

# Drivers of habitat partitioning among three *Quercus* species along a hydrologic gradient

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## Abstract

A critical process that allows multiple, similar species to coexist in an ecological community is their ability to partition local habitat gradients. The mechanisms that underlie this separation at local scales may include niche differences associated with their biogeographic history, differences in ecological function associated with the degree of shared ancestry, and trait-based performance differences, which may be related to spatial or temporal variation in

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habitat. In this study we measured traits related to water-use, growth, and stress tolerance in mature trees and seedlings of three oak species (*Quercus alba* L., *Quercus falcata* Michx., and *Quercus palustris* Münchh), which co-occur in temperate forests across the eastern United States but tend to be found in contrasting hydrologic environments. The three species showed significant differences in their local distributions along a hydrologic gradient. We tested three possible mechanisms that influence their contrasting local environmental distributions and promote their long-term co-existence: 1) differences in their climatic distributions across a broad geographic range, 2) differences in functional traits related to water use, drought tolerance and growth, and 3) contrasting responses to temporal variation in water availability. We identified key differences among the species in both their range-wide climatic distributions (especially aridity index and mean annual temperature) and physiological traits in mature trees and seedlings, including daily water loss, hydraulic conductance, stress responses, growth rate, and biomass allocation. Taken together, these differences explain the habitat partitioning that allows three closely related species to co-occur locally.

## Introduction

Understanding the mechanisms that permit the coexistence of multiple closely related species in a community has been fundamental to ecological research for over a century (Volterra 1926, Connell 1961, May and MacArthur 1972). Local-scale abiotic heterogeneity in factors like water, nutrients, light, or physical space affects the biotic community composition because performance differences among species provide competitive advantages in different parts of the gradient (Hutchinson 1959, Silvertown et al. 1999, Silvertown 2004). Variation in a small number of abiotic factors can allow a large number of closely related species to coexist within a landscape (Cavender-Bares et al. 2004a). Temporal variation or intermittent stressors can provide an additional “axis” on which species can partition local environments (Levins 1966, 1969, May and MacArthur 1972, Tilman 1994). The broad question of coexistence thus narrows: how do similar species exploit temporal and spatial variability to coexist sympatrically?

Trait-based approaches (e.g. Shipley et al. 2017) have focused on the ways that physiological differences between species affect community assembly processes or predict habitat preferences. Wei et al. (2017) identified several key traits in Salicaceae species that showed variation along a hydraulic gradient associated with fitness that predicted species distribution. The traits that support local diversity may operate at different timescales: plants can adjust solute concentration or stomatal opening

within minutes and alter wood vascular growth or phenology along growing seasons or lifetimes (Munns 2002, Chenu et al. 2008). The magnitude of these responses may be very sensitive to changes in water availability, or may be coordinated to allow plants to maintain a relatively constant water status despite environmental changes (Meinzer et al. 2016), and different combinations of traits may affect similar fitness responses in an environment (Reich et al. 2003).

Biogeographic history may offer a macro-scale explanation for how species sort into local niches; species whose lineages stem from different climate regimes may sort into different local habitats where their ranges overlap (Cavender-Bares et al. 2016, Ackerly 2003). For example, Sedio et al. (2013) found that a plant’s microhabitat on Barro Colorado Island, Panama, is associated with the climate of the region where it originated. This pattern is also seen in communities which sort along elevation gradients, reflecting the water availability and temperatures of climates of origin (Harrison et al. 2010).

Close relatives, which may be ecologically similar due to shared ancestry (Webb et al. 2002, Wiens and Graham 2005) are often expected to exhibit functional differences in resource use and/or stress tolerance that promote niche differentiation (Donoghue 2008). Research has shown that niche differentiation can occur directly through competition to meet similar resource requirements, or indirectly via density-dependent mortality (Violle et al. 2011, Gilbert and Webb 2007, Parker et al. 2015). Experimental tests in plants (e.g. Cahill et al. 2008) are equivocal, however, and there are many instances of plant communities without this pattern (e.g. Kluge and Kessler 2011), especially in cases where changing environments or stressors can drive similar species to cluster (Burns and Strauss 2011, Mayfield and Levine 2010).

In this study, we examined whether the local distribution patterns of three oak species showed evidence for differences in physiological and growth responses to gradients of water availability and stress that promote habitat (and thus niche) partitioning. We further considered these factors in relation to their biogeographic history and phylogenetic relatedness. *Quercus alba* L., *Quercus falcata* Michx., and *Quercus palustris* Münchh. are three forest canopy species at the Smithsonian Ecological Research Center near coastal Maryland. Red (*Q. falcata* and *Q. palustris*, *Quercus* section *Lobatae*) and white (*Q. alba*, *Quercus* section *Quercus*) oaks have been shown to have a long history of parallel and sympatric diversification in eastern North America (Hipp et al. 2018), and the two lineages therefore coexist across the continent (Cavender-Bares et al. 2018). While these three species coexist broadly, they have been qualitatively described as being found in contrasting hydrologic niches (Gleason and Cronquist 1991, le Hardy de Beaulieu and Lamant 2006). We hypothesized that the apparent habitat partitioning along a hydrologic gradient shown among these

three species could be demonstrated quantitatively. If large-scale patterns predicted local-scale partitioning, we hypothesized that partitioning can be explained by some combination of the following factors (Figure S1):

1. Climatic envelopes of the full ranges of each species, especially considering moisture, are predictive of the distribution of species across the local elevation gradient in our study site
2. Species more able to tolerate water stress induced by temporal variation (i.e. a drought versus wet year) will occupy a more varied environmental range than less tolerant species
3. Trade-offs in growth and physiological (e.g. transpiration and water use) performance will emerge among species across the gradient, consistent with an interpretation of contrasting adaptive advantages at either end of the elevation gradient.

We further expected to see more habitat separation between *Q. falcata* and *Q. palustris* than between either of those species and *Q. alba*, as both are red oaks and thus more closely related to each other than either is to *Q. alba* (Cavender-Bares et al. 2004b), though with only three species we could not meaningfully quantify phylogenetic niche partitioning in this study system.

We focused on a set of traits, centered around sap flow measurements in mature trees and gas exchange measurements in seedlings, to understand the trait differences that might explain differences in distribution driven by water availability. In mature trees heat-dissipation measurement of xylem sap flow offers an approximation of whole-tree transpiration (Granier 1987, Ladefoged 1960, Cohen et al. 1981, Hogg et al. 1997, Catovsky et al. 2002); although concerns exist that it may fail to account for variable tree anatomy (Clearwater et al. 1999, Lu et al. 2000, Burgess et al. 2001, Delzon et al. 2004), this method continues to provide one of the best approaches for capturing water fluxes in mature trees (Poyatos et al. 2016). Overall, the selected traits indicate water use and hydraulic performance, growth and productivity, and stress response.

Associating the variability in particular traits - even small differences - with both the local and broader ranges and phylogenetic relationships of these three species can help us to subsequently understand how spatially and temporally varied habitats allow close relatives to coexist.

# Methods

## Study System

### Site Description

Our study sites for mature trees were located in a continuous tract of forest within the Smithsonian Environmental Research Center (SERC), located in Edgewater, Maryland, along the Rhode River. Our study site was an approximately 50 ha tract (the “Big Tree Plot”, BTP) within the 1100 ha main forest situated around the SERC photobiology tower (38.89 N, 76.56 W) and included an elevation gradient ranging from sea level to 22m, shown in Figure 1a. Mean slope angle at sampled sites was  $6.69^\circ$  (SD =  $4.70^\circ$ ), and compound topographical index (CTI, Moore et al 1991) was 3.62 (SD = 1.29). Historically used for dairy farming, the study area was reclaimed as forest approximately 100 years ago, and is currently made up of 50-100 year old stands in the “tulip poplar” association. Since the time of data collection, a portion of this site has been added to the Forest Global Earth Observatory Network of the Center for Tropical Forest Studies (CTFS-ForestGEO).

The elevation gradient in the plot was treated categorically, such that trees sampled at 0-5m were considered at low elevation and labeled “wet” sites, 10-22m were upland or “dry”, and those in between were at “mid” elevation. These elevation categories are characterized by different soil types with contrasting hydrologic qualities (Soil Survey Staff and Natural Resources Conservation Service 2018); six wells were installed in the Big Tree Plot from 1 to 10m in 2018, and the water table depth and soil moisture measurements show a strong relationship with elevation (Supplement Figures S3 and S4). The low elevation sites were dominated by “Widewater and Issue” (WBA) soils, a poorly drained soil with high flood frequency and a typical summer water table depth of 35 cm; the mean water table depth among all soil types at low elevation was 108 cm. Measured water table depth from May through September 2018 in wells at 1m and 2m elevation ranged from 12 cm to 105 cm, with a mean of 46 cm. The mid-elevation sites included several soil types, typically moderate-to-well drained but with lower flood frequency than the low elevation sites. Mean water table depth estimated from soil types was 158 cm, while measured depths ranged from 16 cm (immediately following heavy rain) to 330 cm. The high elevation sites from which trees were sampled were primarily Collington and Annapolis (CRD) soils, which are well-drained, sandy soils with a summer water table depth of more than 200 cm, which is the reporting threshold for USGS soils data. Soil moisture data for the study site during the experiment are given in Table 1a, and key differences in soil characteristics are summarized in Table 2. A map of the study trees including

167 elevation and soil type can be found in Figure S2.

## 168 Mature Tree Sampling

169 Physiological measurements were collected from June to October 2002 and 2003 on  
 170 the three most common oak species in the SERC forest tract: *Quercus alba* L. (white  
 171 oak), *Quercus falcata* Michx. (Southern red oak), and *Quercus palustris* Munchh.  
 172 (pin oak). *Q. palustris* is commonly found in floodplains with limited drainage, and  
 173 is considered water-loving; *Q. falcata* grows in drier areas, including slopes and ridges  
 174 above the floodplain. *Q. alba* preferentially grows in more moderately watered areas  
 175 and does not typically tolerate habitats with very high or very low water availability.  
 176 Figure 1c shows the proportion of total basal area for each species found across the  
 177 elevation gradient.

178 The number of trees sampled per species and elevation category in each year  
 179 is summarized in Table S2. Trees were all mature, with diameter-at-breast-height  
 180 (DBH) between 50-70cm in similarly-aged forest stands and were selected to cover the  
 181 elevation range of the site, with considerations made for proximity to power sources.  
 182 A map of study trees and elevation categories is included as supplemental Figure  
 183 S2. Soil moisture at each tree was measured approximately weekly each summer  
 184 using time domain reflectometry (TDR): steel probes were installed to a depth of 1m  
 185 and 5cm apart, and readings were collected with a metallic cable tester (Tektronix  
 186 1502C, Tektronix Inc., Beaverton, Oregon).

187 Sapwood area (SA, cm<sup>2</sup>) was measured in all sample trees. Tree cores were taken  
 188 in late summer each year at a height of 1.4m, away from the sap flow sensors and ab-  
 189 normal wood formations. Sapwood depth is the distance between the outermost ring  
 190 of xylem and the point of color change marking the beginning of inactive heartwood.  
 191 This approach was cross-validated with injection of Safranin-O dye. These cores were  
 192 also used to estimate growth rate as basal area increment (BAI, cm<sup>2</sup>/year). Average  
 193 values of sapwood depth and DBH are reported in supplemental Table S4.

## 194 Seedling Common Garden

195 In addition to *in situ* measurements of mature trees, a common garden of oak  
 196 seedlings was established. Acorns from each species were collected from within a  
 197 2 ha region of the SERC forest and planted in three blocks of an experimental gar-  
 198 den. Seedlings were grown under 50% shade cloth for their first year of growth, then  
 199 moved to an open-air rain-out shelter with an automatic irrigation system. Three  
 200 water treatments were established: plants in the low water treatment were irrigated  
 201 every 10 days, in the medium water treatment every four days, and in the high water

202 treatment daily. Soil moisture was monitored using TDR probes; mean values are  
 203 given for each treatment in Table 1b.

## 204 **Species Geographic and Climatic Ranges**

205 The geographic ranges for each species were captured using occurrence data aggre-  
 206 gated by the Global Biodiversity Information Facility (GBIF, accessed December  
 207 2016); only occurrences in the United States with valid latitude and longitude co-  
 208 ordinates were included. Climatic envelopes were produced for those ranges using  
 209 the bioclimatic variables (chiefly mean annual temperature (MAT) and mean an-  
 210 nual precipitation (MAP) generated by WorldClim Global Climate Data (Hijmans  
 211 et al. 2005) and potential evapotranspiration (PET) and the aridity index (MAP  
 212 over mean annual PET) data from the Consortium for Spatial Information (Zomer  
 213 et al. 2008, Trabucco and Zomer 2010). We rename aridity index as "wetness index"  
 214 (WI) for clarity. All data were processed using R (R Core Development Team 2017).

## 215 **Spatial and Temporal Variation in Water Availability**

216 The SERC site falls within the humid subtropic climate zone, with warm summers  
 217 and cool, wet winters. From 1990-2010, the mean daily temperature in the sum-  
 218 mer was 21.9°C (SD = 7.1°C), with mean monthly summer rainfall of 28.1 mm (SD  
 219 = 11.2 mm, Global Historical Climatology Network Database), with a consistent  
 220 pattern of interannual variation. Data were collected for this study over two sum-  
 221 mers with contrasting weather conditions. Weather during the "dry year" (2002)  
 222 saw significantly less rainfall, warmer temperatures, more solar radiation, and higher  
 223 vapor pressure deficit (VPD) than the "wet year" (2003) (Figure 2a, additional in-  
 224 formation in supplementary table S1). The differences in these weather conditions  
 225 from 2002 to 2003 were consistent with year-to-year differences for the region (Figure  
 226 2b). All site-specific climate data were collected at the climate monitoring station  
 227 at SERC; measurements include global solar flux between 285 to 2800 nm (Eppley  
 228 Precision Spectral Pyranometer, The Eppley Laboratory, Newport, Rhode Island),  
 229 temperature and relative humidity (Vaisala HMP45AC, Vaisala, Helsinki, Finland),  
 230 and rainfall (TE525 "Tipping Bucket" rain gauge, Texas Electronics, Dallas, Texas).  
 231 Saturated vapor pressure ( $VP_{sat}$ ) and vapor pressure deficit (VPD) were calculated  
 232 from temperature and relative humidity as per the National Weather Service.

## Trait Measurements

The traits measured in mature trees and seedlings fall into three broad categories: water use, stress, and growth/productivity. In mature trees, water use and stress traits were compared among species and across both space and time; growth rate was calculated as an average basal area increment over 20 years and was thus only compared among species and along the elevation gradient.

### Water Use: Sap Flow, Conductance, and Water-Use Efficiency

We used constant-heat dissipation sap flow sensors consisting of a heated temperature sensor inserted into the sapwood 4 cm (per manufacturer recommendation) above an unheated reference temperature probe (Granier 1985, 1987). We used both commercial sensors (TDP 30; Dynamax, Inc.; Houston, Texas) and constructed custom shorter sensors (Phillips et al. 2002, Meinzer et al. 2004); all probes used copper-constantin thermocouples to measure temperature. The current applied to constructed sensors was regulated by a circuit board to produce the same power density (wattage per unit volume of the resistor) to compensate for differences in resistance. The median temperature increase above ambient was 5.17°C for the Dynamax sensors and 8.24°C for the short sensors; this variation similar in magnitude to other studies (e. g. McCulloh et al. (2007)). Data from different sensor types showed no more variation than data from sensors of the same type in different positions in the tree (Supplemental Figures S5 and S6). Sap flow was measured for 15 weeks beginning in mid-August in 2002 and 17 weeks beginning in early July in 2003.

Dynamax sensors were installed in each of 20 trees in both the dry and wet year: probes were inserted 0-30mm into the cambium at 1.4m in height on the north- and south-facing sides of each tree. In the wet year, when 19 additional trees were added to the study, two short sensors were also installed in each tree. These probes were inserted 11, 16, or 21mm (depending on probe length) into the cambium; if Dynamax probes were already installed, the short probes were inserted at the same height 20cm away. All sensors were insulated from water and heating, and connected to a current regulator (AVRD; Dynamax, Inc; Houston, Texas) and data logger (23X, 21X or 10X; Campbell Scientific, Inc.; Logan, Utah), powered by AC power with a battery backup. The temperature difference between the pairs of thermocouples for each probe were sampled every 10 seconds and averages were logged every 10 or 30 minutes. Data was downloaded weekly and potentially problematic data (due to malfunctioning sensors or electrical storms) was flagged.

Sap flow velocity ( $v$ , cm/s) was calculated from the maximum ( $\Delta T_0$ ) and actual ( $\Delta T$ ) temperature difference between probes at each time point, following the equa-



tions established by Granier (1987), Granier et al. (1994) as shown in equations 3 and 4; volumetric sap flow rate ( $F$ , cm<sup>3</sup>/s) is velocity multiplied by sapwood area. Total daily water loss (TDWL) was calculated as the integral of sap flow rate over a 24 hour period and maximum sap velocity ( $V$ , cm/s) is the maximum value of  $v$  in the same period.

$$v = 0.0119k^{1.231} \quad (1)$$

where

$$k = \frac{\Delta T_0 - \Delta T}{\Delta T} \quad (2)$$

267 Sap flow measurements taken with Dynamax sensors, which were generally longer  
268 than the sapwood depth, and thus in contact with non-conducting tissue, were cor-  
269 rected per Clearwater et al. (1999) to account for overestimated sap flux velocity.

270 In seedlings, transpiration ( $E$ , mol H<sub>2</sub>O m<sup>-2</sup>s<sup>-1</sup>) was measured directly ( $n = 108$ ,  
271 12 plants per species per treatment) with a LI-COR 6400 Portable Photosynthesis  
272 System (LI-COR; Lincoln, Nebraska) rather than approximating via sap flux. Other  
273 water use traits, including stomatal conductance ( $g_{sw}$ , mol H<sub>2</sub>O m<sup>-2</sup>s<sup>-1</sup>) and intrinsic  
274 water use efficiency ( $WUE_i$ ,  $A/g_{sw}$ ), were measured at the same time as  $E$  with the  
275 LI-COR 6400. Data were collected twice for each plant, over the last weeks of June  
276 and July, between 7:00 AM and 9:00 AM.

277 In both mature trees and seedlings, predawn (3:00 am - 6:00 am) and midday  
278 (10:00 am - 3:00 pm) leaf water potential ( $\Psi_{PD}$  and  $\Psi_{MD}$ , respectively) were mea-  
279 sured with a pressure chamber (Plant Water Status Console, 3000 series; Soilmois-  
280 ture; Santa Barbara, California). Leaves for measuring  $\Psi_{PD}$  were taken from the  
281 most accessible location on tree, usually a low or mid canopy, while  $\Psi_{MD}$  was mea-  
282 sured for high, mid and low canopy leaves. Between cutting and measurement, leaves  
283 were stored in moist, sealed plastic bags inside a dark cooler to minimize water loss.  
284 In mature trees, measurements were collected over the first three weeks of July in  
285 each year; in seedlings measurements were taken in the last two weeks of July.

286 In mature trees, the change in water potential from predawn to midday and  
287 steady-state sap flow rate ( $F$ ) were used to calculate whole plant hydraulic conduc-  
288 tance ( $K$ , cm<sup>2</sup>s<sup>-1</sup>MPa<sup>-1</sup>):  $K = F/(\Psi_{MD} - \Psi_{PD})$ . Steady-state  $F$  is the average  $F$   
289 over the hour-long period during mid-day leaf collection when the variance in  $F$  was  
290 smallest. If sap flow measurements were not available for a tree on the date water  
291 potential was measured, the value from the most recent day with similar VPD was  
292 used. Whole plant hydraulic conductance in seedlings ( $K_l$ , mmol m<sup>-2</sup> s<sup>-1</sup>MPa<sup>-1</sup>)  
293 was similarly calculated, using steady state transpiration instead of sap flow rate.

294 Water use efficiency ( $WUE$ ,  $A/E$ ) in seedlings was calculated directly from gas  
295 exchange measurements. In mature trees, it was estimated from  $\delta^{13}C$  values (Far-

quhar et al. 1982), although this approach may be confounded by unknown mesophyll conductance (Warren and Adams 2006). In each monitored mature tree, leaves were collected at multiple canopy positions at four time points across both summers. Leaf samples were frozen upon collection and then dried and ground for carbon isotopic analyses with an elemental analyzer (Carlo Erba Instruments, NA 2500 series; Wigan, England) coupled via continuous flow to a stable isotope ratio mass spectrometer (ConFloII to Delta Plus XL; ThermoFinnigan; Waltham, Massachusetts) in the lab of Marilyn Fogel at the Geophysical Lab, Carnegie Institution of Washington, D.C. Stable carbon isotopic values are expressed as  $\delta$  values according to the equation:

$$\delta^{13}C = [(R_{sample}/R_{standard}) - 1]1000 \quad (3)$$

where R is the ratio of  $^{13}C$  to  $^{12}C$  and the standard was the Pee Dee Belemnite (PDB) standard. Instrument error was  $\pm 0.3\%$ . When making comparisons among species and water availability, only mature mid-summer leaves for each tree were analyzed to minimize the problem of early, heterotrophic growth influencing WUE estimates (Terwilliger et al. 2001).

## Water Stress

The change in daily leaf water potential ( $\Delta\Psi$ ) between midday and predawn was used to estimate leaf water stress, where lower values suggest a leaf is closing its stomata or otherwise conserving water during the day and higher values show more water loss relative to the equilibrium indicated by the predawn water potential.

While measuring pre-dawn  $\Psi$ , maximum quantum yield of photosynthesis after dark incubation ( $F_v/F_m$ ) was measured on seedlings with a portable chlorophyll fluorometer (MINI-PAM; Heinz Walz GmbH; Effeltrich, Germany). An indicator of the efficiency of photosynthesis,  $F_v/F_m$  is generally 0.8 in healthy plants and declines as plants experience stress (Maxwell and Johnson 2000).

## Growth and Productivity

Basal area increment (BAI,  $\text{cm}^2/\text{year}$ ) from tree cores collected in 2002 was used in mature trees to compare growth rates among species across the elevation gradient. Basal area was estimated from 1980 to 2002 by subtracting all newer ring growth from the present DBH; average growth rate was the slope of least-squares regression between year and basal area.

Productivity was directly measured in seedlings as carbon assimilation ( $A$ ,  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) with the LI-COR 6400 ( $n = 108$ , 12 plants per species per treatment,

as with *E*). At the conclusion of the experiment, seedlings were harvested for biomass measurements. Leaves, stems, and roots were separated and dried at 70°C for three days before weighing. In addition to biomass, leaf stable isotope ratios were measured following the same protocol as for mature trees.

## Statistical Analysis

All statistical analyses were performed in R (R Core Development Team 2017). For each physiological trait measured in mature trees, we tested the effects of and interactions among species, elevation category, and year using Analysis of Variance (ANOVA) on a fixed effects model including all three attributes and all interactions. The same approach was used for the seedling trait data, with Species and Treatment as the explanatory variables. When ANOVA results were significant ( $p < 0.05$ ), Tukey's Honest Significant Differences (HSD) was used to make pairwise comparisons.

Species climatic ranges were extracted from the raster BIOCLIM and aridity datasets at the coordinates of individuals identified in the GBIF data set using the *raster* package (Hijmans 2016). Coordinate system corrections and conversion of shapefile data to raster format were done using QGIS software (QGIS Development Team 2009). Pairwise species means were compared using a Tukey-adjusted t-test for multiple comparisons (Lenth 2016). All figures were produced using the *ggplot2* package (Wickham 2009).

## Results

### Comparison of Broad and Local Distributions

Comparing the climatic distributions of the oak species across their full ranges, the three species differed in mean bioclimatic variables in a few critical ways that were suggestive of associations with their local distributions at SERC. In particular, *Q. falcata* had a more arid climatic distribution and was found in the sites that have the lowest water availability locally. Across its range, *Q. falcata* was found in locations which were significantly warmer than either *Q. alba* or *Q. palustris*, which were generally not different from each other. The average mean annual temperature (MAT, °C) in *Q. falcata*'s range was 3.2°C warmer than the range of *Q. alba* and 2.8°C warmer than *Q. palustris* ( $p < 0.0001$ , Tukey-adjusted p-value). *Q. falcata* also occurred in regions with higher rainfall than the other species, with an average MAP was 79 mm higher ( $p < 0.0001$ , Tukey-adjusted p-value), but because the higher

temperatures drove a higher rate of potential evapotranspiration (PET), its range had a lower WI value, indicative of a drier environment overall. The temperature and aridity distributions of these three species are shown in Figure 1b. For climate variables, the differences between *Q. alba* and *Q. palustris* were not significant; these and additional bioclimatic variables are summarized in Table 5.

Figure 1c shows the distributions of each species of oaks for all trees in the Big Tree Plot at SERC; these distributions are also summarized in Table S3. Though all three species were found across the elevation gradient (from the sea level floodplain to 22m), each was concentrated in a distinct subset of the gradient from floodplain to higher elevation. Comparing the least-squares means of elevation by species, *Q. palustris* had the lowest mean elevation, showing a preference for locations where soils had higher water availability. As predicted, the largest difference in elevation was between the two red oaks, though both also occurred at significantly different mean elevations from *Q. alba* ( $p < 0.0001$ , Tukey-adjusted p-value).

## Species, Spatial, and Temporal Performance Differences

### Water Use

Figure 3 shows the sap velocity over the course of 24 hours averaged over the season (August - October in the dry year, July - September in the wet year) for each species; mean sap velocity for each species over time is shown in supplemental figure S7. The average maximum daily sap velocity ( $V$ , cm/s) was significantly different among species, elevation categories, and years; each interaction between pairs of variables was also significant (ANOVA,  $p = 0.0251$  for the species by year interaction,  $p < 0.0001$  for all others). Mean values of  $V$  and other key traits measured in mature trees by species, elevation category, and year are summarized in Table 3.

Maximum sap velocity was also slightly but significantly correlated with both VPD (Pearson's  $r = 0.128$ ,  $p < 0.0001$ ) and with solar radiation (Pearson's  $r = 0.107$ ,  $p < 0.0001$ ). The relationship between sap velocity and VPD was found in each species when considered separately and p-values were adjusted with the Holm method for multiple comparisons (*Q. alba*:  $r = 0.120$ ,  $p < 0.0001$ ; *Q. falcata*:  $r = 0.159$ ,  $p < 0.0001$ ; *Q. palustris*:  $r = 0.105$ ,  $p = 1.343 \times 10^{-4}$ ). The relationship between sap velocity and solar radiation persisted in both *Q. alba* and *Q. falcata* when these species were considered separately, but not in *Q. palustris* ( $r = 0.0008$ ,  $p = 0.97$ ).

Average total daily water loss (TDWL) is shown in figure 5a. TDWL was significantly lower at low elevation than at either middle or high elevation sites ( $p = 0.013$  and  $p = 0.046$  respectively, Tukey's HSD); mean values did not differ among species

398 or between years. There was a significant ( $p = 0.024$ ) interaction between elevation  
 399 and species: *Q. palustris* exhibited a decline in water loss with increased elevation  
 400 (and therefore decreased soil moisture), while both *Q. alba* and *Q. falcata* generally  
 401 exhibited increased water loss. In *Q. alba*, peak TDWL in both years occurred at  
 402 high elevation sites (dry), while in *Q. falcata* peak values were seen at mid elevation.

403 In mature trees, whole-plant hydraulic conductance ( $K$ ) was similar to TDWL in  
 404 its relationships with species, elevation, and year (figure 4a): there were significant  
 405 differences in mean values among elevation categories ( $p = 0.002$ ) but not species ( $p$   
 406  $= 0.38$ ) or year ( $p = 0.13$ ). Much of this difference was driven by the much higher  
 407  $K$  seen in *Q. falcata* growing at mid-elevation in the dry year. There was also a  
 408 significant interaction ( $p = 0.003$ ) between species and elevation: among both *Q.*  
 409 *alba* and *Q. falcata*, the lowest values of hydraulic conductance occurred in the wet  
 410 floodplain, while in *Q. palustris*, trees in the floodplain had higher values of  $K$  than  
 411 at other elevations.

412 Contrasting with mature trees, seedlings of all three species showed a significant  
 413 decline in hydraulic conductance under the low water treatment; mean differences  
 414 among species were not significant, and no significant interaction between species  
 415 and water treatment when seedlings of all three species were included (Table 4).  
 416 *Q. palustris* does show a steeper decline in hydraulic conductance than *Q. falcata*  
 417 (Figure 4b), but this difference is marginal ( $p = 0.07$ ).

418 In mature trees, the strongest predictor of increased  $\delta^{13}\text{C}$  ratios (and thus in-  
 419 creased WUE) was leaf developmental stage indicated by calendar day. There were  
 420 significant differences in  $\delta^{13}\text{C}$  by species ( $p = 0.028$ ) and marginal differences by year  
 421 ( $p = 0.07$ ). There was also a change in the relationship between water use efficiency  
 422 and elevation between the years: on average,  $\delta^{13}\text{C}$  increased when comparing wet to  
 423 dry sites in the dry year and decreased in the wet year ( $p = 0.023$ ). *Q. palustris* had  
 424 a higher WUE than the other two species in both years and at both wet and dry  
 425 sites. It also exhibited the largest change in WUE at dry sites between the dry and  
 426 wet years, as seen in figure 5c.

427 Seedlings exhibited significant differences in transpiration rates ( $E$ ) and stomatal  
 428 conductance ( $g_{sw}$ ) when grown under different water-availability conditions ( $E$ :  $p <$   
 429  $0.0001$ ,  $g_{sw}$ :  $p < 0.0001$ ), shown in figure 7. Performance in all species was highest at  
 430 the moderate water treatment for both traits; transpiration and  $g_{sw}$  were significantly  
 431 higher at moderate water availability than either dry or wet conditions ( $p < 0.0001$   
 432 for both traits, Tukey's HSD). There were no significant differences in either  $A$  or  $E$   
 433 among species, though  $g_{sw}$  was significantly higher in *Q. alba* than in the other two  
 434 species ( $p = 0.001$ , Tukey's HSD).

435 Water use efficiency in seedlings was measured using both carbon isotope ratio

( $\delta^{13}\text{C}$ ) and gas exchange measurements ( $A/g_{sw}$ , abbreviated as  $\text{WUE}_i$ ). There were significant differences among species ( $p = 0.04$ ) and treatments ( $p = 0.045$ ) in  $\delta^{13}\text{C}$ , though pairwise differences were small. *Q. falcata* and *Q. palustris* were the most similar in their isotope ratios ( $p = 0.99$ ), while *Q. alba* showed slightly, though non-significantly, higher WUE by this metric.  $\text{WUE}_i$  was not significantly different among species but was among treatments, and was highest under dry conditions ( $p < 0.0001$ , Tukey's HSD). This pattern was also seen with  $\delta^{13}\text{C}$ , though the results were not significant.

## Stress

Pre-dawn water potential ( $\Psi_{PD}$ ) (shown in supplemental Figure S8) was significantly lower at all elevations and for all mature trees in the dry year, reflecting significant differences in measured soil moisture. Mid-day water potential ( $\Psi_{MD}$ ) was also significantly different between years. Here we focus on the difference ( $\Delta\Psi$ ) between these values as an indicator of plant stress to incorporate information about both changing water availability and changing evaporative demand. Figure 5b illustrates the changes among species in  $\Delta\Psi$  between years and elevation categories in mature trees. All species exhibited higher mean  $\Delta\Psi$  in the dry year, though this general trend was not observed at all sites. The differences between years were most pronounced at dry sites, and the difference in  $\Delta\Psi$  at wet and dry sites was significant in the dry year ( $p = 0.007$ , Tukey's HSD) but not the wet year ( $p = 0.25$ , Tukey's HSD). The compounding effect of the drought and elevation gradient on water stress appeared most pronounced in *Q. palustris*, though differences among species in mature trees were not significant.

*Q. palustris* seedlings also exhibited higher levels of  $\Delta\Psi$  in the low water treatment than at high water, as did *Q. alba*. Differences in  $\Delta\Psi$  between water treatment categories and species were significant (ANOVA,  $p = 0.0005$  and  $p = 0.04$ , respectively). The interaction between species and water treatment was not significant when *Q. alba* was included, but differences among species in which water treatment caused the most stress were significant when only *Q. palustris* and *Q. falcata* seedlings were compared ( $p = 0.05$ ).

Stress response measured by chlorophyll fluorescence ( $F_v/F_m$ ), however, suggested that seedlings exhibited increased photoinhibition ( $F_v/F_m$  below 0.8) at high water treatments (ANOVA,  $p < 0.0001$ ). This response was seen in both *Q. falcata* and *Q. palustris*, but not in *Q. alba* (Figure 7).

## 470 Growth and Productivity

471 There was a weak ( $p = 0.08$ , linear least squares regression), positive relationship  
 472 between increasing growth rate (average BAI per year) and elevation, shown in Figure  
 473 6b, suggesting slightly higher growth rates in individuals at drier sites at higher  
 474 elevation. *Q. palustris*, however, had a significantly different ( $p = 0.02$ ) relationship  
 475 than the other two species, having its fastest growth in the floodplain and decreased  
 476 growth rate at higher elevation.

477 In seedlings, the relationship between growth and water availability was not as  
 478 strong; all three species produced less total biomass at both high water and low water  
 479 availability, as compared to the moderate water treatment (Figure 7). However, the  
 480 differences in biomass between high and low water were not significant, nor were  
 481 the differences among species. *Q. palustris* seedlings did show a different pattern of  
 482 biomass allocation than the other two species, with significantly lower allocation of  
 483 biomass below ground. This was especially apparent in the high water treatment.  
 484 There was a significant difference in carbon assimilation ( $A$ ) among treatment groups  
 485 ( $p < 0.0001$ ), with plants given moderate water showing higher  $A$  than those at high  
 486 water ( $p < 0.0001$ , Tukey's HSD). There were no significant differences in  $A$  among  
 487 species, nor was a significant interaction between species and treatment observed.

488 Mature trees in all three species did exhibit a strong ( $p < 0.0001$ ), positive rela-  
 489 tionship between hydraulic conductance ( $K$ ) and average annual growth rate, shown  
 490 in Figure 6a. The slope of this relationship was significantly ( $p = 0.03$ ) higher in *Q.*  
 491 *palustris* than the other two species, meaning for the same increase in  $K$ , *Q. palustris*  
 492 had a larger annual basal area increment. In *Q. palustris*, this increased slope was  
 493 the same at both dry and wet sites (slope = 0.02 at wet site and 0.01 at dry site,  
 494  $p = 0.23$ ); by contrast, *Q. falcata* had a steeper slope at dry site (increasing from 0  
 495 to 0.016,  $p = 0.04$ ) and *Q. alba* had a lower one (decreasing from 0.02 to 0.002,  $p =$   
 496 0.07), suggesting that each species responded differently to environmental conditions  
 497 that vary with elevation.

## 498 Discussion

499 These results provide evidence that the three most abundant species of oaks in the  
 500 "Big Tree Plot" at SERC, *Quercus alba*, *Quercus falcata*, and *Quercus palustris*,  
 501 partitioned an elevation (and thus hydrologic) gradient. *Q. palustris* and *Q. falcata*  
 502 showed the largest differences in local distributions, while *Q. alba* was more evenly  
 503 distributed from low to high elevation. The difference in local distribution between *Q.*  
 504 *falcata* and *Q. palustris* was also reflected in differences in growth rate, with *Q. palus-*

505 *tris* experiencing its highest growth rates at low elevation, in the floodplain, where  
 506 *Q. falcata* exhibited its lowest growth rates. This habitat partitioning was supported  
 507 in part by climatic differences in the broad geographic ranges of these species, as well  
 508 as key differences in functional traits of both mature trees and seedlings. Considered  
 509 in sum, these results underline the complexity of the factors that drive local species  
 510 distributions in natural systems.

511 Differences in climatic conditions across the broad geographic ranges of the three  
 512 species were associated with local habitat partitioning, as hypothesized in Ackerly  
 513 (2003) and Cavender-Bares et al. (2016), particularly in wetness index and mean  
 514 annual temperature. The overall geographic range of *Q. falcata* was associated with  
 515 significantly warmer and more arid climate than the other two species, despite higher  
 516 overall rainfall, and locally was found in sites with the lowest seasonal water avail-  
 517 ability. *Q. alba* had a broad geographic and climatic range that largely overlaps the  
 518 other two species, a trend consistent with the local distributions at SERC. However,  
 519 the distribution of oaks in the BTP showed significant separation between *Q. palus-*  
 520 *tris* and the other two species, while the full climatic distributions of *Q. palustris* and  
 521 *Q. alba* across their ranges showed no significant differences in average temperature,  
 522 rainfall, or aridity. One caveat to note is that we may not have completely captured  
 523 the full North American ranges of these species with GBIF data alone. Beck et al.  
 524 (2014) demonstrated that the spatial bias in specimen records can significantly skew  
 525 range reconstructions, and the accuracy of species identification and the precision  
 526 of geographic location can introduce error (Goodwin et al. 2015, Wieczorek et al.  
 527 2004). Nevertheless the consistency between aridity and temperature ranges and  
 528 habitat preference at SERC provides compelling evidence of a connection between  
 529 broad scale and local distributions.

530 Among plant functional traits, the hydraulic conductance of mature trees sup-  
 531 ported the hypothesis that contrasting water-use strategies help *Q. palustris* and *Q.*  
 532 *falcata* exploit opposite ends of a hydrologic gradient. With decreasing water avail-  
 533 ability, in both a dry and wet year, the hydraulic conductance in mature trees of *Q.*  
 534 *palustris* declined while that of *Q. falcata* increased or did not change. The conduc-  
 535 tance of *Q. palustris* also declined consistently with decreasing water in seedlings,  
 536 while conductance in *Q. falcata* showed a small increase in the moderate water treat-  
 537 ment, though the mean values were not significantly different among seedlings of  
 538 different species. Conductance has been shown to be highly correlated with growth  
 539 rate, a trend seen in both the the literature (e. g. Poorter et al. 2010) and in our  
 540 data (Figure 6a). In our study, the relationship between growth and conductance  
 541 was strongest in *Q. palustris*: the same increase in conductive ability was associated  
 542 with a significantly larger increase in growth rate in *Q. palustris* than the other two



species, suggesting it is adapted to take advantage of greater water availability.

The higher conductance seen in *Q. palustris* may come at the cost of increased stress during drought years. Values reported in the literature show that *Q. palustris* typically has a larger vessel diameter than *Q. falcata* (Lobo et al. 2018, Robert et al. 2017), which suggests it may be trading high hydraulic efficiency when water is available for increased vulnerability when it is not (Sperry et al. 2008). We observed mature *Q. palustris* trees experiencing the largest difference between predawn and midday water potential, indicative of drought stress, at the highest elevation in the dry year.  $\Delta\Psi$  was also higher in *Q. palustris* seedlings when water was limited, and higher in *Q. falcata* without water limitation.

Other traits in both mature trees and seedlings also provided evidence of partitioning. *Q. palustris* seedlings allocated less of their total biomass below ground, especially at high water availability, indicating a relatively shallow rooting system compared to the other species. Shallow roots have been shown to significantly decrease the survival of tree seedlings in drought (Padilla and Pugnaire 2007), and at a global scale lower rooting depth is associated with wet environments (Canadell et al. 1996). Though both species demonstrated an increase in water use efficiency with decreasing water, the change in WUE in drier conditions was the smallest in *Q. falcata*, consistent with the species' preference for drier habitats.

We found limited evidence to support the hypothesis that *Q. alba*'s broader distribution would be supported by an ability to maintain homeostasis under stress. In the high water treatment, both *Q. palustris* and *Q. falcata*, but not *Q. alba*, seedlings exhibited stress (as indicated by low  $F_v/F_m$ ). Though it might be unexpected to see a water-loving species like *Q. palustris* exhibit higher stress in very well-watered conditions, even wetland species show decline in photosynthetic rates in response to the oxygen deprivation caused by flooding (Pezeshki 2001), and lowered  $F_v/F_m$  is a documented response to flooding stress (Nash and Graves 1993). In general, oaks show a preference for drier, well-drained soils and do not grow in the wettest climates in their geographic ranges (Cavender-Bares et al. 2018).

The depressed performance of seedlings under high water conditions illustrates that drought was unlikely to be the only environmental factor affecting plant function. Lower vapor pressure deficit or light limitation in the rainy season may have augmented plant response to water stress, helping to explain why we observed a smaller response than expected to the drought conditions of the dry year. We found sap flux to be correlated with both light levels and VPD; it is possible that decreases in transpiration from lower water availability were offset by stronger driving gradients in the dry year, explaining why we did not see a change in total daily water loss. Aranda et al. (2005) found a higher stress response to drought in cork oak

581 (*Quercus suber* L.) in low light conditions compared to high light. High light could  
 582 alternatively cause depressed performance or stress due to photoinhibition (Long  
 583 et al. 1994), which we were not able to test for in this study.

584 Finally, while three species are too few to draw strong conclusions about the  
 585 effects of phylogeny on habitat sorting, the distributions of these three oak species at  
 586 SERC did match the expectation that more closely related species will show greater  
 587 habitat separation, drawn from microcosm experiments (Violle et al. 2011), across  
 588 environmental gradients (Cavender-Bares et al. 2004a, Fallon and Cavender-Bares  
 589 2018), and on continental-scale observations of different subgenera (Cavender-Bares  
 590 et al. 2018). *Q. palustris* and *Q. falcata*, both red oaks (Section *Lobatae*) are more  
 591 closely related to each other and more separated along the elevation gradient than  
 592 either is from *Q. alba*, a white oak (Section *Quercus*). The pattern suggested by  
 593 these three oak species was consistent with phylogenetic relatedness as a driver for  
 594 community structure and functional diversification.

595 In addition to concerns about the accuracy of GBIF data and limited power for  
 596 phylogenetic analysis, there are a few cautions which may limit the scope of these  
 597 results. Heat dissipation sap flow measurements may fail to accurately estimate  
 598 transpiration rate, in particular because there can be a high amount of radial and  
 599 circumferential variation in sap flow that may not be captured by one or two mea-  
 600 surements per tree (González-Altozano et al. 2008); we observed a high degree of  
 601 dispersion in results from pairs of sensors installed in the same tree (Figures S5 and  
 602 S6), which could be attributed to natural variation or could be an artifact of dif-  
 603 ferences between sensors (Lu et al. 2004). Bush et al. (2010) have observed that  
 604 the calibration constants published by Granier (1987) may not be accurate for ring-  
 605 porous tree species, like oaks. Second, the design of this study was not optimal for  
 606 testing competition or local adaptation directly. This was not a reciprocal transplant  
 607 experiment, nor were genotype or maternal line controlled (Bengtsson et al. 1994).  
 608 Our results should, however, motivate further research that does explicitly control  
 609 these variables, because the distribution pattern and trait differences we found war-  
 610 rant additional investigation.

## 611 Conclusion

612 We have provided evidence supporting the hypothesis that *Quercus alba*, *Quercus fal-*  
 613 *cata*, and *Quercus palustris* coexist in the forest community at SERC by partitioning  
 614 a hydrologic gradient driven by elevation. Our findings suggest that a combination  
 615 of biogeographic legacy effects, functional traits, response to temporal variation, and  
 616 phylogeny may play a role in driving this variation. Among functional traits, the

hydraulic conductance of mature trees offers the clearest support to the idea that the two red oaks partition the gradient through contrasting water-use strategies. A lack of a single phenomenon among those we tested can explain the local distribution of our study species is consistent with other recent work (Morueta-Holme et al. 2016), and future research in habitat partitioning and community assembly will be strengthened by addressing multiple potential drivers of observed patterns.

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	Water	SWC (SE)		Water	SWC (SE)
Dry Year	Wet	0.186 (0.016)			
	Mid	0.246 (0.017)			
	Dry	0.157 (0.014)			
Wet Year	Wet	0.466 (0.003)		Dry	0.124 (0.012)
	Mid	0.469 (0.005)		Mid	0.263 (0.017)
	Dry	0.485 (0.005)		Wet	0.462 (0.019)

(a) Mature trees

(b) Seedlings

Table 1: Mean soil moisture (volumetric water content,  $V_w/V_s$ ) as measured by TDR probes in the mature tree field sites and seedling common garden. Differences among sites, years, and treatments are all significant. Standard error (SE) is reported for each value in parentheses.

	Wet (<5m)	Mid (5-10m)	Dry (>10m)
AWS (cm)	31.0	31.1	26.9
AWC (cm/cm)	0.17	0.16	0.14
Water Table Depth (cm)	108.2	157.8	>200
$K_{sat}$ ( $\mu\text{m/s}$ )	15.7	16.3	13.4
% SOM	1.28	0.64	0.38

Table 2: Mean values of selected soil characteristics at SERC by elevation category. Available Water Storage (AWS) is the quantity of water available to plants for all soil layers. Available Water Capacity (AWC) is the water available for use by plants given in centimeters of water per centimeter soil. Water Table Depth is the average from May to September, matching the months of measurements on mature trees; the maximum water table depth measured is 2m and soils with a deeper water table were assigned this maximum value. Saturated hydraulic conductivity ( $K_{sat}$ ) represents the rate of water movement through soil pores in a fully saturated soil. Soil Organic Matter (SOM) is measured as percentage by weight. Data were provided by the Web Soil Survey using a soil map of the minimum rectangular bounding box covering all trees measured in the experiment. All differences in means among elevation categories are significant (ANOVA,  $p < 0.0001$ ).

Trait	Species			Site				Year		
	<i>Q. alba</i>	<i>Q. falcata</i>	<i>Q. palustris</i>	Wet	Mid	Dry		Dry	Wet	
V (cm s <sup>-1</sup> )	4.29 × 10 <sup>-3</sup>	5.18 × 10 <sup>-3</sup>	4.51 × 10 <sup>-3</sup>	4.51 × 10 <sup>-3</sup>	5.09 × 10 <sup>-3</sup>	4.66 × 10 <sup>-3</sup>	**	4.91 × 10 <sup>-3</sup>	4.55 × 10 <sup>-3</sup>	
TDWL (l)	13.17	12.28	12.28	8.72	15.56	14.07		12.83	12.47	
K (cm <sup>2</sup> s <sup>-1</sup> MPa <sup>-1</sup> )	945.14	814.15	573.38	511.77	1165.68	744.52	**	876.96	729.65	
ΔΨ (MPa)	1.58	1.43	1.68	1.61	1.48	1.60	.	1.66	1.47	*
δ <sup>13</sup> C (‰)	-29.190	-29.241	-28.645	*	-29.002	-29.142		-28.791	-29.138	.

Table 3: Mean values of selected physiological traits measured in mature trees. Significance stars are the result of an ANOVA test and correspond to the following p-values: . : p < 0.1; \* : p < 0.05; \*\* : p < 0.01, \*\*\* : p < 0.001. Significant interactions between variables are described in Figure 5. V: maximum sap flux velocity; TDWL: total daily water loss; K: hydraulic conductance; ΔΨ: change in leaf water potential from pre-dawn to mid-day; δ<sup>13</sup>C: Water use efficiency.

Trait	Species				Treatment			
	<i>Q. alba</i>	<i>Q. falcata</i>	<i>Q. palustris</i>		Dry	Moderate	Wet	
Total Biomass (g)	10.36	8.96	10.89	*	7.28	14.05	8.59	***
Proportion Belowground	0.664	0.627	0.605	***	0.625	0.645	0.608	**
Leaf Area (cm <sup>2</sup> )	201.41	219.26	288.95	***	186.25	325.78	200.04	***
A ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	11.71	11.20	11.31		11.42	11.99	10.29	***
E (mol H <sub>2</sub> O m <sup>-2</sup> s <sup>-1</sup> )	3.64	3.58	3.51		3.46	3.91	3.20	***
$g_{sw}$ (mol H <sub>2</sub> O m <sup>-2</sup> s <sup>-1</sup> )	0.177	0.159	0.162	**	0.149	0.190	0.153	***
WUE <sub>i</sub> (A/ $g_{sw}$ )	75.21	77.54	74.73		81.52	72.81	70.31	***
$\delta^{13}\text{C}$ (‰)	-28.780	-29.666	-29.632	*	-28.752	-29.717	-29.688	*
$K_l$ (mmol m <sup>-2</sup> s <sup>-1</sup> MPa <sup>-1</sup> )	0.422	0.519	0.593		0.272	0.582	0.724	***
$\Delta\Psi$	11.55	9.13	9.23	.	11.29	10.66	6.91	***
F <sub>v</sub> /F <sub>m</sub>	0.807	0.784	0.767	*	0.811	0.804	0.749	***

Table 4: Seedling data means for a variety of physiological traits. Significance stars are the result of an ANOVA test and correspond to the following p-values: . :  $p < 0.1$ ; \* :  $p < 0.05$ ; \*\* :  $p < 0.01$ , \*\*\* :  $p < 0.001$ . Total biomass, leaf area, photosynthesis (A), transpiration (E), stomatal conductance ( $g_{sw}$ ), and F<sub>v</sub>/F<sub>m</sub> each also show significant interactions between species and treatment.

	<i>Q. alba</i>	<i>Q. falcata</i>	<i>Q. palustris</i>
Wetness (WI)	1.022	0.959	1.023
PET	1077.1	1219.6	1077.9
MAT (°C)	11.12	14.28	11.51
Min. T(°C)	-7.08	-3.08	-6.71
Max. T(°C)	29.39	31.48	29.87
MAP (mm)	1091.16	1168.00	1090.59
Wettest Month (mm)	112.86	122.84	112.51
Driest Month (mm)	68.71	74.49	67.14
Permeability (in/hr)	3.43	3.53	3.57
Flood frequency	3.77	3.70	3.67

Table 5: Mean values of bioclimatic and soil hydrology variables in the North American ranges of *Q. alba*, *Q. falcata*, and *Q. palustris*.

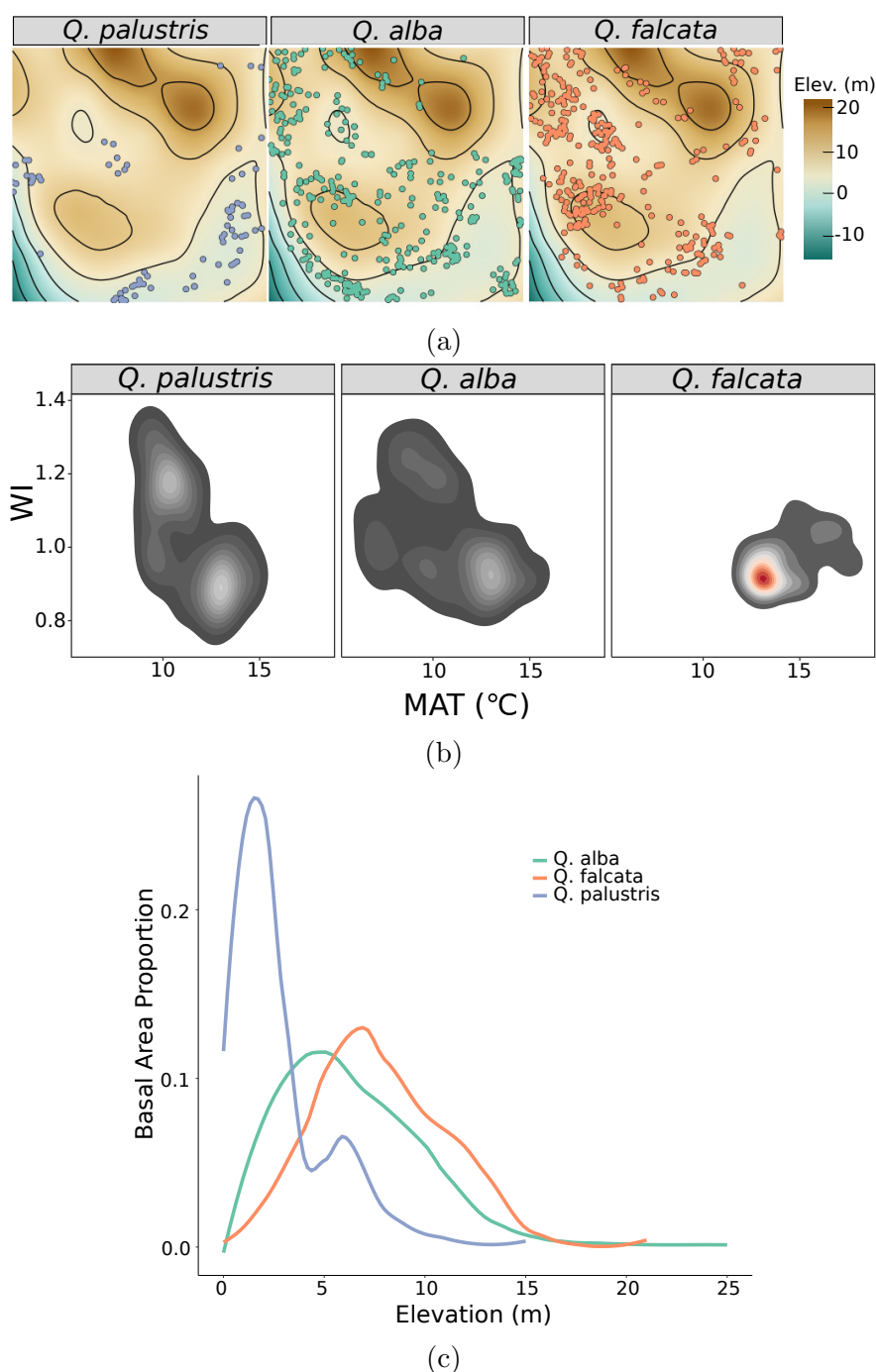


Figure 1: Broad and local distributions of *Q. alba*, *Q. falcata*, and *Q. palustris*. 1a: Distribution of the three oak species across SERC's Big Tree Plot (BTP), 700 m by 700 m. with elevation (m above sea level). 1b The climatic envelopes of the North American ranges of the three study species. Wetness Index, on the vertical axis, was developed by Zomer et al. (2008) and calculated as mean annual precipitation over mean annual evapotranspiration. The horizontal axis is mean annual temperature in degrees Celsius. The distribution of *Q. falcata* is significantly drier (lower WI,  $p < 0.001$ ) and hotter ( $p < 0.001$ ) than the other two species. 1c Proportion of total basal area for each oak species found across the elevation gradient in the BTP. These distributions are further summarized in Table S3.

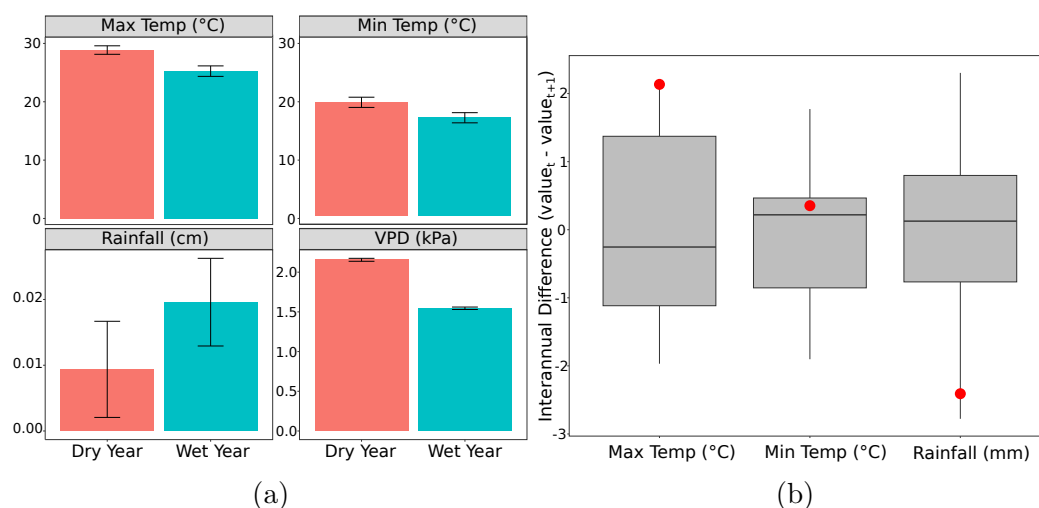


Figure 2: 2a: Mean total daily rainfall, minimum and maximum daily temperatures, and VPD for each summer during which data was collected, showing that dry summer was significantly warmer and drier than the wet summer. Error bars are 2\*SE. 2b: Year-to-year difference in average summer minimum and maximum daily temperature and monthly rainfall totals, 1980-2010. The vertical axis gives the difference in average summer weather from year  $t$  and year  $t + 1$ . Dark bar is the mean, boxes are interquartile distance, and whiskers are 95% confidence interval. Red dots highlight the difference in values between the study years, i.e. the value in 2003 minus the value in 2002.



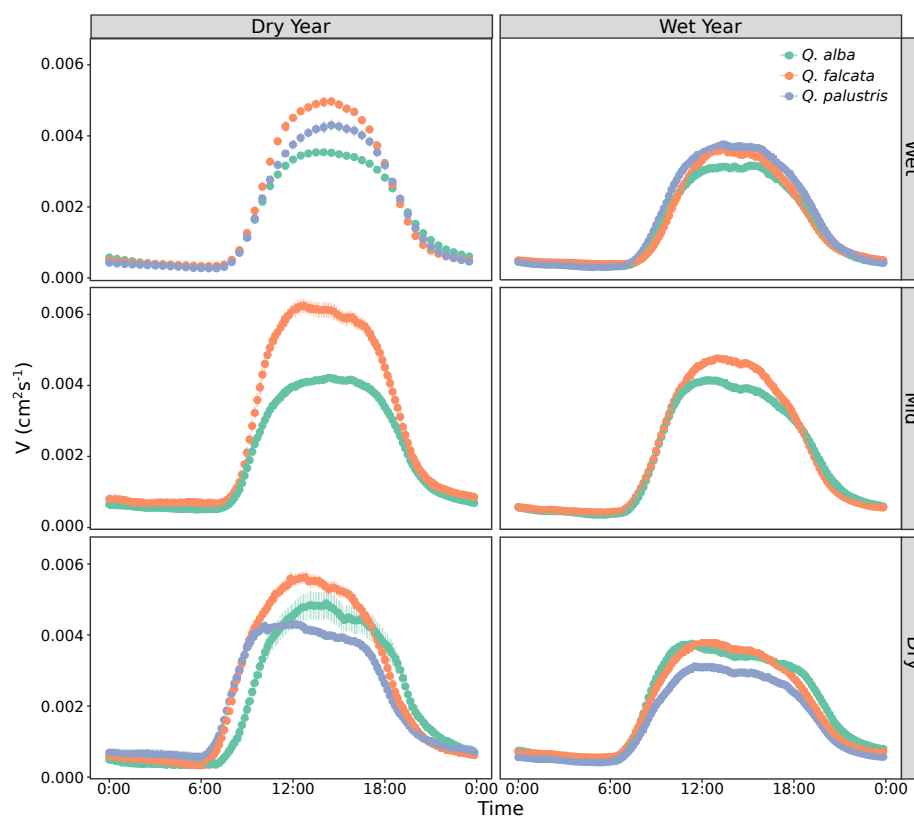


Figure 3: Average daily sap flow patterns for each species at each elevation and in the wet (July-September) and dry (August-October) year; the error bars are standard error. Daily maximum velocity is more variable in the dry year (SD in wet year = 0.00194, SD in dry year = 0.00239;  $p = 0.0008$ , Welch's Two-Sample t-test), and at low elevation (SD at low elevation = 0.00246, SD at high elevation = 0.00169;  $p < 0.0001$ , Welch's Two-Sample t-test).

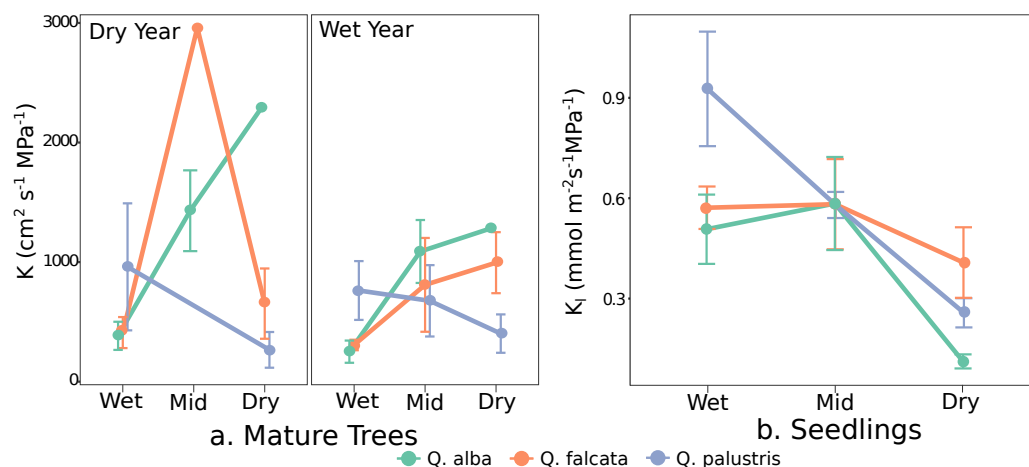


Figure 4: Differences in hydraulic conductance with water availability in mature trees (a) and seedlings (b). In mature trees,  $K$  ( $\text{cm}^2 \text{s}^{-1} \text{MPa}^{-1}$ ) differed significantly by site-based water availability (ANOVA,  $p = 0.00225$ ); interactions between water availability and species (ANOVA,  $p=0.003$ ) and the three-way interaction between year, elevation, and species (ANOVA,  $p= 0.03$ ) were also significant. In seedlings, conductance varied significantly by species (ANOVA,  $p < 0.0001$ ) but not by water availability.

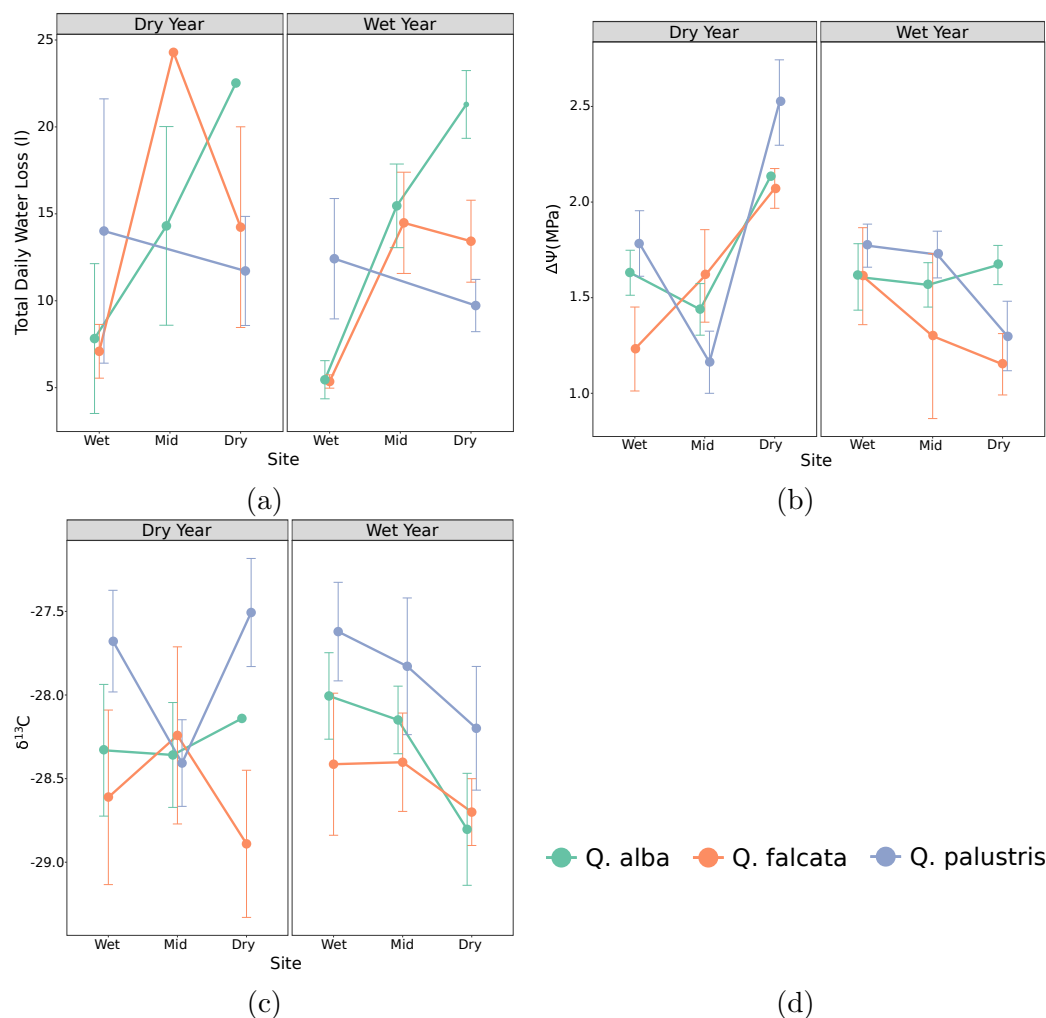


Figure 5: Differences by species, year, and elevation in four water-use traits measured in mature trees. 5a There were significant differences in total daily water loss (l) by elevation (ANOVA,  $p = 0.009$ ), as well as a significant interaction between elevation and species (ANOVA,  $p = 0.024$ ). 5b  $\Delta\Psi$  was significantly higher in the drought year than in the wet year (ANOVA,  $p = 0.037$ ), and there was a significant interaction between elevation category and year (ANOVA,  $p < 0.0001$ ). 5c There were significant species differences (ANOVA,  $p = 0.0167$ ) in water use efficiency ( $\delta^{13}C$ ) by species.

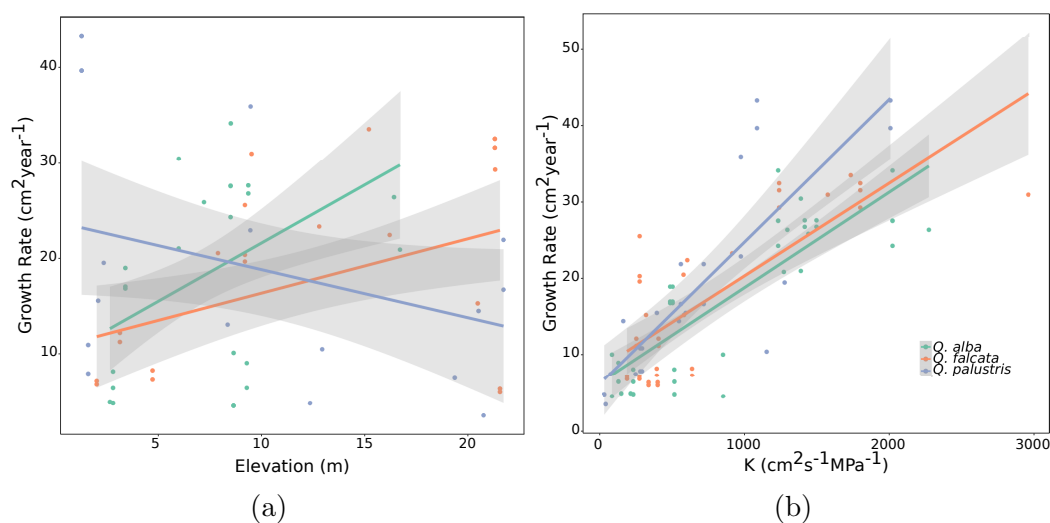


Figure 6: Growth rate (basal area increment,  $\text{cm}^2/\text{year}$ ) versus 6a: elevation (m) and 6b: hydraulic conductance ( $K$ ,  $\text{cm}^2\text{s}^{-1}\text{MPa}^{-1}$ ), measured in mature trees. There is a strong, positive linear relationship between growth rate and hydraulic conductance (Multiple  $R^2 = 0.67$ ), and the slope of that relationship is significantly higher ( $p = 0.0312$ ) in *Q. palustris*, which also exhibits a significantly different ( $p = 0.0178$ ) relationship between growth rate and elevation than the other two species.

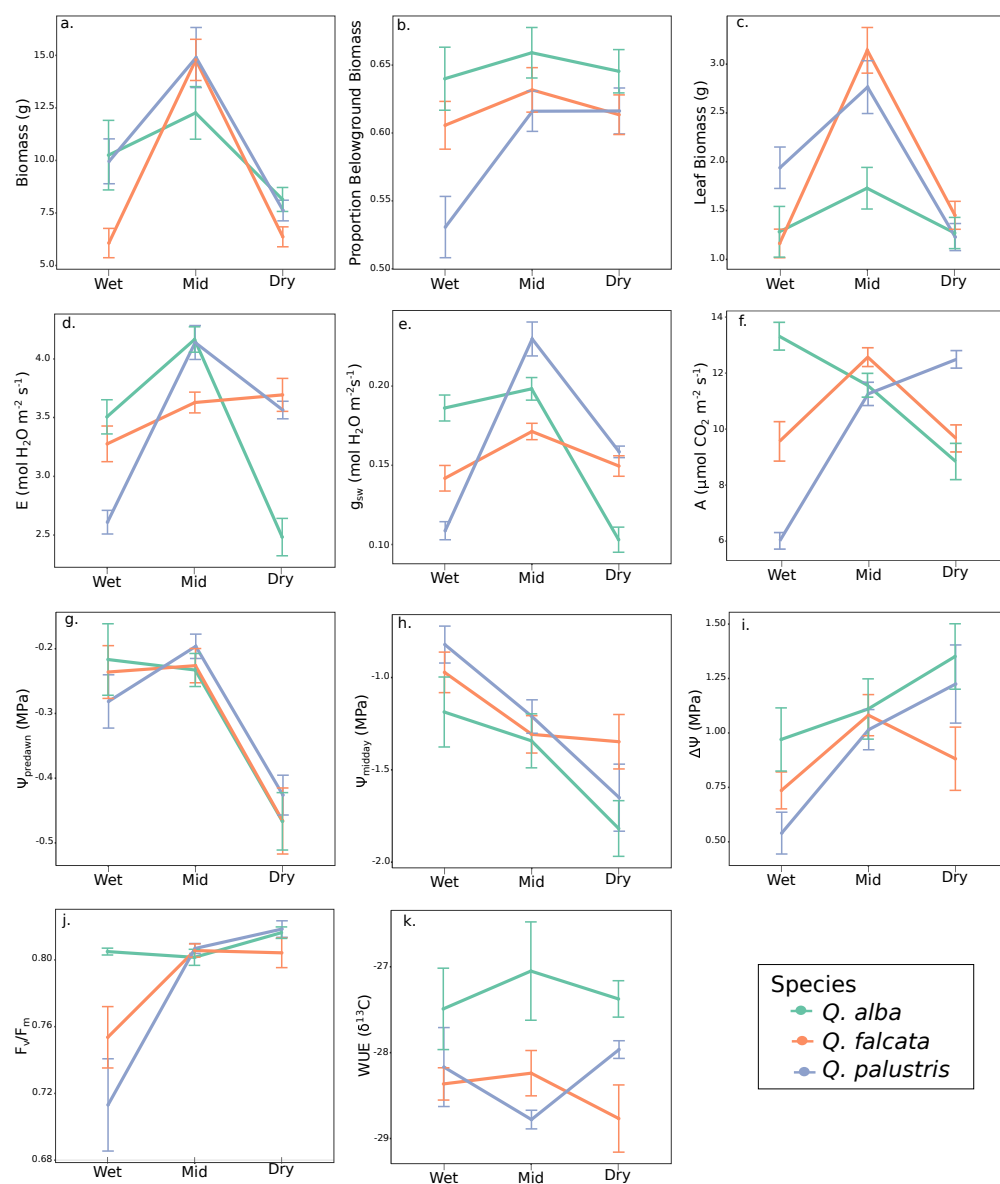


Figure 7: Seedling traits demonstrating (from top to bottom): growth (a. total biomass, b. proportion belowground biomass, and c. leaf biomass), gas exchange (c. transpiration rate, d. stomatal conductance, and e. photosynthesis), stress response and water status (g.  $\Psi_{predawn}$ , h.  $\Psi_{midday}$ , i.  $\Delta\Psi$ , and j.  $F_v/F_m$ ), and water use (k.  $\delta^{13}C$ ). Significant differences by treatment and species are summarized in Table 4.