# Physiological and Structural Mechanisms of Niche Differentiation for Three Sky Island Oaks in Relation to Light and Temperature

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## ABSTRACT
In an effort to identify the influence of light and temperature on the physiology and leaf structural characteristics of three species of *Quercus* from Coahuila, Mexico, we measured a comprehensive suite of plant traits as functions of light and temperature intensity. We tested the hypotheses that 1) species' physiological responses to light and temperature were related to their distributions in their native habitats; and 2) that species' physiological responses corresponded to similar variation in leaf anatomical and morphological traits. *Quercus sideroxyla* was adapted to high elevation forest overstories as evidenced by its high photosynthetic rate, transpiration rate, relative water content (RWC), leaf density (LD), and thick palisade and spongy parenchyma. *Quercus rugosa* displayed typical characteristics of a forest understory species including a low photosynthetic rate and light saturation point, thick spongy parenchyma tissue and high RWC, leaf density, and leaf mass per unit area. *Quercus laceyi* was adapted to hot, dry sites based on its lower RWC and LD, intermediate photosynthetic rate, thick cuticle and upper epidermis, and low transpiration rates at high temperatures. Our results suggest that the physiological and structural adaptations of Mexican oaks to changing environmental conditions across resource gradients are key regulators of plant community structure.

Keywords: *Quercus*, Mexico, ecophysiological response, temperature response, light response, photosynthesis

## INTRODUCTION
Interspecific differences in seedling functional traits are closely associated with light, temperature, and moisture gradients (Bazazz, 1991; Ackerly et al., 2000; Ackerly, 2003; Fittter and Hay, 2002; Larcher, 2003). The distribution patterns of the genus *Quercus* (Fagaceae) in response to environmental heterogeneity has been extensively studied in the United States (Neilson and Wullstein, 1987; Abrams, 1990; Cavender-Bares et al., 2004). While Mexico is considered the source of oak diversification for North America and harbors the highest oak species richness in the world (Rzedowski, 1978; González, 1993; Nixon, 1993), virtually no information exists that characterizes the mechanisms that underscore the diversification and spatial distribution patterns of *Quercus* to the south of the United States (but see Alvarez Moctezuma et al., 1999; Martínez Cabrera, 2003; Poulos et al., 2007).

The majority of *Quercus* ecophysiological research in North America has been devoted to understanding how differences in species' drought tolerances influence their specialization across landscapes (Abrams, 1990, 1996; Kubiske and Abrams, 1992; Dickson and Tomlinson, 1996; Ehleringer and Phillips, 1996; Cavender-Bares and Bazazz, 2000; Cavender-Bares et al., 2004; Poulos et al., 2007). While limited information suggests that Mexican oak drought tolerance is an important influence on species' distributions (Poulos et al., 2007), other abiotic factors including light and temperature intensity also influence vegetation mosaics across landscapes (Berry and Björkman, 1980; Seemann et al., 1984; Ninemets and Tenhunen, 1997; Fitter and Hay, 2002). Interspecific differences in oak anatomy, morphology, and physiology in response to high light or deep shade environments (Callaway, 1992; Knapp, 1992; Ashton and Berlyn, 1994; Balaguer et al., 2001; Gardiner and Krauss, 2001) and low or high temperature regimes (Hamerlynck and Knapp, 1994; Hammerlynck and Knapp, 1996; Bolstad et al., 2003; Haldimann and Feller, 2004) are closely associated with species' dominance across environmental gradients and forest strata. However, no information exists regarding the light and temperature responses of oaks in Mexico. Nor has any prior research investigated oak leaf anatomical and morphological variability in relation to both light and temperature in this region.

Our goal was to investigate the relationships between the physiology (water status, temperature, and heat tolerance) and the leaf anatomy and morphology of three species of *Quercus* from northern Mexico including *Quercus laceyi* Small-subgenus Leucobalanus-Fagaceae, *Q. sideroxyla* Humb. et Bonpl. -subgenus Erythrobalanus-Fagaceae, and *Q. rugosa* Née–subgenus Leucobalanus-Fagaceae. We employed a common garden experiment to test the following hypotheses: 1) Each species' physiological responses to instantaneous changes in temperature and light levels would correspond to its distribution in high elevation forest overstories (*Q. sideroxyla*), high elevation understories (*Q. rugosa*), or low elevation savannas (*Q. laceyi*), and 2) The physiological responses of each species to light and temperature variability would correspond to similar variation in leaf structural characteristics.

## MATERIALS AND METHODS
### Species distribution patterns
The three species of *Quercus* in this study dominate uplands of the Sierra del Carmen of the Sierra Madre Oriental in northern Coahuila, Mexico. The high-elevation forests of the Sierra Madre Oriental are post-Pleistocene relics that are bound at lower elevations by deserts dominated by shrub and succulent desert flora, where tree establishment and growth is inhibited due to high temperatures and moisture-limited conditions. No climatic data exist for the Sierra del Carmen, however mean annual precipitation ranges from 20 to 180 cm in the uplands of the Sierra La Encantada

and Sierra Santa Rosa, which abut the Sierra del Carmen to the south. Mean annual temperature in these two mountains ranges from 12 to 32.6 °C (CONABIO, 2006). The soils of the natural habitats of the three species are generally shallow to moderately deep and are volcanic in origin. The underlying rocks are predominantly extrusives, consisting of lavas and pyroclastics.

*Quercus laceyi* is distributed across Texas and northern Mexico, and is a low elevation tree species that is distributed across dry, hot habitats (Correll and Johnston, 1970). *Quercus sideroxyla* inhabits cooler, wetter habitats at high elevations (Poulos, 2007), and is entirely endemic to northern Mexico (Encina Domínguez and Villarreal Quintanilla, 2002). It exists as an understory seedling or overstory co-dominant in closed canopy forests that are approximately 30 m in height. *Quercus rugosa* coexists with *Q. sideroxyla,* but it dominates high elevation forest understories in the Sierra del Carmen (Poulos, 2007). *Quercus rugosa* has a wide distribution in comparison to *Q. laceyi* and *Q. sideroxyla,* in that it ranges from Arizona and Texas in the United States to Guatemala. Taxonomy and distributional ranges follow Corell and Johnston (1970) for the United States and Encina Domínguez and Villarreal Quintanilla (2002) for Mexico.

### Experimental conditions and experimental design
Ripe acorns were collected from 20 mature trees of each species in the Sierra del Carmen in Coahuila, Mexico in November 2004. While stratification is necessary for the germination of some oaks of the subsection Erythrobalanus, oaks in the southwestern United States and Mexico germinate readily after maturation (Nyandiga and McPherson, 1992). Acorns were submerged in water and placed in a 5°C refrigerator for 24 hours to promote germination. Acorns were planted in a Metromix seedbed (Scott's Co., Marysville, Ohio) inside a greenhouse in New Haven, Connecticut on March 22, 2005 (lat. 41°16' N, long.72° 55' W) coincident with typical seedling germination times under field conditions. The daily temperature and relative humidity were recorded at 30-minute intervals during the experiment using a HOBO Micro Station Data Logger (Onset Computer, Bourne, MA). Temperatures and relative humidity in the greenhouse were similar to those experienced by seedlings in the field (Poulos, unpublished data), with temperature ranging from 18 to 42°C and mean relative humidity of 12-45 % over the course of the experiment. Photosynthetically active radiation (PAR) was also measured at 30-minute intervals across the greenhouse bench used in the experiment with a HOBO Photosynthetic Light Smart Sensor attachment to a HOBO Microstation Data Logger (Onset Corporation, Bourne, Massachusetts). The mid-day peak in PAR varied from 1100 to 1561 $\mu$mol m-2 s-1.

After three weeks, when the radical was 3 cm long, germinants were transplanted to 10 cm plastic pots. Seedlings were transplanted again to 18 cm plastic pots that were filled to the rims with Metromix growing medium on September 18th, 2005. A modified Hoagland's nutrient solution (Hoagland and Arnon, 1950) was applied monthly to all plants prior to the onset of the experiment. Metromix growing medium was chosen for this study as it a commercially available medium that drains well.

### Light response measurements
Photosynthetic light response curves were measured on 10 seedlings of each species (N = 30) on intact, fully mature leaves using a LI-6400 Portable Photosynthesis system (LI-COR, Lincoln, Nebraska, USA) between April 23 and 26, 2006. We used a standard broadleaf chamber with a built-in red + blue light-emitting diode light source (LI-COR 6400-02B). The $CO_2$ level in the reference chamber was held constant at 400 $\mu$mol/mol air, and relative humidity in the sample chamber was held above 50%. Leaves were given 10 minutes in the chamber to reach equilibrium, which was assessed visually by graphing photosynthesis and stomatal conductance over time. Light curves were constructed by measuring photosynthesis at light levels of 50, 200, 400, 600, 800, 1000, 1500, 1800, and 2000 $\mu$mol PAR m-2 s-1. A minimum wait time of 90 sec was used at each light level, and each measurement was taken after photosynthesis and stomatal conductance stabilized according to visual interpretation of the photosynthesis and stomatal conductance graphs.

Photosynthetic parameters were derived from the light response curve data to approximate the maximum photosynthesis (Amax), the light saturation level (PARsat), and the quantum efficiency (QE) for each species using Photosyn Assistant software (Dundee Scientific, Scotland, UK). The highest stomatal conductance logged for each species' light response curve was used as the maximal stomatal conductance (gmax).

### Temperature response measurements
Photosynthetic temperature and transpiration response curves were measured on 10 seedlings of each species (N = 30) on intact, fully mature leaves using the same LI-6400 Portable Photosynthesis system (LI-COR, Lincoln, Nebraska, USA) used for constructing the light response curves. Photosynthesis, transpiration, and stomatal conductance were measured at 18, 25, 32, 37, and 40°C on each leaf. The leaf temperatures used in this study were chosen based on the range of temperatures experienced by the three species in the field and common temperatures used in similar studies as reported by Medlyn et al. (2002). The highest photosynthesis logged for each species' temperature response curve was used as Tmax. Each leaf was given a minimum of 10 minutes in the chamber at each temperature to reach equilibrium, which was assessed visually by plotting photosynthesis and stomatal conductance using the same methods employed in the light response curve measurements.

### Leaf anatomy
Fully mature leaves from four seedlings were randomly selected from each species (N = 12) to identify anatomical traits that could relate to the physiology of each species. Measurements in this study were designed to investigate species-level variability in stomatal characteristics (density, size, and distribution), upper epidermal features (cuticle, epidermal, and upper cell wall thickness), and the dimensions of the leaf blade, palisade parenchyma, spongy parenchyma, and lower epidermis. Mature sample leaves were randomly selected from fully expanded, undamaged leaves with no signs of scarring, disease, or herbivory.

Stomate density, size, and distribution were measured by taking leaf peels of the abaxial side of a randomly selected leaf on four plants of each species. Only the abaxial sides of the leaves were sampled based on the absence of stomates on the adaxial sides of the leaves of the three species. Leaf peels were taken using clear nail polish that was applied at 10 a.m. on April 27, 2006 to ensure that stomates were fully open. Polish was applied in a thin coat and allowed to dry for two days prior to removal. Each peel was placed on a slide with a No. 1 ½ cover slip (0.15-0.19 mm) that was affixed with clear nail polish and observed at x 200. Digital images of each specimen were taken using a Sony digital camera (model no. MVC-CD500), and the anatomical measurements were taken using ImageJ digital image analysis software (Version 1.36b, National Institutes of Health, USA). Each image was calibrated using a micrometer prior to taking the anatomical measurements. The stomata were counted and the lengths of 10 stomata were measured for each leaf peel. Five different fields of view were counted and the mean stomate density and length was recorded for each individual plant. The stomate data were combined into a Stomate Area Index (SAI) that was used as a measure of stomate area per unit area of leaf for each species. SAI was calculated by taking the product of the mean stomate length and the stomate density per unit area for each individual plant in five fields of view (N = 12).

Leaves were randomly selected from four individuals of each species (N = 12) for analyzing the thickness of the cuticle, upper epidermis, upper cell wall, palisade parenchyma, spongy parenchyma, and leaf blade. Each individual seedling was sampled by cutting a 0.5 x 1.0 cm strip from the middle portion of the lamina across the midrib, which was immediately fixed in FAA (formalin: acetic acid: alcohol, formula of Berlyn and Miksche, 1976), dehydrated in ethanol, immersed in a Tertiary Butyl Alcohol series, and embedded in wax. Tissue sections were cut on a microtome at a thickness of 12μm, and ribbons were mounted on slides prepared with a gelatin-chrome alum adhesive, with each slide representing a different leaf strip (Berlyn and Miksche 1976). Slides were stained in Safranin O and fast green FCF, and then dehydrated and mounted with synthetic resin using No. 1 ½ cover slips following a modified procedure of Berlyn and Miksche (1976).

The leaf anatomical sections were examined for each species using objectives of 2 x, 3.5 x, 6 x, and 40 x that were combined with oculars of 5 x and 6 x, depending on the cellular or histological attributes to be measured. For each slide, five measurements of the thickness of the palisade parenchyma, spongy parenchyma, and lower epidermis were taken and the mean for each anatomical measurement was recorded for each individual plant. Measurements were taken in portions of the slide that did not include the leaf midrib. Cuticle, upper epidermal, upper cell wall, and total leaf blade thickness were measured in the same manner on separate sections of the slide, and in different places within each section around the leaf midrib.

**Leaf morphology**
Leaf area, leaf dry mass, leaf mass per unit area (LMA), and the number of leaves per plant were used as measures of the leaf morphological characteristics of each species. The total leaf area of 20 plants per species (N = 60) were measured using a CI-202 portable leaf area meter (CID Inc., Vancouver, Washington). Leaves were dried in a 70°C oven until a constant mass was reached. Leaf mass was recorded for each leaf using a digital balance (A & D Systems, Milpitas, California), and LMA (g/cm2) was calculated as the ratio between leaf mass and area.

**Water relations**
Relative water content (RWC) and leaf density (LD) were calculated as measures of plant water status and water holding capacity for each species. RWC was measured on one randomly selected leaf on 30 plants of each species (N = 60). Leaves were collected and immediately weighed to determine their fresh mass (FM). Leaves were then saturated in water to full turgor by immersing them in distilled water and leaving them in the dark for 24 hours at constant temperature. Leaves were reweighed to obtain their turgid mass (TM) and put into an oven at 70° C for 3 days to obtain their dry mass (DM). RWC was calculated as: RWC = (FM - DM)/(TM − DM) x 100. LD (mg/μm3) was calculated by dividing leaf dry mass by leaf volume (leaf thickness x leaf area) for four individuals of each species (N = 12).

**Statistical analyses**
Species-level differences in light and temperature responses were analyzed using ANOVA by a mixed model procedure with species as a fixed effect and light and temperature as random effects. Mixed models were used to account for the repeated measures nature of the light and temperature data. Mixed models were chosen for analysis rather than repeated measures general linear models (GLMs) to account for the covariance structures of the repeated measures data. Differences among species' water status and leaf anatomical and morphological characteristics were analyzed using ANOVA by a GLM procedure. Pairwise differences between species were identified using Tukey's pairwise comparisons. All statistical analyses were conducted using the R Statistical Language (R Core Development Team, 2007).

**RESULTS**
**Light response curves**
The three species demonstrated significantly different responses to light (P < 0.001). *Quercus sideroxyla* had the highest photosynthetic rate across all light levels above 200 μmol PAR m-2 s-1, followed by *Q. laceyi*, and *Q. rugosa*, respectively (Table 1; Fig. 1). *Quercus rugosa* had the highest photosynthetic rate below 200 μmol PAR m-2 s-1, but was light stressed at higher light intensities. Maximum photosynthesis (Amax), and PARsat showed the same trend, with *Q. sideroxyla* having the highest Amax and PARsat followed in order by *Q. laceyi* and *Q. rugosa*. Quantum efficiency (QE) was highest for *Q. rugosa*, followed successively by *Q. laceyi* and *Q. sideroxla*. Maximum stomatal conductance (gmax) differed significantly by species, occurring at 50 μmol PAR m-2 s-1 for *Q. rugosa*, 2000 μmol PAR m-2 s-1 for *Q. laceyi*, and 1800 μmol PAR m-2 s-1 for *Q. sideroxyla* (P < 0.001). Transpiration rates did not differ significantly among the three species.

## Temperature response curves

*Quercus sideroxyla, Q. laceyi,* and *Q. rugosa* differed significantly in their responses to temperature (P < 0.001) (Fig. 2). Photosynthesis and transpiration were highest for *Q. sideroxyla,* intermediate for *Q. laceyi,* and lowest for *Q. rugosa.* Tmax occurred at 32°C for *Q. laceyi* and *Q. rugosa,* and at 37°C for *Q. sideroxyla.* While photosynthesis declined at high temperatures for all species, *Q. sideroxyla* maintained high transpiration rates at high temperatures relative to the other two species.

## Leaf anatomy

Leaf anatomical characteristics differed significantly among species (P < 0.05) (Table 2, Figs. 3 and 4). Total leaf blade thickness was highest for *Q. sideroxyla,* followed by *Q. rugosa* and *Q. laceyi,* respectively. *Quercus laceyi* leaves were thinner than *Q. rugosa* and *Q. sideroxyla,* but had greater cuticle and upper epidermal thickness. *Quercus rugosa* had intermediate leaf blade thickness, and was distinguished from the other two species by its thinner palisade parenchyma and thicker spongy parenchyma tissue. *Quercus sideroxyla* had the thickest leaf blades, which were primarily composed of palisade and spongy parenchyma tissue. The mean stomate length, density, and SAI also differed among species (P < 0.05), and *Q. rugosa* had significantly fewer and smaller stomates than *Q. laceyi* and *Q. sideroxyla.*

## Leaf morphology

The three *Quercus* species demonstrated significant differences in leaf morphology (P < 0.05) (Table 3). *Quercus rugosa* had fewer, but larger and heavier leaves than the other two species, and had high LMA. *Quercus laceyi* leaves were intermediate in leaf mass and area, but had lower LMA. *Quercus sideroxyla* had the smallest and lightest leaves, although this species bore more leaves per plant. LMA values for *Q. sideroxyla* were similar to its understory counterpart, *Q. rugosa.*

## Water relations

Leaf density and RWC differed significantly among species (P < 0.05) (Fig. 5). Leaf density and RWC were highest for *Q. rugosa,* intermediate for *Q. sideroxyla,* and lowest for *Q. laceyi.*

## DISCUSSION

Our results suggest that while seedlings of all three Quercus species were well adapted to the hot temperatures that commonly occur in uplands of the Chihuahuan Desert, they differed significantly in their physiological and leaf structural characteristics. Oak species sorting across the Sierra del Carmen was consequently related to each species'ability to partition resources across light, temperature, and moisture gradients. The topographically dissected landscape of the native habitat of these species provided spatial variation in local environmental conditions which are known to contribute strongly to landscape- and regional-scale differences in woody plant distribution and diversity in southwestern North America (Whittaker, 1965; Allen et al., 1991; Urban et al., 2000).

While other prior ecophysiological research on oak distributions in North America demonstrated clear physiologi-

cal and anatomical differences in species according to local growing conditions (i.e. Neilson and Wullstein, 1987; Abrams, 1990, 1996; Kubiske and Abrams, 1992; Dickson and Tomlinson, 1996; Ehleringer and Phillips, 1996; Cavender-Bares and Bazazz, 2000; Donovan et al., 2000; Cavender-Bares et al., 2004; Poulos et al., 2007), our work is the first to examine instantaneous oak light and temperature responses in the context of leaf histological variation. Moreover, this research represents the first attempt to identify the functional and structural mechanisms responsible for the differentiation and diversification of the oaks Mexico.

The physiological response and the anatomical and morphological characteristics of *Q. sideroxyla* were consistent with its distribution in high elevation, forest canopies. Upper elevations of the Sierra del Carmen are cooler and wetter than lower elevations according to adiabatic cooling and increased cloud cover with elevation (Barry, 1992; Poulos, unpublished data). The higher overall photosynthetic rate of *Q. sideroxyla* and its higher PARsat and Tmax values, number of leaves, blade area, LMA, and leaf thickness (comprised mostly of the palisade and spongy parenchyma tissues responsible for carbon fixation) suggested that this species was the most efficient light energy harvesting species in this study (Taiz and Zeiger, 2002; Larcher, 2003).

While the distribution of *Q. rugosa* overlapped with *Q. sideroxyla, Q. rugosa* displayed structural and physiological characteristics that were typical of an understory, shade tolerant species. The low Amax and PARsat, high QE, larger leaves, and thicker spongy parenchyma tissue of *Q. rugosa* were typical adaptations of species to the low light conditions often found in closed canopy forest understories (Bassow and Bazzaz, 1997). The lower light response curve of *Q. rugosa* suggested that it was well adapted to harvesting light energy under low light conditions, where increases in photon flux above PARsat no longer increased photosynthetic rates due to other limiting factors to photosynthesis including electron transport rate, rubisco activity, or triose phosphate metabolism (Taiz and Zeiger, 2002). Photon flux densities above PARsat probably resulted in decreased efficiency of the reaction center of photosystem II (PSII), and the increased dissipation of excess light energy through chlorophyll fluorescence, heat release, the xanthophyll cycle, or photorespiration (Björkman and Deming-Adams, 1995; Taiz and Zeiger, 2002; Larcher, 2003).

In comparison to *Q. sideroxyla* and *Q. rugosa, Q. laceyi* demonstrated characteristics typical of plants adapted to hot, dry, low elevations. The intermediate Amax, PARsat, and Tmax of this species relative to the two others indicated that this species had high photosynthetic potential, but that carbon fixation may have been limited in the hot, high light intensity growing conditions that are typical of the low elevation savanna woodlands of southwestern North America. The lower photosynthetic rate of *Q. laceyi* relative to *Q. sideroxyla* was most likely an adaptation to prevent photodamage to the photosynthetic pigments and thylakoid structures under high photon flux (Björkman and Demmig-Adams, 1995; Larcher, 2003).

The leaf anatomy of *Q. laceyi* was the strongest indicator of this species' adaptation to hot, high light intensity conditions. The thicker cuticle, upper cell wall, and upper epidermis of *Q. laceyi* were typical oak adaptations to high light environments (Abrams, 1990, 1996; Ashton and Berlyn, 1994), as was the high percentage of the total leaf blade thickness being occupied by the palisade parenchyma layer. The cuticle and upper epidermis absorb UV radiation by epicuticular waxes, carotenoids and flavonoids dissolved in the cell sap, thus protecting the lower leaf from radiation injury (DeLucia and Berlyn, 1984; Day et al., 1992; Day, 1993; Larcher, 2003). Likewise, the high percentage of palisade parenchyma tissue also probably facilitated photosynthesis at high light levels.

The thinner leaves of *Q. laceyi* relative to *Q. rugosa* and *Q. sideroxyla* is an atypical trend for North American oaks. While oaks on exposed sites in the northeastern United States have been shown to have thicker leaves than those that dominate valley bottoms or midslopes (i.e. Ashton and Berlyn, 1994; Abrams, 1990, 1996), all previous studies were conducted on species from regions that were much less water limited than our study area. Water availability is the most limiting factor to tree growth in the southwestern United States (Meko et al., 1995; Hidalgo et al. 2001; Adams and Kolb, 2005). The thinner leaves of *Q. laceyi* may have been an adaptation of this species to the hotter, much dryer growing conditions that predominated in the low elevations of its native habitat. Alternatively, thinner leaves dissipate heat at faster rates than thicker leaves, which may also be an adaptation to high temperature growing conditions.

The temperature and transpiration data for *Q. sideroxyla* and *Q. laceyi* suggest that the two species adopted different strategies for tolerating heat stress. The temperature response of plants is a function of the thermal stability of the photosynthetic apparatus at the chloroplast level (Berry and Björkman, 1980). High temperatures reduce the stability of the thylakoid membranes and key photosynthetic enzymes, disrupt electron transport in PS II, or cause photoinhibition (Pearcy, 1977; Armond et al., 1978; Smillie, 1979; Smillie and Nott, 1979; Berry and Björkman, 1980; Björkman et al., 1980; Seemann et al., 1984; Havaux, 1993, 1994; Hikosaka et al., 2005). Such damage can result in a dramatic decline in photosynthesis at high temperatures, even for plants that are well adapted to hot growing conditions. Prior research has shown that the ability of plants to maintain high rates of photosynthesis at high temperatures is correlated with the increased stability and rate of photosynthetic electron transport at high temperatures (Björkman et al., 1976; Pearcy, 1977; Björkman et al., 1978). The higher Tmax and transpiration rates of *Q.sideroxyla* at high temperatures suggest that while this species is distributed across less extreme sites relative to *Q. laceyi*, it maintains high quantum efficiency at high temperatures. This indicates that this species may allocate resources to stabilize PS II, protect against photoinhibition, or maintain higher enzymatic activity than *Q. laceyi*. *Quercus sideroxyla* also maintained high transpiration rates at high temperatures, while transpiration rates declined above 32°C in *Q. laceyi*. *Q. sideroxyla* probably dissipated heat through evaporative cooling in the mesic conditions

that predominate in the high elevations of its native habitat. In contrast, the decline in transpiration by *Q. laceyi* at high temperatures through stomatal closure was probably a product of its adaptation to hotter, drier growing conditions at lower elevations. The thicker cuticle of *Q. laceyi* may have also played an important role in reducing water loss through transpiration in addition to providing protection from high intensity light.

The temperature response data also suggest that all three of the species in this study were well adapted to high temperature growing conditions. The temperature tolerances of these species were most likely related to the location of their native distributions in the middle of the Chihuahuan Desert, where July mean maximum temperatures are 37°C. All three species may have adapted to hot growing conditions through the previously described mechanisms for heat tolerance or through the development of heat shock proteins that ensure the conformational structure of photosynthetic enzymes for increased thermotolerance (Taiz and Zeiger, 2002; Larcher, 2003).

The leaf structural characteristics corresponded closely with our plant water status and light and temperature response data. Light intensity, temperature, and water relations are closely related (Hamerlynk and Knapp, 1994; Holmgren, 2000; Sack and Grubb, 2002; Sack, 2004; Aranda et al., 2005; Quero et al., 2006), with high light and temperature intensity often corresponding to xeric conditions. The higher LMA, leaf density, and RWC of the two high elevation species relative to *Q. laceyi* suggest that harsher growing conditions at low elevations may limit carbon fixation. Upper elevations are cooler and wetter, and upland oaks (*Q. sideroxyla* and *Q. rugosa*) appeared to be adapted to these growing conditions through greater water holding capacity and higher leaf densities, whereas lowland oaks (*Q. laceyi*) probably developed strategies for conserving water under hot, dry, high light conditions. Hence, the niche partitioning of *Q. sideroxyla* and *Q. laceyi* according to moisture regime, as identified by Poulos et al. (2007), may also translate to similar differentiation according to light and temperature gradients in a pattern similar to that observed in oaks from other regions of North America (i.e. Hamerlynck and Knapp, 1994, 1996).

## APPLICATION OF GREENHOUSE RESULTS TO FIELD CONDITIONS

The application of greenhouse experiments to field conditions warrants discussion (e.g., Harper, 1977), because the field environment can differ dramatically from controlled greenhouse conditions. We addressed this by mimicking natural patterns of spring oak germination in the southwestern United States and northern México and by taking our measurements in the late spring when these plants experience a pronounced fore-summer drought in the field. Relative humidity and temperatures within the greenhouse were also similar to field conditions during the experiment (Poulos, unpublished data) to minimize differences between field and greenhouse growing conditions.

Results from this study corresponded to other field-based studies of plant anatomy and water relations in the south-

western United States (i.e., Lajtha and Barnes, 1991; Lajtha and Getz, 1993; Linton et al., 1998), which suggests that our experiment approximated field conditions.

## CONCLUSION

Our results suggest that the physiological and structural adaptations of Mexican oaks to changing environmental conditions across resource gradients are important influences on plant community structure. We identified a close association between oak physiology, leaf structural characteristics and species dominance. Moreover, our results suggested that drought, light, and temperature tolerance were important influences on oak spatial distribution patterns at the landscape scale. Future research that investigates the physiological ecology of other oaks in Mexico is warranted to gain a more complete understanding of the factors influencing oak dominance and diversity patterns.

## ACKNOWLEDGEMENTS

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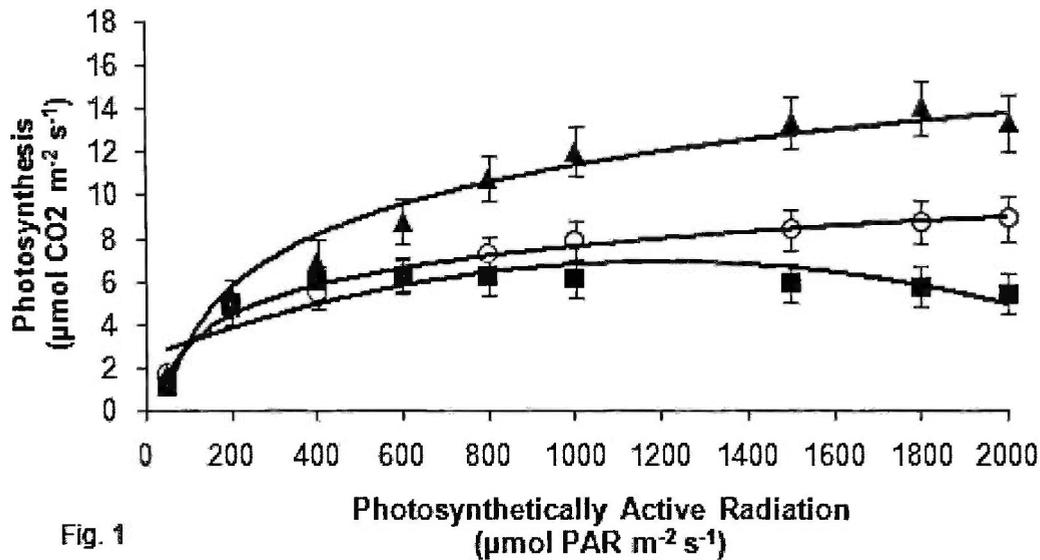Whittaker, R.H. 1965. Dominance and diversity in land plant communities. Science 147:250-260

**Figure 1:** Photosynthetic light response curves for (▲) *Q. sideroxyla*, (○) *Q. laceyi*, and (■) *Q. rugosa*. Light curves of each species were significantly different according to a mixed model procedure ($P < 0.001$). Each point represents the mean of 10 leaves sampled for each species ($N = 30$) with error bars representing ± 1 SE. Best fit curves are modified hyperbolas fit to the mean values for each species.
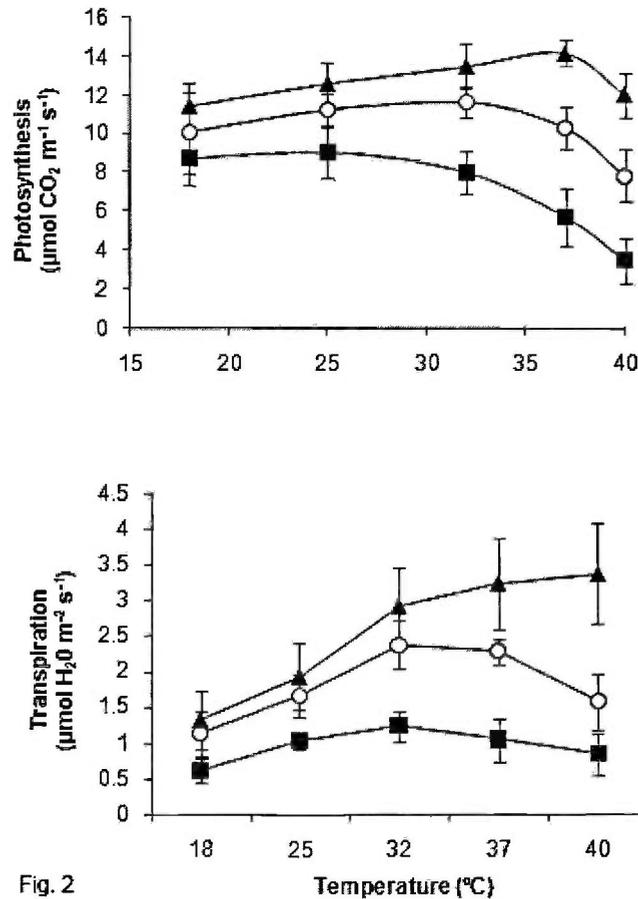


**Figure 2:** Temperature response curves of A) photosynthesis and B) transpiration for (▲) *Q. sideroxyla*, (○) *Q. laceyi*, and (■) *Q. rugosa*. Temperature curves were significantly different among species according to a mixed model procedure ($P < 0.001$). Each point represents the mean of 10 leaves sampled for each species ($N = 30$) and error bars indicate ± 1 SE.
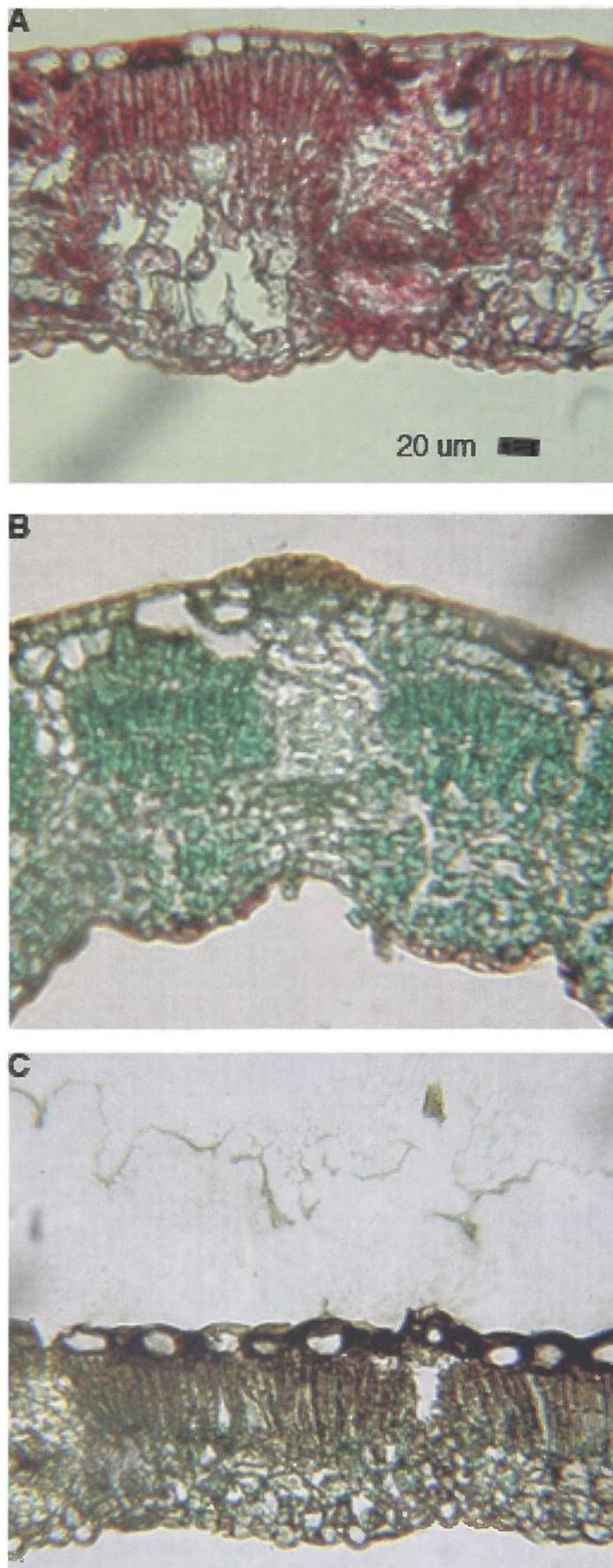
**Figure 3:** Photomicrographs of leaf sections for A) *Q. sideroxyla*, B) *Q. rugosa*, and C) *Q. laceyi.*
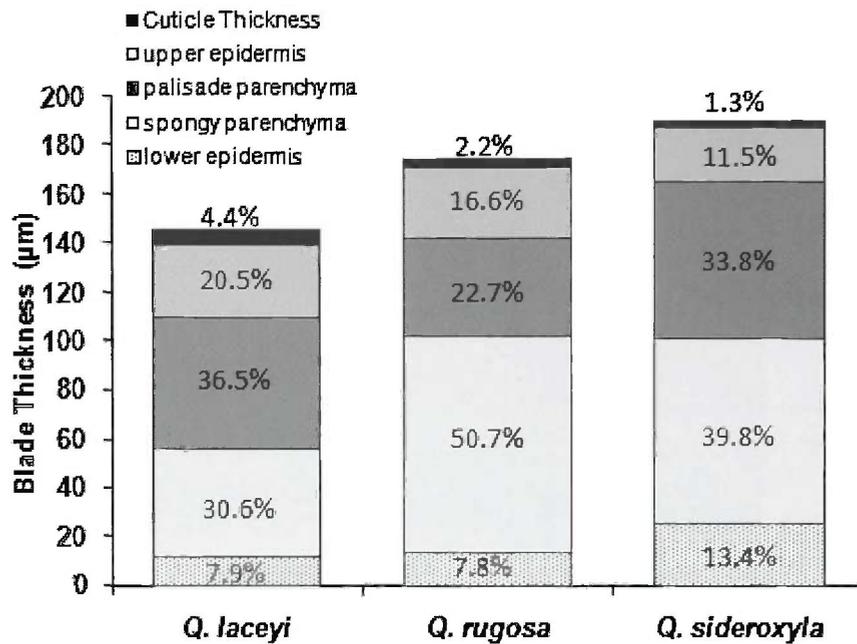
*Desert Plants*



**Figure 4:** Stylized leaf cross-sections of *Q. laceyi*, *Q. rugosa*, and *Q. sideroxyla*. Shadings are the cuticle, upper epidermis, palisade parenchyma, spongy parenchyma, and lower epidermis from top to bottom. The percent of each anatomical characteristic relative to total leaf blade thickness is listed on each bar. Data are means for leaves of four individuals of each species ($N = 12$).
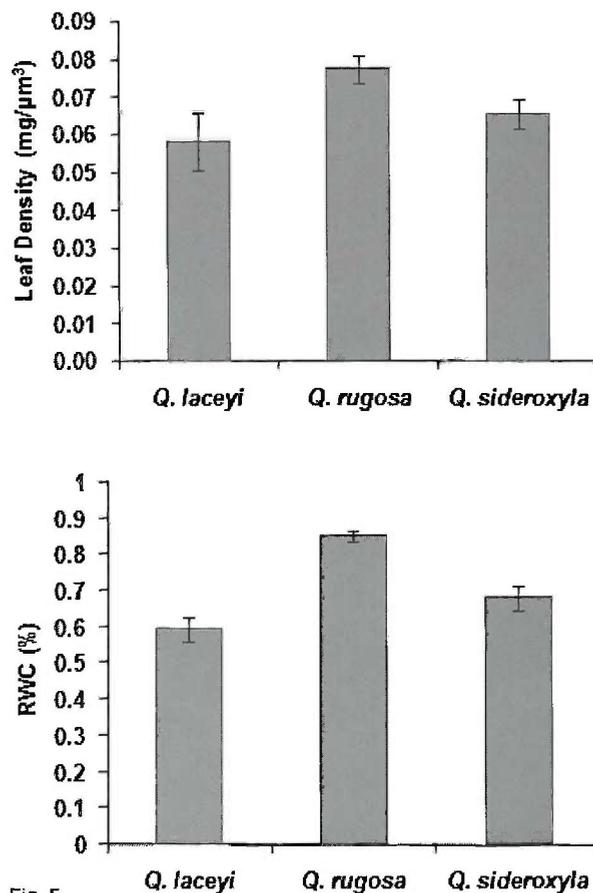


**Figure 5:** Means ($\pm$ 1 SE) of A) leaf density and B) leaf relative water content (RWC) for each of the three species of *Quercus* ($N = 30$).