes it somewhat less than feasible to complete.

The majority of trees being planted across this gradient come from nurseries resulting in a smaller genetic pool than wild plants. (Okon et al 2013, Williams & St. Clair 1993, Miller & Schaal 2006). I chose to focus on trees grown in parks, schools and other public areas to remove potential problems created by measuring both cultivated and wild grown trees. The focus of this work will be primarily on plastic responses of trees in terms of their leaf shape and other leaf metrics and how they

may relate back to temperature and to a lesser degree their natural habitats. Plasticity may be divided into two components: phenotypic and genotypic. This study attempts to focus solely on phenotypic plasticity by using only cultivated specimens of species that do not have multiple varieties commercially available. This allows the assumption that due to low genetic variation within cultivated populations, most of the variation may be attributed to phenotypically plastic responses. For these reasons, specifically strongly controlled water levels and lowered genetic diversity, evenly distributed across a temperature gradient that I chose to use city trees within southern California or research purposes.

People have a wide range of reasons for choosing the species that they do. They may chose to plant trees to suit specific desires including: shade, food, and aesthetics (Eichenberg et al 2009, Weller Clarke et al, 2013), specifically brightly colored flowers which would not be available in just the tree species found in California. Despite the large diversity of plant species in California, the number of native trees is comparatively small, with few of them having aesthetically pleasing blooms. As a result of this low diversity and the desire for showy species, people have selected species from around the world. These trees come from a variety of habitats including riparian habitats, tropical forests, tropical dry forests, and semi-arid regions among others. This widespread planting of trees from a number of different habitats under relatively controlled conditions will allow for assessment of a swath of species from different plant families from around the world.

Previous studies have shown specific characteristics tend to be associated with certain climate types. Research has indicated that when going into cooler climates more trees tend to exhibit smaller, simple leaves and have toothed margins (Velazquez-Rosas 2002, Royer et al. 2008), similarly additional research by Santiago et al 2009 found that within one taxon adaptive radiation resulted in species exhibiting smaller more dissected leaves in warmer more exposed environments and larger less dissected leaves in cooler forested ones. These studies suggest that there is an optimal temperature range (Gurevitch, J. 1988, Wright et al 2004, Wright et al 2005, Okajima et al 2012, Kessler et al 2007) with smaller toothed or dissected leaves at either end of the spectrum. Additional metrics such as Specific Leaf Area (SLA) have also shown differences with different temperatures, with leaves in cooler climates showing higher SLAs than those in warmer climates. Aside from studies showing variations across species there has been extensive research into variation within individual specimens (Royer et al 1008, Hamerlynck & Knapp, 1994). Many species do show some ability to acclimate microhabitats by virtue of the production of sun verses shade leaves. Tree species capable producing these types of leaves tend to produce smaller, more sclerophyllous leaves in the higher light environments and larger, thinner leaves in the lower light environments.

This variation in the shape of the leaf is an important characteristic when it comes to surviving in different environments as leaf shape affects heat dissipation, water loss, and light capture. In high light environments, light will penetrate farther into a leaf. By producing leaves that are smaller, and thicker, a plant may effectively

capture more light while suffering from less water loss. Additionally, breaking up surface area of a leaf by dissection will also reduce water loss by altering the boundary area. As air flows across a leaf's surface, friction creates eddies, which in turn produce a cushion of air over the leaf surface. The broader a leaf blade, the larger this boundary layer will be with larger boundary layers reducing the amount of heat which dissipated from a leaf. This increased temperature results in greater water loss over time. Leaf dissection or elongation reduces the thickness of a boundary layer, conserving water, a trait which will become increasingly important in warmer condition. It is for these reasons that we hypothesized that trees, under warmer conditions would acclimate and produce leaves which were more dissected, more sclerophyllous , or both.

Methods:

For this study as climate change is not limited to just species in California, we chose to focus on several tree species from a number of habitats from different regions of the world, including riparian regions, and temperate, dry tropical, and tropical forests. Two sets of related species, several un-related species. All specimens within this study were cultivated, suggesting limited genetic pool as is typical among cultivate species (Williams & St. Clair, 1993). Tree species that are known to have a variety of cultivars were removed from the studies.

Selected species:

This study will focus on seven species from different habitats and geographic regions. Of these species, there are two pairs within the same genus and two species are California natives. The first of the pairs includes the species *Platanus racemosa* and *Platanus occidentalis*. Both of these species have large, broad, palmately lobed leaves with varying levels of trichome density. *Platanus racemosa* is a California native species found primarily in riparian regions (Baldwin B. G. 2013). *Platanus occidentalis* is native to temperate forests in the eastern side of the United States. The second of the pairs contains the species *Schinus molle* and *Schinus terebinthifolius*. Both of these species are South American in origin, grow in tropical dry forests and have leaves that are pinnately compound one time with entire margins and waxy cuticles. Of the two species, the leaflets are larger and fewer in number on *S. terebinthifolius* than on *S. molle* (Moore 1006). *S. terebinthifolius* has also been documented as becoming invasive in certain regions of the United States (Meyer, 2016).

The remaining three species are *Jacaranda mimosifolia*, *Quercus agrifolia*, and *Koelreuteria bipinnata*. *Jacaranda mimosifolia*, like both the *Schinus* species, is also a South American species found in dry tropical forests. The leaves of *J. mimosifolia* are twice pinnately compound, with many small leaflets, which have entire margins, cuticles and glabrous to lightly trichomed surfaces. *Quercus agrifolia* is the second California native found in a wide variety of habitats it has broad, cup-shaped leaves with trichomes and has slightly toothed margins (Baldwin B. G. 2013, Steinberg 2002). The final species is *Koelreuteria bipinnata* is native to tropical forests in the

Asian continent. The leaves of this species are twice pinnately compound, with large glabrous leaflets with toothed margins.

Sites:

Three sites were selected along a temperature gradient in southern California in Los Angeles, Riverside and Palm Desert. Average temperatures were calculated from data collected from the Western U.S. Historical Climate Summaries, 2012 and local weather stations. In Los Angeles, the average temperature was 17.35 C with an average high of 18.91 C. In Riverside the average temperature is 18.48 C with an average high of 25.54 and the average temperature of Palm Desert is 23.6 C with an average high of 29.4 C. While the average temperature of Riverside is only ~ 1.5 C higher, the differences in average maximums show that summer time temperatures are much higher in Riverside than in Los Angeles. Average temperatures and average highs are several degrees higher in Palm Desert than both Los Angeles and Riverside (figure 1).

Leaf Collection: Each selected tree species had a minimum of three specimens growing within at least two of the selected locations. Trees were selected only in grassy, irrigated areas. Three of the most recently matured, fully sun-exposed leaves were collected from each tree at the end of the growing season in 2012 and 2013.

Leaf processing: Each leaf was then scanned at 300 DPI and saved as a Jpeg. After a leaf was scanned it was run through a LI-3000 area meter to determine the leaf area in cm² then dried in a drying oven at 65 C for 48 hours after which point

dry mass was measured. In species with leaves more than 1x compound several individual leaflets were taken from each leaf and analyzed then an average generated for the leaf. Weight and area values were used to calculate Specific Leaf Areas.

Each image was then processed using several pieces of software. Each image was initially edited using the software Photoline One where the image was converted to a black and white silhouette. Any damage which fundamentally altered the perimeter and area of the leaf, such as tears caused during the collection process or holes from insect activity, were also repaired with the imaging software. The outline of the leaf was not altered in this process. After initial processing, each image was treated as a landscape, with the leaf being treated as a patch within the surrounding matrix, and was run through two different pieces of landscape imaging software. The image was first processed using ArcMaps where it was converted into a TIFF raster file. From here, the image was analyzed using Fragstats which provided a number of landscape metrics, including Area and Perimeter.

Dissection index: The dissection index of each leaf was calculated using

$$DI = \frac{Perimeter}{2\sqrt{Area} \pi} \text{ (Santiago et al, 2009) where a perfect circle is equal to 1 with}$$

increasing values representing higher degrees of dissection or increasing elongation.

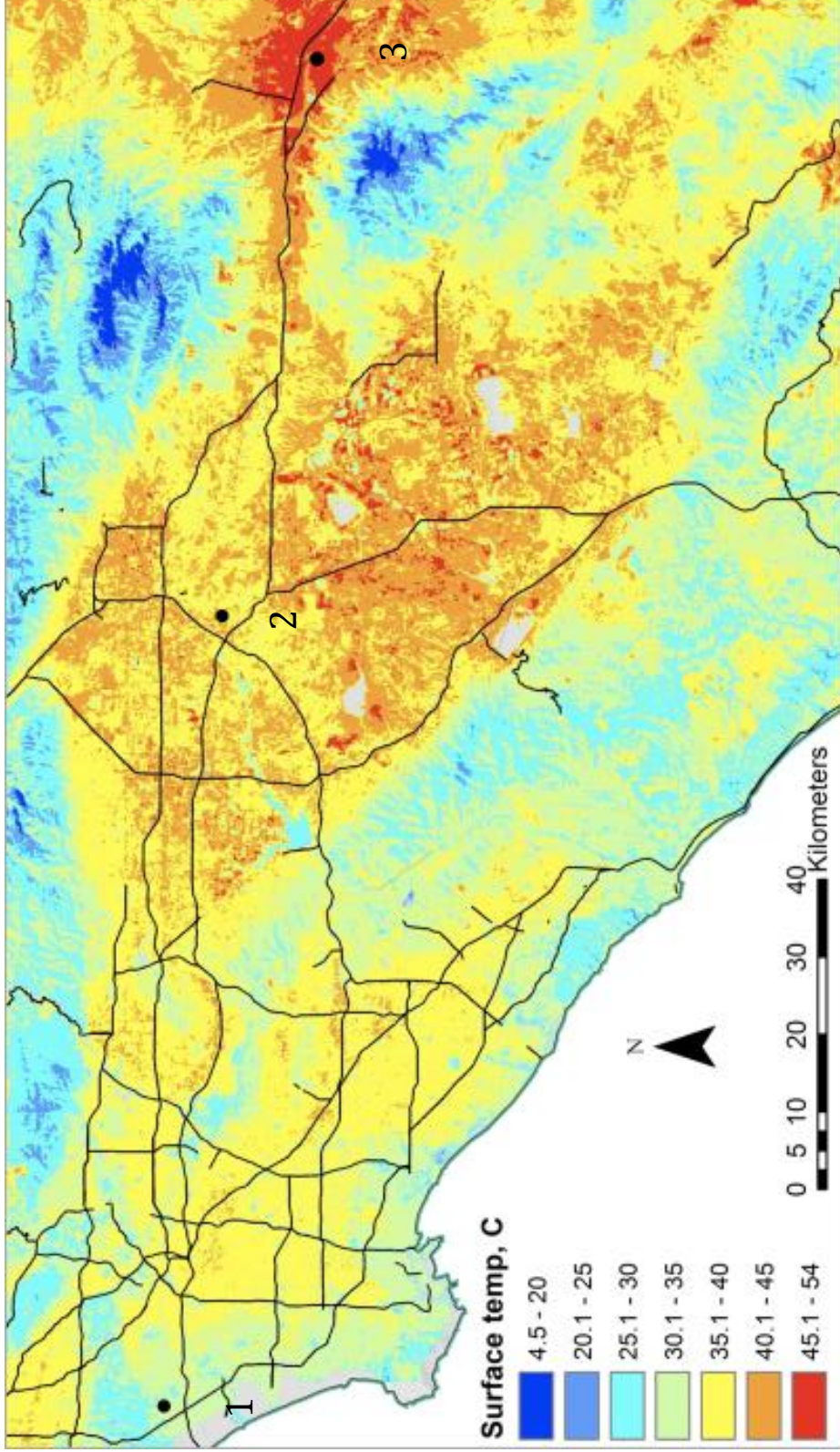


Figure 1. Temperatures Increase along an coastal gradient with sites denoted by black dots, Los Angeles being site 1, Riverside being site 2 and Palm Desert being site 3.

Results:

Statistics were calculated in Matlab, using one-way anovas. Of the seven species in this study, six appeared in two of the sites, while the seventh, *Jacaranda mimosifolia*, was found in all three locations. Of these species, three showed statistically significant changes in at least one metric with increasing temperature while four did not. Of the seven tested species, *Platanus racemosa* and *Platanus occidentalis* showing the most variation. Both species showed increases in dissection ($P = 0.03$ & $P = 0.001$ respectively), figures 2 and 3, decreases in masses ($P = 0.03$ & $P = 0.001$), and decreases in area ($P = 0.01$ & 0.007). Additionally *Platanus occidentalis* showed decreases in SLA as well ($P = 0.01$). *Schinus terebinthifolius* was the only other species to show any changes with increasing leaf dissection with increased temperature $P < 0.001$ (Figure 4). *Platanus racemosa* and *Platanus occidentalis* both show changes in leaf area, and leaf mass with both decreasing with increasing temperature, while *Platanus occidentalis* also showed decreasing SLA with increasing temperature. Of the remaining species, none of them showed any changes among the sites.

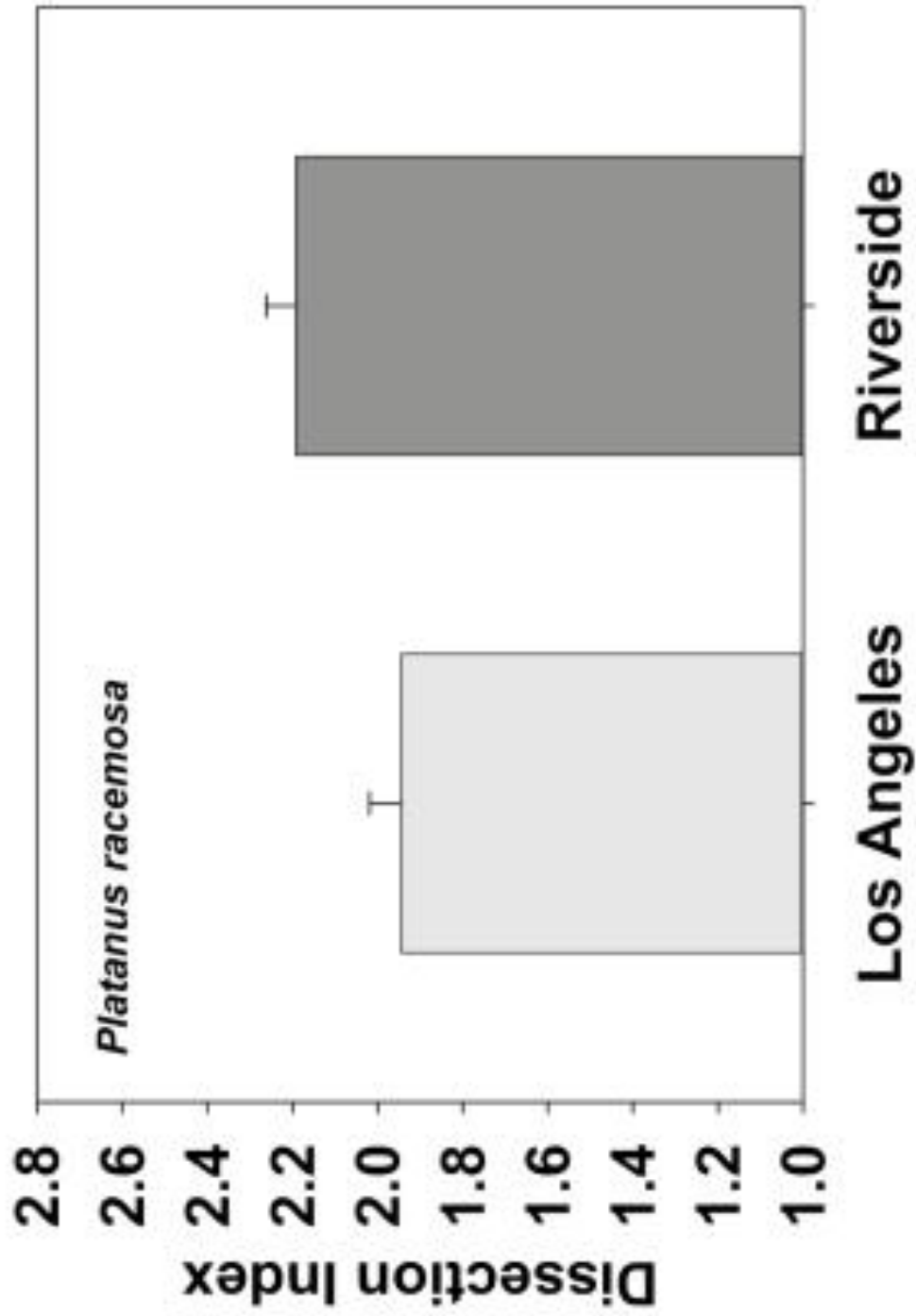


Figure 2. Dissection indexes for *Platanus racemosa*. P = 0.03

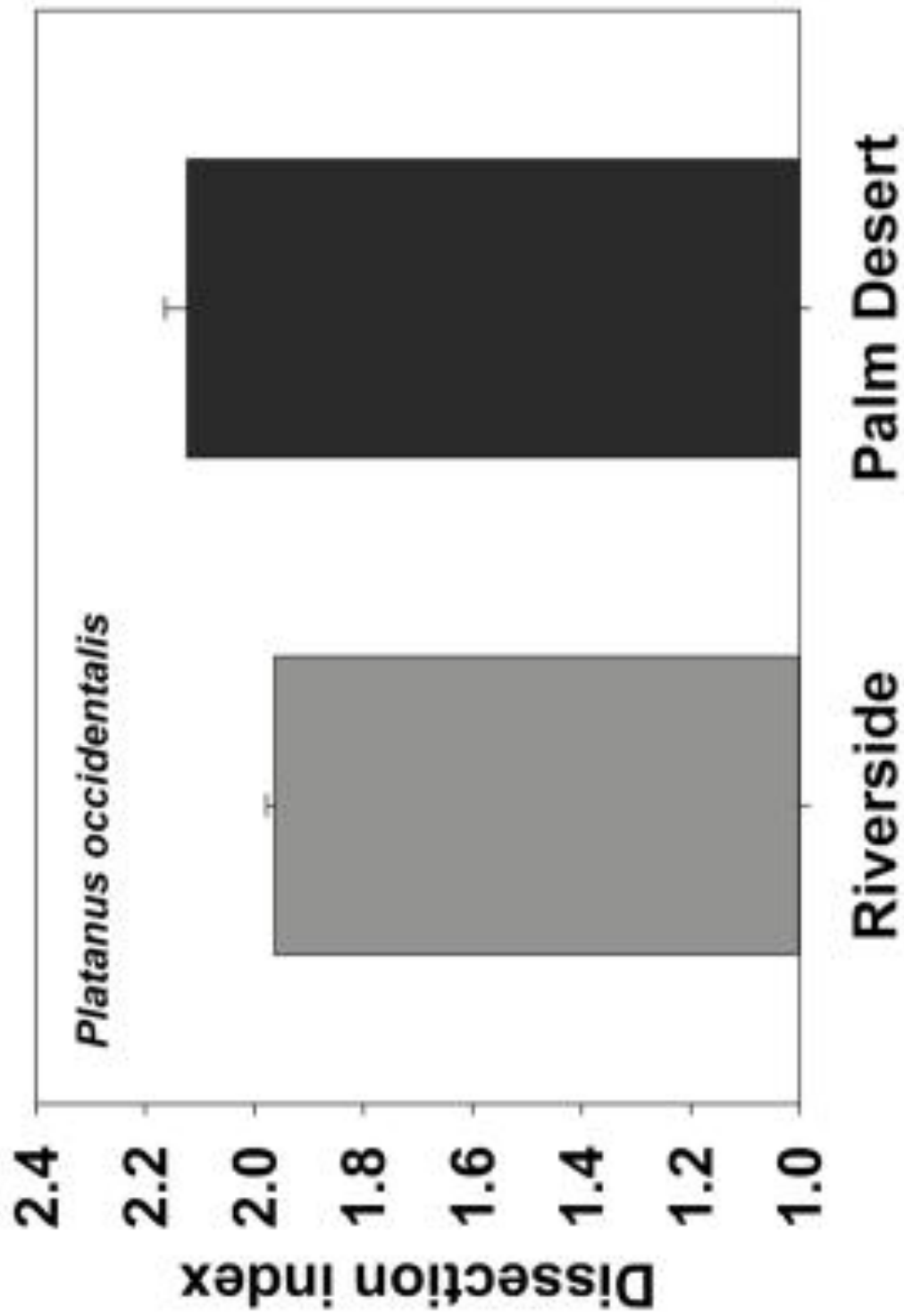


Figure 3. Dissection indexes for *Platanus occidentalis* P = 0.001.

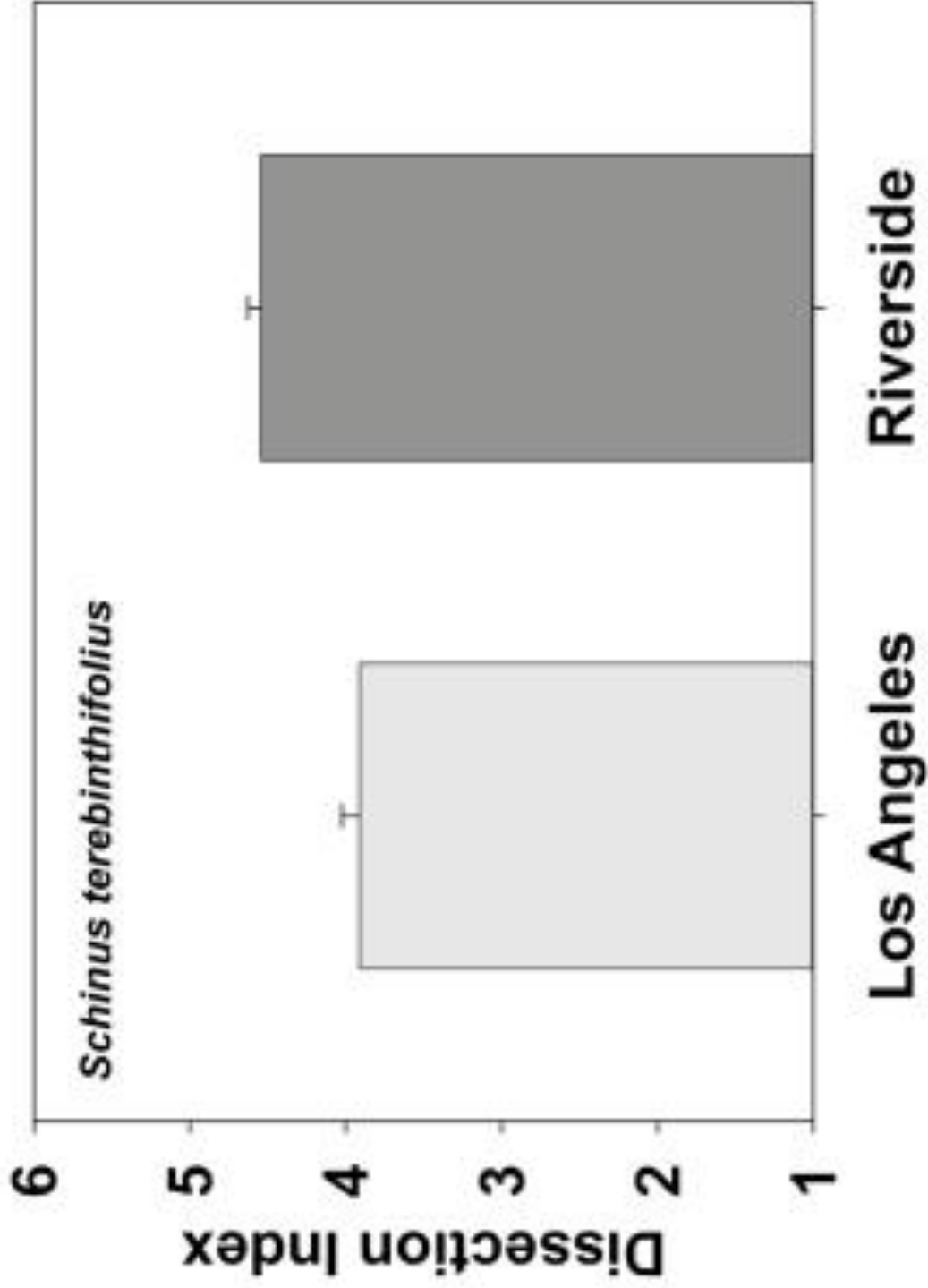


Figure 4. Dissection index for *Schinus terebinthifolius* $P < 0.001$.

Discussion:

These findings suggest that three of the tested species, *Platanus racemosa*, *Platanus occidentalis*, and *Schinus terebinthifolius*, may be more adaptable to changes in temperature. These findings in both species in the *Platanus* genus, suggest that there may be a genetic component to the adaptability of the two species. This will likely be to a significant advantage in *Platanus racemosa* in particular. *Platanus racemosa* is a riparian tree with a distribution limited mostly to the states of California and Arizona. The Southwestern portion of the United States, which encompasses both California and Arizona, is predicted to become both hotter and drier over the coming years, which will have significant impacts in riparian species. Any ability of a riparian species to acclimate to warmer temperature will provide it with a significant advantage over other riparian species. While it will still be of great importance to protect riparian regions in drier conditions, the findings of this study indicate that *Platanus racemosa* may be more hardy than was previously anticipated for a species with such narrow constraints in habitat type.

Within the *Schinus* genus, only one of the two species, *Schinus terebinthifolius*, showed any changes in leaf morphology in response to temperature. There are several potential hypotheses for why one species of a genus showed changes while the other did not. The first hypothesis is that if a genetic component exists allowing for increased adaptability it is either much weaker in *Schinus molle* or it was not passed into this species. A second is that perhaps the smaller size of the leaflets in the *Schinus molle* species are already well adapted to warmer temperatures. A third

hypothesis is that *Schinus molle* is adapting to warmer temperature in some other manner which was not focused on in this study, such as changes in stomatal densities or cuticle thickness. When comparing the two *Schinus* species, the second and third hypotheses are readily plausible. Leaflets on the *Schinus molle* species were found to be smaller overall than those of *Schinus terebinthifolius*. While a loss of genetic adaptability would potentially account for the lack of change seen in *S. molle* it seems unlikely given the similar habitats, distributions, and invasibility seen within both of the species.

The adaptability of *Schinus terebinthifolius* may have greater implications than just the survivability within its home range. *S. terebinthifolius* has already begin to show invasiveness in some areas of the United States (Meyer, 2011) This ability to adapt to potentially warmer, drier, environments could become increasingly problematic as native species begin to struggle under the same conditions.

The lack of changes within the other species studied could have troubling implications for their own survival. *Koelreuteria bipinnata* being a large leaved tree from tropical regions would likely be more susceptible to changes in temperature and precipitation than any of the other species. In the remaining species, at least one of them, *Quercus agrifolia*, has a limited range, being found only in California (Baldwin, 2013) This limited range, in combination with the increased fire hazards within California due to changing climate patterns, as well as the apparent lack of adaptability seen within the leaves, suggests that the Coast Live Oak may fair poorly

in the future. However, the optimistic look at this same species suggests that perhaps, being a California native, with a range extending across several hundred miles in latitude, may just be extremely well adapted to dry temperatures as is. With leathery, cup-shaped leaves, with trichomes on the lower surface, *Quercus agrifolia* may be very efficient reducing water loss, even under higher heat conditions. This efficiency may account for the insignificant differences noted within the study, simply because *Q. agrifolia* has not been forced into stressful enough conditions, particularly when being irrigated, to have a need to acclimate.

The last species, *Jacaranda mimosifolia*, poses interesting questions. Of the species studied, this was the only one found to be growing in large numbers within all three sites. It appeared to grow well across a large temperature range, but showed no noticeable differences in any of the measured metrics. It is possible that *J. mimosifolia*, with its very small leaflets, generally less than a cm long, is just less affected by the temperature or that it has an ability to acclimate in somewhat that has not yet been measured. Given the ability of this species to apparently thrive in a variety of temperatures, if water levels hold steady, it is not likely to be threatened in the immediate future.

One of the goals of this study is to determine which, if any, of the study species may be more susceptible to increasing temperatures. While it is imperative, that riparian species be preserved, the findings suggest that perhaps we should also be looking elsewhere, to those species which are not acclimating, such as the broad-

leaved trees of tropical regions as well as species such as the oaks, with their more limited ranges.

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