Drought Tolerance and Climatic Distributions of the American Oaks

Matthew A. Kaproth* and Jeannine Cavender-Bares
Department of Ecology, Evolution and Behavior, University of Minnesota
Saint Paul, MN 55108, USA
corresponding author: mkaproth@umn.edu*

ABSTRACT

Plants employ contrasting strategies to survive in different environments. Adaptations to environmental stress may involve investment in resistance mechanisms that enhance survivorship under stress, potentially at the cost of limiting growth. We test the hypothesis that among the American oaks that have radiated into contrasting habitats varying in water availability, some species will have greater drought resistance at the cost of reduced growth capacity. We investigate patterns of trait variation in relation to native environments in species representing lineages across the American oak phylogeny, and experimentally test the response of species to experimental water treatments. Trade-offs between drought tolerance strategies, such as solute accumulation in leaves (known to help plants regulate water potential), and growth appear in all lineages – indicating both adaptation and evolutionary constraints in physiological traits. We find that species from mesic environments have enhanced growth and resource acquisition traits when experimentally well watered. In contrast, xeric species do not have the capacity to increase growth when well watered; however they do accumulate solutes and show a greater propensity to prevent plant dieback under drought conditions. We postulate that the drought resistance traits exhibited by xeric species may require investment of resources that limits growth under mesic conditions.

Keywords: functional traits, Moisture Index (I_m), osmotic adjustment, trade-offs

Introduction

Life history trade-offs between competitive ability and stress tolerance are a long standing concern in ecology (Grime 1977). The same physiological attributes that confer stress tolerance may compromise a plant's ability to grow (Lambers and Poorter 2004; Reich 2014) as some stress tolerance traits or strategies can be nutrient or resource intensive. Lower growth rates can reduce the ability of plants to compete for resources or survive disturbance, however, stress-tolerance may allow them to survive prolonged events, such as flooding (Carter and Grace 1990; Bailey-Serres and Voesenek 2008), pests (Fine et al. 2006) freezing (Koehler et al. 2012; Savage and Cavender-Bares 2013) or drought (Shipley et al. 2006; Reich 2014).

In mesic environments, plants have high resource supply that can support high growth rates and promote the evolution of traits that maximize resource acquisition and growth, thereby enhancing competitive ability. In contrast, plants from drier environments would be expected to have higher drought resistance traits and/or avoidance strategies that enhance likelihood of survival and competitive ability under drought stress. One well-understood strategy for increasing drought resistance is the increase of solute concentrations in the leaves, lowering leaf turgor loss points (Ψ_{TLP}; critical wilting), to prevent wilting and loss of leaf function under drought stress (Bartlett et al. 2012b). Alternatively, or in addition, plants may drop leaves in response to drought stress, reducing leaf and canopy area as a means to prevent water loss. The latter strategy prevents plants from continued carbon uptake, and hence a trade-off may be expected between these two alternatives.

These two strategies for conferring drought resistance or tolerance can be categorized as isohydry, where a plant maintains a uniform water status by regulating stomata and leaf area, and anisohydry, where a plant will allow its water potential (Ψ) to change but accumulate solutes (osmotically adjust) to continue to draw water into the leaves and conduct gas exchange for photosynthesis (carbon assimilation, A, and stomatal conductance, g_s). Through osmotic adjustment, a plant may maintain leaf function and the ability to fix carbon (C) during prolonged drought and thereby continue basic metabolism and maintenance (Bartlett et al. 2012b). Alternatively, species may shed leaf area to maintain plant water potential (isohydry) and fail to fix C at sufficient rates to maintain plant function. Consequently, these species may be at risk of woody tissue loss and mortality during prolonged droughts (Breshears et al. 2008; McDowell et al. 2008). Recently, Bartlett et al. (2012a) showed that rapid measurement of leaf solute concentration (π_o) using an osmometer can be used to infer the leaf turgor loss point (Ψ_{TLP}) or wilting point, which is otherwise assessed using more time consuming methods (e.g., pressure-volume curves, Koide et al. 1989)

Quercus L. species found in the Americas have wide-ranging distributions across gradients of water availability and drought stress (Abrams 1990; Cavender-Bares and Holbrook 2001; Cavender-Bares et al. 2004; Manos and Stanford 2001; Nixon 2006), providing an excellent study system for examining these trade-offs. Species adaptations to different water-stress environments may be evident in their morphology and investment strategies (Cavender-Bares et al. 2004; Reich 2014). Mesic environments, which often allow for enhanced nutrient uptake, may select for species with leaves that are thin and large, which might be nutrient-expensive but promote rapid growth. Xeric environments, alternatively, may select for plants with more durable, carbon-rich leaves with low nutrient costs, which are thick and small enough to endure multiple growing seasons and resist water stress.

We took a two-pronged approach to examine evidence for adaptation of oaks to contrasting environments with respect to water availability and drought stress. In the first approach, we used leaf and stem traits from herbarium specimens of oaks species from across the Americas to test for associations between plant morphology and species' native climates. In the second approach, we established an experiment with 40 oak species in three different watering treatments to examine the range of drought-tolerance strategies and test the extent to which stress-tolerance traits trade-off with growth traits. We hypothesize that species from mesic environments will show traits associated with growth, while species from xeric environments will have drought-tolerance strategies and traits that allow for survivorship in dry climates. As a consequence, species adapted for xeric conditions will have lower enhancement of growth rates when grown in well-watered conditions compared to mesic species.

Methods

To characterize the functional trait and physiology variation in American *Quercus* species, we used both measurements from a herbarium trait survey and a common garden[1]. The herbarium survey included 125 species from both spontaneous and garden-grown specimens comprising the majority of the oaks native to North America (and roburoids of Eurasia). Ecologically relevant leaf traits can be acquired from herbarium samples, like Specific Leaf Area (SLA), which measures the light-capturing blade area per unit of dry-mass investment, and has been shown to correlate with water use, growth, nutrient use and other life histories (Cornelissen et al. 2003; Wright et al. 2004; Reich 2014). Perimeter to area (P/A) relates the distance blade tissue is from primary veins, desiccation risk and leaf hydraulic conductance (Sack et al. 2003). A leaf with low P/A would be rounded while a higher value P/A may be asssociated with a dissected and/or smaller leaf. Leaves were scanned to assess leaf area and perimeter length via ImageJ and weighed for dry mass. Leaf pubescence was qualitatively rated into four categories ranging from glabrous to dense trichome coverage obscuring the blade surface with the highest two values indicating a range of functional coverage.

Additionally, seedling growth and physiology was measured in a common garden with forty species representing all major American clades (subset in Figure 1). A total of 1,200 plants were grown from seed for two years in a greenhouse at the University of Minnesota and maintained at a constant growing season temperature of 22-32 °C (8-16 °C in the winter). Each species included seeds from one to thirteen populations. Plants were grown in 1.5 m pots (two stacked Stuewe & Sons T616) with 1:1 Sunshine LC8 potting mix and sand by volume. Over the second growing season, we regulated watering to impose long-term water treatments within and among species across the clade – watering when soil moisture dropped below 7, 14, and 21% by volume (low, medium and high watering treatments, respectively). Starting in April of the second growing season, plants were fertilized with 0.2 g N in a 1:1 ratio of Scotts EXCEL Cal-Mag 13-2-13 and All Purpose 21-5-2, after which 0.2 g N Peter's 21-7-7 was applied bimonthly.

Aboveground functional traits and π_o (Bartlett et al. 2012a) were measured on a minimum of three replicates per species per watering treatment over the second growing season. Stomatal Pore Index (SPI; stomatal density (SD) × stomatal pore length^2 (SPL)), a measure of the stomatal area per unit leaf area that is directly tied to the leaf maximum

---

[1] A « common garden experiment » brings together different species of plants to grow in a uniform environment.

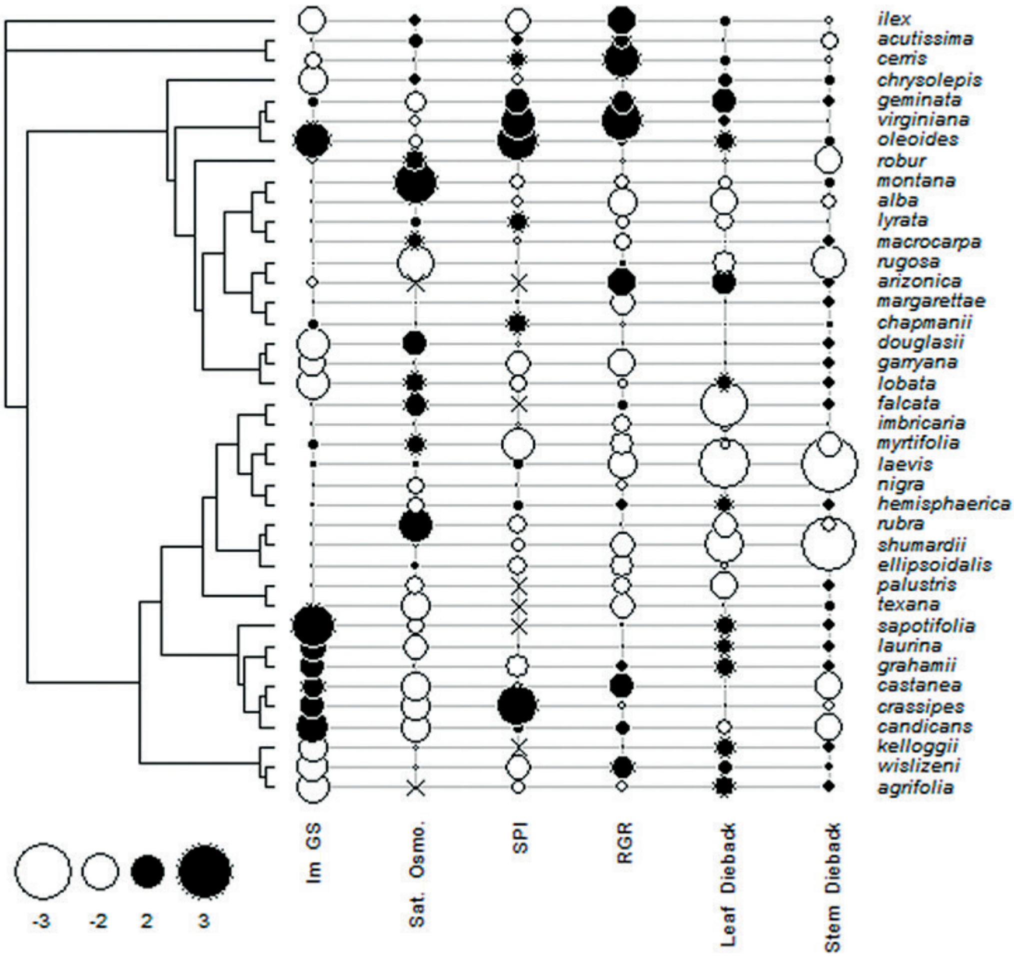

Figure 1/ Common garden species traits aligned with a RAD-seq phylogeny (pruned from McVay et al. *unpublished*) to show correlated patterns among and across clades (via 'adephylo' package in R v3.2.1). Species mean traits include climate of origin in the growing season (Im GS), drought treatment response variables Osmo. indicating π_o (leaf solute concentration) and dieback indicating portion of leaf area lost or stem length lost, and high water treatment response variables RGR of total biomass over one year and Stomatal Pore Index (SPI). Circles are scaled with higher values being more positive – in the case of dieback, the more negative the value, the greater the proportion of tissue loss.

gas exchange volume, was also measured on three replicates per species (Figure 1). To determine SPI (Sack et al. 2003), stomatal peels were taken on the most recent mature leaf of three plants to assess mean abaxial SD at 20× and mean SPL at 40× (three random stomates per peel). Species mean values were derived from 611 specimens overall.

At the end of the second growing season, biomass absolute growth rate (AGR; g/day; 578 days of the experiment) and second year relative growth rate (RGR g/g/day; 365 days) were determined for each plant through species-specific allometric coefficient associations with suites of above-ground traits (i.e., combinations of height, basal diameter, longest leaf length and number of leaves). The reference dry biomass values were determined through destructive harvests of a common garden of 1,700 seedlings over the course of two growing seasons. Curve fit coefficients of trait suites and biomass varied by species with a mean fit of R^2=0.84 ±0.02 for 46 *Quercus* species (available on the TRY Plant Database; Kaproth and Cavender-Bares 2016).

Climatic dataset

Species native climate values were calculated from occurrence records of herbarium vouchered specimens. An average of 1,085 ±228 unique presence records per species were compiled, totaling 135,611 records for 125 species overall. Ten species measured in herbarium records did not have digitized occurrence points available. Geo-referenced records were obtained from clearinghouses and herbariums [GBIF data portal (available at http://www.gbif.org), USGS BISON (http://bison.usgs.ornl.gov/#home), Consortium of Northeast Herbaria (http://portal.neherbaria.org/portal), C.V. Starr Virtual Herbarium (New York Botanical Garden; http://sciweb.nybg.org/science2/hcol/allvasc/index.asp.html), Southeast Regional Network of Expertise and Collections (http://sernec.appstate.edu/), Robert K. Godfrey Herbarium (FSU; http://herbarium.bio.fsu.edu), USFS Forest Inventory and Analysis (FIA; http://apps.fs.fed.us/fia/fido/index.html), Morton Arboretum (quercus.mortonarb.org), Missouri Botanical Garden’s Tropicos (http://www.tropicos.org/Home.aspx), INBio (http://atta.inbio.ac.cr), Plants of Iowa (http://plantsofiowa.com/oaks.html) and data published by Herbario del Instituto de Ecología, A.C., MEXU/Tipos de Plantas Vasculares, Catálogo de Autoridad Taxonómica del Género Quercus, Fagaceae en México]. This data complemented our own records, compiled from field observations and specimens deposited in US and Mexican herbaria.

For each occurrence point, we sampled climate records (e.g., mean annual temperature and precipitation) from current 30” BioClim and WorldClim layers (available at http://www.worldclim.org/). Additionally, monthly precipitation and temperature values were sampled to calculate a moisture index (I_m = 100 × (precipitation – PET) / (PET)) to quantify water stress of each site where precipitation did not meet evapotranspiration demand (*sensu* Edwards 2006). The values range from negative (xeric) to positive (mesic). The potential evapotranspiration (PET) was calculated from WorldClim mean monthly air maximum and minimum temperature values and day length for each location (*sensu* Thornthwaite 1948). The I_m from May-August was calculated to capture the water stress during the critical growing season (hereafter I_m GS).The data were averaged by species and allow for comparisons of the range climate conditions to which they may be adapted.

Analysis

Species means of measured traits were compared to their mean climatic conditions (I_m GS) through linear regressions using JMP PRO v12.0.1. ANCOVA analyses were used to assess treatment differences of physiological, RGR and dieback traits over the species I_m GS. Initial biomass prior to the start of the water treatments was used as a covariate when conducting analyses with the response of AGR.

Results

Functional traits from herbarium samples across 125 species show significant associations with native climate. In environments with high precipitation exceeding PET (mesic; positive I_m GS), oaks show higher leaf area and reduced leaf perimeter per area (P/A) (Figure 2). Specifically, leaf area increased and P/A decreased in more mesic environments. Leaf pubescence also varied with water availability in the native habitat (I_m GS; adaxial; $F=6.32_{DF=1,n=125}$, $p<0.0001$). Leaves of xeric species had pubescence covering a higher proportion of leaf surface than in mesic species. We observed that in extremely

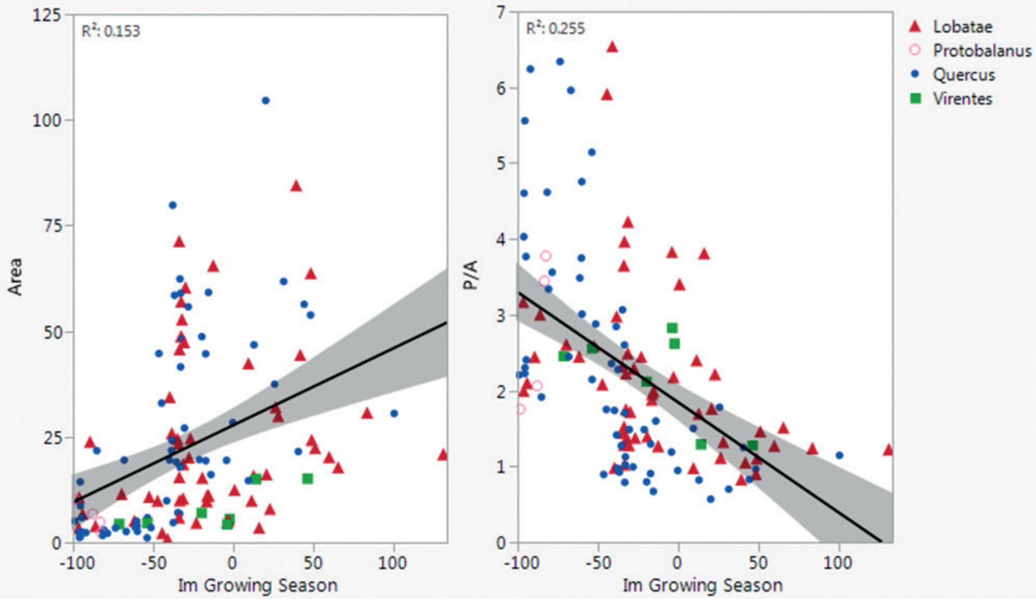

Figure 2/ Leaf trait variation, from herbarium records, across species climatic water availability in the growing season (I_m GS). Species mean leaf area (cm^2) and perimeter to area (cm) show adaptive responses from xeric (negative) to mesic (positive) climates ($F_{DF=1,n=125}=22.19$, $p<0.0001$, $F_{DF=1,n=125}=54.87$, $p<0.0001$ respectively).

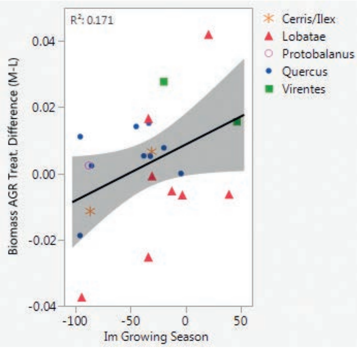

Figure 3/ Biomass AGR treatment differences medium minus low indicates a trend of enhancement in growth in mesic species (M-L $F_{n=22,\ df=1}=4.11$, $p<0.06$). A similar, non-significant pattern can be seen in other water treatment comparisons.

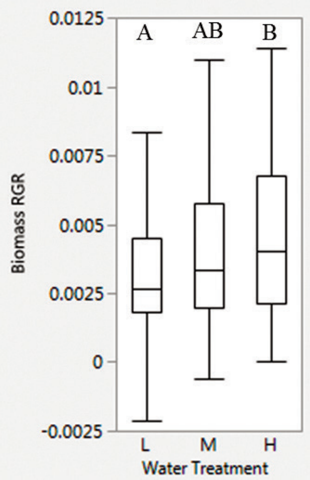

Figure 4/ Biomass RGR among water treatments, using maternal lines with replicates ($F_{n=170,\ df=2}=3.29$, $p<0.04$). Under low-water conditions the collections had a RGR=0.0032 ±0.0003 g/g/day, which was 32% lower than the high-water treatment.

xeric species, the upper-blade surface may be entirely covered with trichomes, which may increase reflectance and reduce light absorption and heat load. Other traits, including abaxial leaf pubescence, SLA, specific stem density or leaf lobedness (perimeter per area × length, P/A*L) were not associated with climate.

Traits measured on oaks in the common garden, likewise, showed significant associations with native climate. Xeric species tended to exhibit traits that enhance drought resistance while minimizing woody-tissue loss. In particular, xeric species had higher solute concentrations than mesic species. They also showed a greater increase in solute concentration between the well-watered (H) treatment relative to the low-watered (L) treatments compared to mesic species (Figure 5C: I_m GS $F_{n=57,\ df=1}=8.51$, $p<0.01$; Water Treatment $F_{n=57,\ df=1}=12.26$, $p<0.001$; Interaction $F_{n=57,\ df=3}=2.82$, $p<0.1$), a response associated with drought resistance. Across species, drier soil moisture treatments increased stem and leaf dieback, with the L treatment plants having 11.8× and 2.4× higher dieback compared to the H (Figure 5A and 5B: $F_{n=79,\ df=2}=10.24$, $p<0.0001$, $F_{n=79,\ df=2}=2.45$, $p=0.09$, respectively). However, xeric and mesic species responded differently to water limitation. Specifically, under low water, more xeric species had less stem dieback than mesic species ($F_{n=22,\ df=1}=5.69$, $p<0.03$; $F=3.12$, $p=0.09$); stem dieback is also correlated with leaf loss (Figure 1; $R^2=0.52$, $F_{n=22,\ df=1}=21.49$, $p=0.0002$).

As hypothesized, growth and growth-related traits varied with climate of origin and in response to water limitation in a manner that suggests a trade-off between drought resistance and growth. Mesic species had greater enhancement of growth in well-watered treatments relative to low-water treatments (absolute growth rate – AGR – based on biomass; Figure 3). Overall, species mean relative growth rate based on biomass (RGR) among water treatments was 32% higher under well-watered (H) conditions compared to the drought treatment (Figure 4). Similar patterns were observed for RGR based on other measures (height, number of leaves, longest leaf). Stomatal pore area (reported as SPI) was correlated with growth (RGR; Figure 1; $R^2=0.16$, $F_{n=22,\ df=1}=3.75$, $p=0.07$), with more mesic species having greater SPI.

Importantly, the accumulation of solutes in leaf tissue, which confers drought resistance, and increased RGR in response to well-watered conditions are inversly related (Figure 5D). Xeric species showed no change in growth rates under well-watered and drought stress conditions (H-L), while more mesic species, which had lower solute concentrations, significantly decreased growth ($F_{n=22,\ df=1}=5.24$, $p=0.03$).

Discussion

Using a broad survey of traits from herbarium specimens for 125 oak species, and careful experimental analysis of 40 species, we provide evidence that species from mesic environments show traits associated with rapid growth, while species from xeric environments have traits that increase drought tolerance and survival in dry climates. Furthermore, we demonstrate that oaks show evidence of an important life history trade-off such that species adapted to xeric conditions have higher resistance to drought but do not increase their growth in response to water addition, while species adapted to mesic conditions do have the capacity to increase growth in response to water addition but have lower drought resistance.

Traits that confer drought tolerance are found in species occurring in xeric climates

Under experimental conditions, we find that species from xeric climates have higher

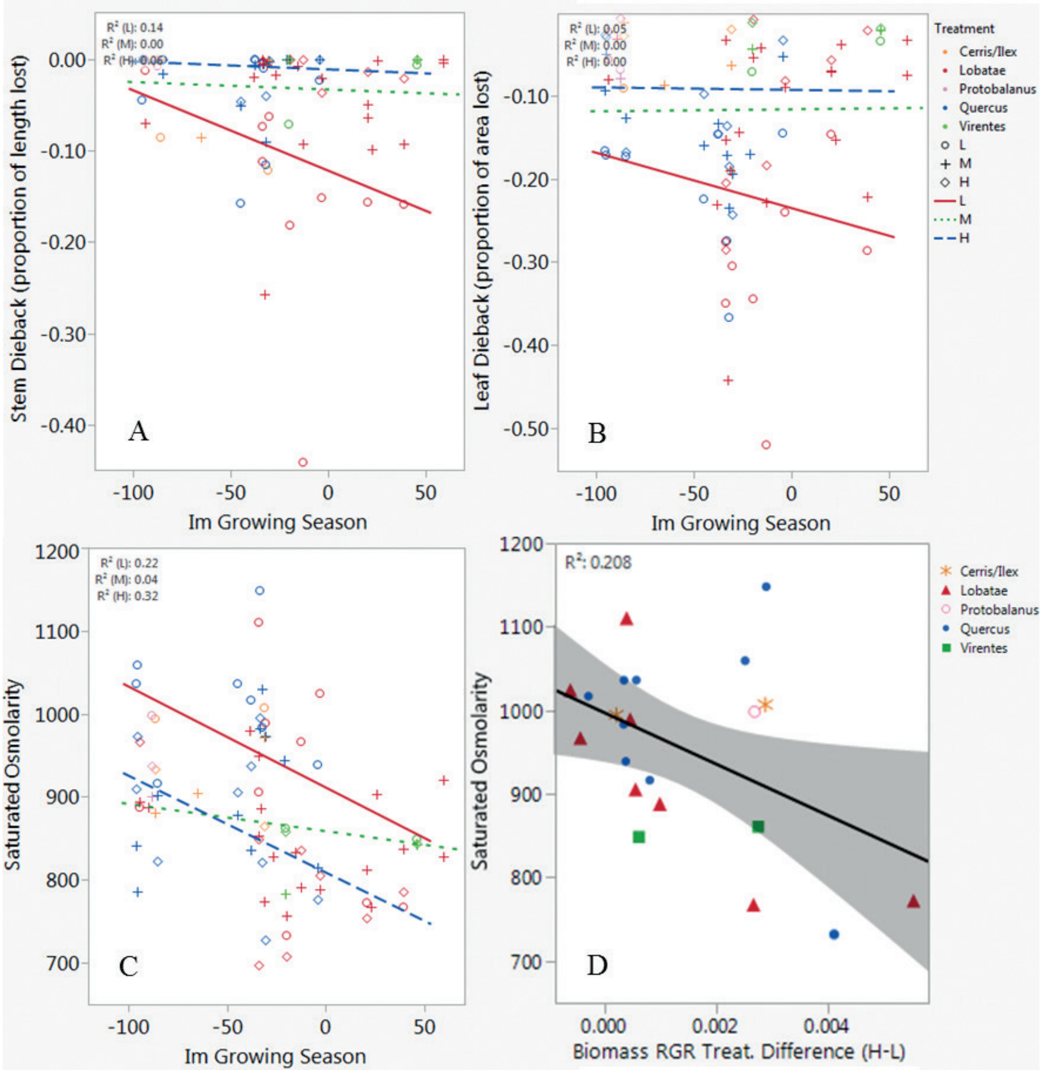

Figure 5/ Common garden species responses to water treatments. A) Species mean stem and B) leaf dieback in relation to species climate of origin I_m GS (negative values indicate water deficit). C) Species mean leaf solute concentrations in relation to species native range I_m GS. D) Trade-off between species mean leaf solute concentrations when grown under low water and growth rates differences between high and low water treatments. Positive RGR values indicate enhanced growth when well watered.

drought tolerance compared to species from mesic environments. In particular, we found that species from xeric environments are able to increase solute concentration and avoid dieback in response to imposed drought. This pattern of varying species acclimation to water treatment corresponds with water availability in their climate of origin (Moisture Index during the growing season, I_m GS). The association of species traits and climate is very practical because it allows for characterization of species drought resistance or tolerance using environmental indices of species native range (e.g., I_m GS). As a consequence, environmental indices can serve as important indicators of drought response, and parameters for modeling responses to climate change. The correlation between water availability in species native ranges and their stress tolerance under experimental drought conditions is a strong indication of adaptation of species to their native environment and environmental sorting (Diaz et al. 1998; Reich et al. 2003).

Results from the larger 125-species herbarium functional trait survey reinforces this pattern, showing evidence for a functional association of species with their native hydrologic regime. For example, species with leaves that have higher perimeter-to-area ratios, i.e., those that are more dissected or smaller, are found in drier environments. Previous work has shown P/A relates to leaf (and subsequently whole-plant) hydraulic conductance (Sack et al. 2003); plants with higher P/A leaves tend to have shorter vascular distances within leaf tissue preventing desiccation risk in dry environments. Thus, a more dissected or smaller leaf would have a higher proportion of the leaf blade closer to primary and secondary veins, providing a greater ability to hydrate the leaf blade and reduce the likelihood of leaf dieback in xeric conditions. Additional traits, such as increased adaxial pubescence, were also associated with drier climates. Pubescence often increases reflectance and can reduce the amount of light and heat that reach the leaf blade, thereby reducing light and heat stress (Manetas 2003; Banowetz et al. 2008).

Trade-off between drought resistance traits under drought stress and capacity to enhance growth under well-watered conditions

We found that the accumulation of leaf solutes (π_o) in oaks is inversely related to their capacity to enhance growth rate (RGR) in response to well-watered conditions. Species from dry environments had higher solute concentrations, reduced stomatal area *and* reduced growth rates compared to mesic species (when well-watered). We also found that species stomatal pore area (as measured by stomatal pore index, SPI) and growth rates are positively correlated, while negatively associated with higher π_o. SPI is strongly linked with greater capacity for gas exchange and leaf hydraulic conductance (Sack et al. 2003), both of which support growth (Sack and Holbrook 2006). This trade-off indicates that at the extremes of a climate spectrum, species invest either in drought resistance via solute accumulation or in leaves with high potential gas exchange area.

A trade-off is also present between specific leaf area (SLA) and π_o – species with higher SLA have higher concentrations of solutes under medium or low water treatments. The relationship improves when omitting the only *Protobalanus* (Trelease) A. Camus species, *Q. chrysolepis* Liebm., a xeric species that has one of the lowest SLA values in the common garden but a π_o near the mean of all tested oaks, equivalent to $\Psi_{TLP} <$ -2.5 MPa. Higher SLA is often positively associated with photosynthetic rates, growth and nutrient uptake rates, traits that are typically higher in more mesic environments (Lambers and Poorter 2004; Wright et al. 2004; Reich 2014).

Generally, the trade-off between drought tolerance strategies and the capacity to increase growth in response to water addition is consistent across the major lineages of the Americas *Quercus* phylogeny. However, clades within particular regions may fall at one extreme or another. For example, Mexican and Central American species, which represent two of the major clades, grow in the most mesic I_m GS in the Americas, and have the lowest solute concentrations, greatest growth enhancement and the most pronounced trade-off.

Synthesis

In the common garden study, mesic species are more likely to utilize isohydric strategies in drought conditions, reducing stomatal conductance (Kaproth et al. *unpublished*) and leaf area at the cost of carbon fixation, in order to prevent water loss, cavitation and mortality. After cessation of drought, plants then produce new leaf tissue to increase photosynthesis (although with some delay). Xeric species, in contrast, tend to be more anisohydric, maintaining their leaf tissue to allow for gas exchange whenever possible. The maintenance of thicker (Kaproth et al. *unpublished*) and more dissected/smaller leaves allows for the tissue to maintain carbon fixation, and the plants can be opportunistic – taking advantage of ephemeral well-watered conditions. As a result, xeric species have high survivorship and minimal leaf and stem dieback under all water treatments. Many of the xeric species show no differences in growth rates across water treatments, although their solute concentrations varied in response to soil moisture treatments. Similar patterns of an osmotic adjustment drought resistance strategy has been observed across the genus *Acer* L. over a growing season (Sjöman et al. 2015), with increased solutes developing in drier conditions.

An interesting pattern occurs between xeric and mesic species under controlled water treatments. It is well known that plant growth is controlled by water availability, which can alter nutrient availability and physiological processes, including photosynthesis and stomatal conductance. With higher water availability, more N and P become available due to nutrient cycling and microbial mobilization and a plant can acquire and allocate more nutrients for growth, light capture and photosynthesis. As expected, we see that mesic species' growth is enhanced with increased water. The xeric species however, do not show increased growth rates in response to increased watering (despite higher photosynthesis rates under well-watered conditions; Kaproth et al. *unpublished*). We speculate the xeric species could allocate resources in a different way than mesic species. For example, a portion of photosynthates may be channeled to belowground ectomycorrhizae. While mycorrhizae colonization may enhance a plant's ability to absorb water or nutrients, the C lost may not be enhancing plant growth under mesic conditions. Greater investment in drought tolerant tissues is another possible allocation difference. The morphology of structures like low SLA (typically thicker leaves) and high wood density are more carbon-intensive but necessary to withstand water stress. In other words, for xylem to continue functioning under low water potential, small-diameter xylem vessels with dense pit membranes are required to reduce cavitation and embolism risk (Meinzer et al. 2014). This anatomical form requires a higher amount of C for many small vessels at high density to equal the flow of a few large vessels. Greater allocation to solutes also appears to be a xeric oak species strategy. Xeric species maintain elevated solute concentrations compared to mesic species regardless of the water treatment. The solutes, organic osmolytes (e.g., proline, sugars) or inorganic elements (e.g., K, Cl, Na), require energy for biosynthesis/acquisition *and* for transportation across membranes against concentration gradients in order to increase solute concentration (Delauney and Verma 1993; Pate and Jeschke 1993; Hare et al. 1998). Future work investigating these patterns is needed to understand the response differences among species to water stress.

By examining the patterns of performance in response to experimental watering treatments, we show that the oaks of the Americas have developed adaptive plasticity in water use and drought-tolerance traits. We see evidence of acclimation within species to water treatments, and associations between traits and their native climates, providing evidence for adaptation. Further analysis can examine whether trait plasticity is labile across clades or conserved using the newly developed *Quercus* phylogeny (sensu Hipp et al. 2014).

Assessment of species functional traits in relation to their climates of origin may assist in forecasting how a species will respond to climate change. Leaf osmolarity, and subsequent estimations of turgor loss point can provide rapid determination of a species drought resistance and water-stress dieback. Leaf osmolarity and morphology may also reveal if a species may have competitive growth under more mesic conditions. These traits are likely to be useful in future studies to forecast species performance under varying rainfall conditions – especially important given a changing climate predicted to be more variable and extreme.

Acknowledgements

This work was funded by NSF 1146488: Phylogeny of the New World oaks: Diversification of an ecologically important clade across the tropical-temperate divide, awarded to A. Hipp, J. Cavender-Bares, P. Manos, J. Romero-Severson, A. Gonzalez-Rodriguez. We thank these researchers as well as A. Scollard, S. Schnifer, S. Seramur, J. Nockwicki, B. Fredericksen, N. McMann, G. Perez, J.A. Ramírez-Valiente, B. Fallon; seed collectors (R. Kipfer, B. Kipfer, C. Sulak, C. Brodersen); and data sources (H. Rodríguez-Correa, B. Brown, I. Pearse, and N. Stoynoff).

Photographers. Title page: Matthew Kaproth (*Quercus candicans*).

Works cited

Abrams, M.D. 1990. Adaptations and responses to drought in *Quercus* species of North-America. *Tree physiology* 7: 227-238.

Bailey-Serres, J. and L. Voesenek. 2008. Flooding stress: Acclimations and genetic diversity. *Annual review of plant biology* 59: 313-339.

Banowetz, G.M., M.D. Azevedo, and R. Stout. 2008. Morphological adaptations of hot springs panic grass (*Dichanthelium lanigunosum* var. *sericeum* (Schmoll) to thermal stress. *Journal of Thermal Biology* 33: 106-116.

Bartlett, M.K., C. Scoffoni, R. Ardy, Y. Zhang, S. Sun, K. Cao, and L. Sack. 2012a. Rapid determination of comparative drought tolerance traits: using an osmometer to predict turgor loss point. *Methods in Ecology and Evolution* 3: 880-888.

Bartlett, M.K., C. Scoffoni, and L. Sack. 2012b. The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: A global meta-analysis. *Ecology Letters* 15: 393-405.

Breshears, D.D., O.B. Myers, C.W. Meyer, F.J. Barnes, C.B. Zou, C.D. Allen, N.G. McDowell, and W.T. Pockman. 2008. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment* 7: 185-189.

Carter, M. F. and J. B. Grace. 1990. Relationships between flooding tolerance, life history, and short-term competitive performance in three species of *Polygonum*. American Journal of Botany 77: 381-387.

Cavender-Bares, J. and N.M. Holbrook. 2001. Hydraulic properties and freezing-induced cavitation in sympatric evergreen and deciduous oaks with contrasting habitats. Plant, Cell & Environment 24 :1243-1256.

Cavender-Bares, J., K. Kitajima, and F.A. Bazzaz. 2004. Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. *Ecological Monographs* 74: 635-662.

Cornelissen, J., S. Lavorel, E. Garnier, S. Diaz, N. Buchmann, D. Gurvich, P. Reich, H. Ter Steege, H. Morgan, and M. Van Der Heijden. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335-380.

Delauney, A. J. and D. P. S. Verma. 1993. Proline biosynthesis and osmoregulation in plants. *The Plant Journal* 4: 215-223.

Diaz, S., M. Cabido, and F. Casanoves. 1998. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* 9: 113-122.

Edwards, E. J. 2006. Correlated Evolution of Stem and Leaf Hydraulic Traits in Pereskia (*Cactaceae*). *New Phytologist* 172: 479-489.

Fine, P. V. A., Z. J. Miller, I. Mesones, S. Irazuzta, H.M. Appel, M.H.H. Stevens, I. Sääksjärvi, J.C. Schultz, and P.D. Coley. 2006. The growth–defense trade-off and habitat specialization by plants in Amazonian forests. *Ecology* 87: S150-S162.

Grime, J.P. 1977. Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. *The American Naturalist* 111: 1169-1194.

Hare, P.D., W.A. Cress, and J. Van Staden. 1998. Dissecting the roles of osmolyte accumulation during stress. *Plant, Cell & Environment* 21: 535-553.

Hipp, A. L., D.A.R. Eaton, J. Cavender-Bares, E. Fitzek, R. Nipper, and P.S. Manos. 2014. A Framework Phylogeny of the American Oak Clade Based on Sequenced RAD Data. PLoS ONE 9:e93975.

Kaproth, M.A. and J. Cavender-Bares. 2016. Allometric coeffecients for seedling *Quercus* (oaks) of the Americas. TRY Plant Trait Database.

Koehler, K., A. Center, and J. Cavender-Bares. 2012. Evidence for a freezing tolerance–growth rate trade-off in the live oaks (*Quercus* series Virentes) across the tropical–temperate divide. *New Phytologist* 193: 730-744.

Koide, R., R. Robichaux, S. Morse, and C. Smith. 1989. Plant water status, hydraulic resistance and capacitance. Pages 161-183 *in*

R. Pearcy, J. Ehleringer, H. Mooney, and P. Rundel, editors. *Plant Physiological Ecology*. Springer Netherlands.

Lambers, H. and H. Poorter. 2004. Inherent Variation in Growth Rate Between Higher Plants: A Search for Physiological Causes and Ecological Consequences. Pages 283-362 *in* H. Caswell, editor. *Advances in Ecological Research*. Academic Press.

Manetas, Y. 2003. The importance of being hairy: the adverse effects of hair removal on stem photosynthesis of Verbascum speciosum are due to solar UV-B radiation. *New Phytologist* 158: 503-508.

Manos, P. S. and A. M. Stanford. 2001. The Historical Biogeography of Fagaceae: Tracking the Tertiary History of Temperate and Subtropical Forests of the Northern Hemisphere. *International Journal of Plant Sciences* 162: S77-S93.

McDowell, N., W.T. Pockman, C.D. Allen, D. D. Breshears, N. Cobb, T. Kolb, J. Plaut, J. Sperry, A. West, D.G. Williams, and E.A. Yepez. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* 178: 719-739.

Meinzer, F.C., D.R. Woodruff, D.E. Marias, K.A. McCulloh, and S. Sevanto. 2014. Dynamics of leaf water relations components in co-occurring iso-and anisohydric conifer species. *Plant, Cell & Environment* 37: 2577-2586.

Nixon, K.C. 2006. Global and Neotropical Distribution and Diversity of Oak (genus Quercus) and Oak Forests. Pages 3-13 *in* M. Kappelle, editor. *Ecology and Conservation of Neotropical Montane Oak Forests*. Springer Berlin Heidelberg.

Pate, J.S. and W.D. Jeschke. 1993. Mineral uptake and transport in xylem and phloem of the proteaceous tree, *Banksia prionotes*. *Plant and soil* 155: 273-276.

Reich, P., I.J. Wright, J. Cavender-Bares, J.M. Craine, J. Oleksyn, M. Westoby, and M.B. Walters. 2003. The evolution of plant functional variation: Traits, spectra, and strategies. *International Journal of Plant Sciences* 164: S143-S164.

Reich, P.B. 2014. The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology* 102: 275-301.

Sack, L., P.D. Cowan, N. Jaikumar, and N.M. Holbrook. 2003. The ‘hydrology’ of leaves: co-ordination of structure and function in temperate woody species. Plant, Cell & Environment 26: 1343-1356.

Sack, L. and N. M. Holbrook. 2006. Leaf hydraulics. Annual review of plant biology 57: 361-381.

Savage, J.A. and J. Cavender-Bares. 2013. Phenological cues drive an apparent trade-off between freezing tolerance and growth in the family *Salicaceae*. *Ecology* 94:1708-1717.

Shipley, B., M.J. Lechowicz, I. Wright, and P.B. Reich. 2006. Fundamental trade-offs generating the worldwide leaf economics spectrum. *Ecology* 87: 535-541.

Sjöman, H., A.D. Hirons, and N.L. Bassuk. 2015. Urban forest resilience through tree selection—Variation in drought tolerance in Acer. *Urban Forestry & Urban Greening* 14: 858-865.

Thornthwaite, C.W. 1948. An approach toward a rational classification of climate. *Geographical Review* 38: 55-94.

Wright, I.J., P.B. Reich, M. Westoby, D.D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J.H.C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P.K. Groom, J. Gulias, K. Hikosaka, B.B. Lamont, T. Lee, W. Lee, C. Lusk, J.J. Midgley, M.-L. Navas, U. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet, S.C. Thomas, M.G. Tjoelker, E.J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821-827.