

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

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15 November 1, 2019

16 **Abstract**

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

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

40 Introduction

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

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

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

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

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

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

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

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

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

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

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

131 **Methods**

132 **Study System**

133 **Site Description**

134 Our study sites for mature trees were located in a continuous tract of forest within the
135 Smithsonian Environmental Research Center (SERC), located in Edgewater, Mary-
136 land, along the Rhode River. Our study site was an approximately 50 ha tract (the
137 “Big Tree Plot”, BTP) within the 1100 ha main forest situated around the SERC
138 photobiology tower (38.89 N, 76.56 W) and included an elevation gradient ranging
139 from sea level to 22m, shown in Figure 1a. Mean slope angle at sampled sites was
140 6.69° (SD = 4.70°), and compound topographical index (CTI, Moore et al 1991) was
141 3.62 (SD = 1.29). Historically used for dairy farming, the study area was reclaimed
142 as forest approximately 100 years ago, and is currently made up of 50-100 year old
143 stands in the “tulip poplar” association. Since the time of data collection, a portion
144 of this site has been added to the Forest Global Earth Observatory Network of the
145 Center for Tropical Forest Studies (CTFS-ForestGEO).

146 The elevation gradient in the plot was treated categorically, such that trees sam-
147 pled at 0-5m were considered at low elevation and labeled “wet” sites, 10-22m were
148 upland or “dry”, and those in between were at “mid” elevation. These elevation cat-
149 egories are characterized by different soil types with contrasting hydrologic qualities
150 (Soil Survey Staff and Natural Resources Conservation Service 2018); six wells were
151 installed in the Big Tree Plot from 1 to 10m in 2018, and the water table depth and
152 soil moisture measurements show a strong relationship with elevation (Supplement
153 Figures S3 and S4). The low elevation sites were dominated by “Widewater and
154 Issue” (WBA) soils, a poorly drained soil with high flood frequency and a typical
155 summer water table depth of 35 cm; the mean water table depth among all soil types
156 at low elevation was 108 cm. Measured water table depth from May through Septem-
157 ber 2018 in wells at 1m and 2m elevation ranged from 12 cm to 105 cm, with a mean
158 of 46 cm. The mid-elevation sites included several soil types, typically moderate-to-
159 well drained but with lower flood frequency than the low elevation sites. Mean water
160 table depth estimated from soil types was 158 cm, while measured depths ranged
161 from 16 cm (immediately following heavy rain) to 330 cm. The high elevation sites
162 from which trees were sampled were primarily Collington and Annapolis (CRD) soils,
163 which are well-drained, sandy soils with a summer water table depth of more than
164 200 cm, which is the reporting threshold for USGS soils data. Soil moisture data for
165 the study site during the experiment are given in Table 1a, and key differences in
166 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, cm²) 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, cm²/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.

233 Trait Measurements

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

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

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

254 Dynamax sensors were installed in each of 20 trees in both the dry and wet year:
 255 probes were inserted 0-30mm into the cambium at 1.4m in height on the north-
 256 and south-facing sides of each tree. In the wet year, when 19 additional trees were
 257 added to the study, two short sensors were also installed in each tree. These probes
 258 were inserted 11, 16, or 21mm (depending on probe length) into the cambium; if
 259 Dynamax probes were already installed, the short probes were inserted at the same
 260 height 20cm away. All sensors were insulated from water and heating, and connected
 261 to a current regulator (AVRD; Dynamax, Inc; Houston, Texas) and data logger (23X,
 262 21X or 10X; Campbell Scientific, Inc.; Logan, Utah), powered by AC power with a
 263 battery backup. The temperature difference between the pairs of thermocouples for
 264 each probe were sampled every 10 seconds and averages were logged every 10 or 30
 265 minutes. Data was downloaded weekly and potentially problematic data (due to
 266 malfunctioning sensors or electrical storms) was flagged.

Sap flow velocity (v , cm/s) was calculated from the maximum (ΔT_0) and actual (ΔT) 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^3/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 , $\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$) 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} , $\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$) 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 (Ψ_{PD} and Ψ_{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 Ψ_{PD} were taken from the
 281 most accessible location on tree, usually a low or mid canopy, while Ψ_{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 , $\text{cm}^2\text{s}^{-1}\text{MPa}^{-1}$): $K = F/(\Psi_{MD} - \Psi_{PD})$. 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 , $\text{mmol m}^{-2} \text{s}^{-1}\text{MPa}^{-1}$)
 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 $\delta^{13}\text{C}$ values (Far-

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

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

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

311 **Water Stress**

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

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

321 **Growth and Productivity**

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

327 Productivity was directly measured in seedlings as carbon assimilation (A , μmol
 328 $\text{CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) with the LI-COR 6400 ($n = 108$, 12 plants per species per treatment,

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

333 **Statistical Analysis**

334 All statistical analyses were performed in R (R Core Development Team 2017). For
335 each physiological trait measured in mature trees, we tested the effects of and in-
336 teractions among species, elevation category, and year using Analysis of Variance
337 (ANOVA) on a fixed effects model including all three attributes and all interac-
338 tions. The same approach was used for the seedling trait data, with Species and
339 Treatment as the explanatory variables. When ANOVA results were significant (p
340 < 0.05), Tukey’s Honest Significant Differences (HSD) was used to make pairwise
341 comparisons.

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

349 **Results**

350 **Comparison of Broad and Local Distributions**

351 Comparing the climatic distributions of the oak species across their full ranges, the
352 three species differed in mean bioclimatic variables in a few critical ways that were
353 suggestive of associations with their local distributions at SERC. In particular, *Q.*
354 *falcata* had a more arid climatic distribution and was found in the sites that have
355 the lowest water availability locally. Across its range, *Q. falcata* was found in lo-
356 cations which were significantly warmer than either *Q. alba* or *Q. palustris*, which
357 were generally not different from each other. The average mean annual temperature
358 (MAT, °C) in *Q. falcata*’s range was 3.2°C warmer than the range of *Q. alba* and
359 2.8°C warmer than *Q. palustris* ($p < 0.0001$, Tukey-adjusted p-value). *Q. falcata* also
360 occurred in regions with higher rainfall than the other species, with an average MAP
361 was 79 mm higher ($p < 0.0001$, Tukey-adjusted p-value), but because the higher

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

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

376 Species, Spatial, and Temporal Performance Differences

377 Water Use

378 Figure 3 shows the sap velocity over the course of 24 hours averaged over the season
 379 (August - October in the dry year, July - September in the wet year) for each
 380 species; mean sap velocity for each species over time is shown in supplemental figure
 381 S7. The average maximum daily sap velocity (V , cm/s) was significantly different
 382 among species, elevation categories, and years; each interaction between pairs of
 383 variables was also significant (ANOVA, $p = 0.0251$ for the species by year interaction,
 384 $p < 0.0001$ for all others). Mean values of V and other key traits measured in mature
 385 trees by species, elevation category, and year are summarized in Table 3.

386 Maximum sap velocity was also slightly but significantly correlated with both
 387 VPD (Pearson's $r = 0.128$, $p < 0.0001$) and with solar radiation (Pearson's $r =$
 388 0.107 , $p < 0.0001$). The relationship between sap velocity and VPD was found in
 389 each species when considered separately and p -values were adjusted with the Holm
 390 method for multiple comparisons (*Q. alba*: $r = 0.120$, $p < 0.0001$; *Q. falcata*: $r =$
 391 0.159 , $p < 0.0001$; *Q. palustris*: $r = 0.105$, $p = 1.343 \times 10^{-4}$). The relationship
 392 between sap velocity and solar radiation persisted in both *Q. alba* and *Q. falcata*
 393 when these species were considered separately, but not in *Q. palustris* ($r = 0.0008$,
 394 $p = 0.97$).

395 Average total daily water loss (TDWL) is shown in figure 5a. TDWL was signifi-
 396 cantly lower at low elevation than at either middle or high elevation sites ($p = 0.013$
 397 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

436 ($\delta^{13}\text{C}$) and gas exchange measurements (A/g_{sw} , abbreviated as WUE_i). There were
437 significant differences among species ($p = 0.04$) and treatments ($p = 0.045$) in $\delta^{13}\text{C}$,
438 though pairwise differences were small. *Q. falcata* and *Q. palustris* were the most
439 similar in their isotope ratios ($p = 0.99$), while *Q. alba* showed slightly, though
440 non-significantly, higher WUE by this metric. WUE_i was not significantly different
441 among species but was among treatments, and was highest under dry conditions (p
442 < 0.0001 , Tukey's HSD). This pattern was also seen with $\delta^{13}\text{C}$, though the results
443 were not significant.

444 Stress

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

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

466 Stress response measured by chlorophyll fluorescence (F_v/F_m), however, sug-
467 gested that seedlings exhibited increased photoinhibition (F_v/F_m below 0.8) at high
468 water treatments (ANOVA, $p < 0.0001$). This response was seen in both *Q. falcata*
469 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

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

544 The higher conductance seen in *Q. palustris* may come at the cost of increased
545 stress during drought years. Values reported in the literature show that *Q. palustris*
546 typically has a larger vessel diameter than *Q. falcata* (Lobo et al. 2018, Robert et al.
547 2017), which suggests it may be trading high hydraulic efficiency when water is
548 available for increased vulnerability when it is not (Sperry et al. 2008). We observed
549 mature *Q. palustris* trees experiencing the largest difference between predawn and
550 midday water potential, indicative of drought stress, at the highest elevation in the
551 dry year. $\Delta\Psi$ was also higher in *Q. palustris* seedlings when water was limited, and
552 higher in *Q. falcata* without water limitation.

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

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

572 The depressed performance of seedlings under high water conditions illustrates
573 that drought was unlikely to be the only environmental factor affecting plant func-
574 tion. Lower vapor pressure deficit or light limitation in the rainy season may have
575 augmented plant response to water stress, helping to explain why we observed a
576 smaller response than expected to the drought conditions of the dry year. We found
577 sap flux to be correlated with both light levels and VPD; it is possible that decreases
578 in transpiration from lower water availability were offset by stronger driving gradi-
579 ents in the dry year, explaining why we did not see a change in total daily water
580 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

617 hydraulic conductance of mature trees offers the clearest support to the idea that
618 the two red oaks partition the gradient through contrasting water-use strategies. A
619 lack of a single phenomenon among those we tested can explain the local distribu-
620 tion of our study species is consistent with other recent work (Morueta-Holme et al.
621 2016), and future research in habitat partitioning and community assembly will be
622 strengthened by addressing multiple potential drivers of observed patterns.

623 **Funding**

624 Funding for this project was provided by the Smithsonian Institution and the Oaks
625 of the Americas Project (NSF DEB 1146380).

626 **Acknowledgments**

627 We thank the Smithsonian Environmental Research Center for logistical support,
628 William Brinley and Nathan Phillips for technical assistance in construction of the
629 sapflow sensors and Geoffrey Parker for providing access to the 50-ha plot and for
630 other support. We thank Marilyn Fogel for allowing us to use her former facilities the
631 Geophysical Lab at the Carnegie Institution in Washington, D.C. for isotopic anal-
632 yses, Lauren Urgenson, George Raspberry (posthumously), Roxane Bowden, Kati
633 Dawson, Andrea Krystan, and Patrick Neale for technical and other assistance. The
634 water table and soil moisture data were gathered as part of an NSF funded project
635 to Sean McMahon (NSF Grant 1137366) and is curated by Rutuja Chitra-Tarak.

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		Water	SWC (SE)		
Dry Year	Wet		0.186 (0.016)	Water	SWC (SE)
	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 ⁻¹)	4.29 × 10 ⁻³	5.18 × 10 ⁻³	4.51 × 10 ⁻³	4.51 × 10 ⁻³	5.09 × 10 ⁻³	4.66 × 10 ⁻³	**	4.91 × 10 ⁻³	4.55 × 10 ⁻³	
TDWL (l)	13.17	12.28	12.28	8.72	15.56	14.07		12.83	12.47	
K (cm ² s ⁻¹ MPa ⁻¹)	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 ¹³ 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; δ¹³C: 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 ²)	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 ₂ O m ⁻² s ⁻¹)	3.64	3.58	3.51		3.46	3.91	3.20	***
g_{sw} (mol H ₂ O m ⁻² s ⁻¹)	0.177	0.159	0.162	**	0.149	0.190	0.153	***
WUE _i (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 ⁻² s ⁻¹ MPa ⁻¹)	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 _v /F _m	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_v/F_m 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*.

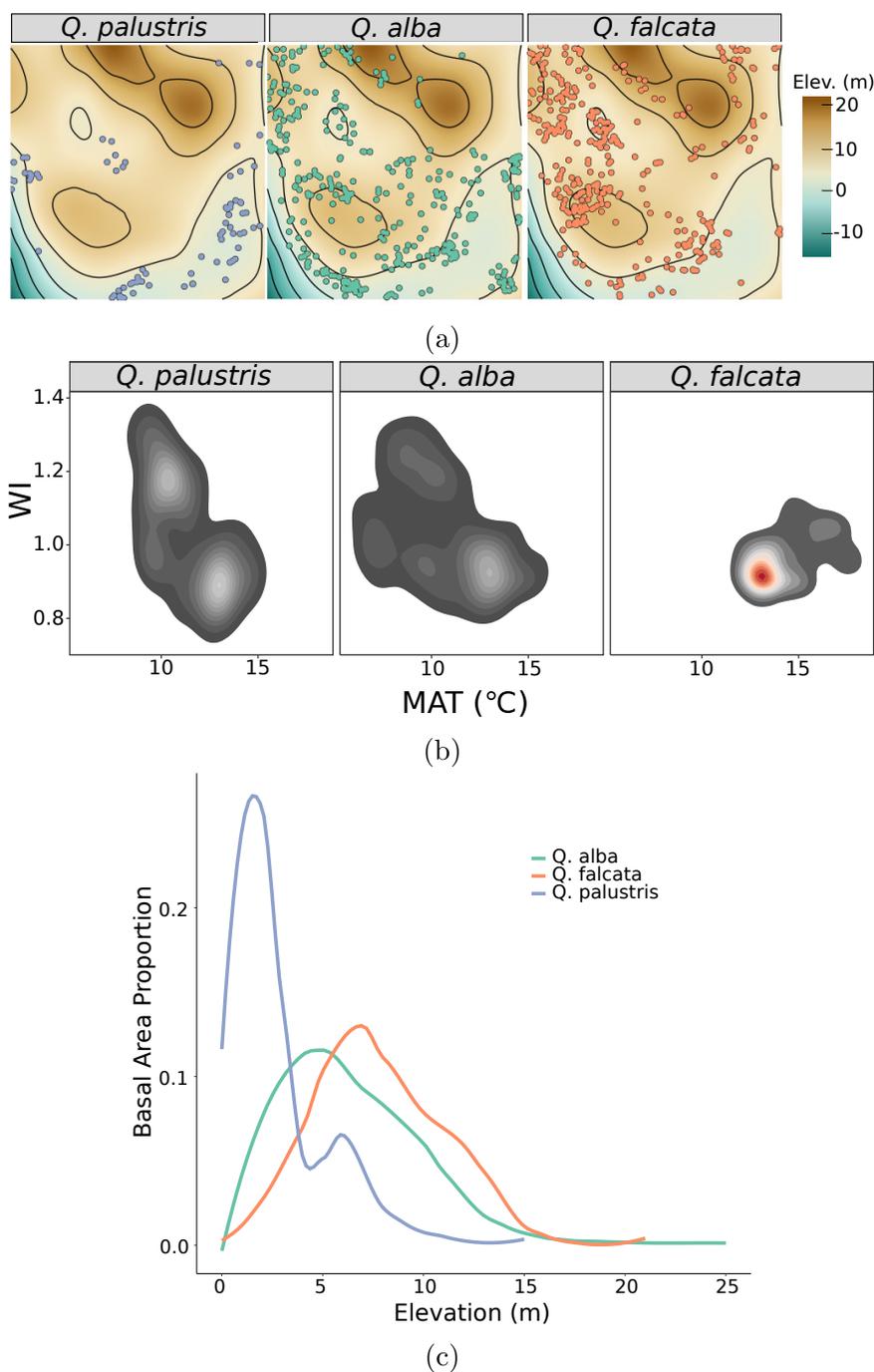


Figure 1: Broad and local distributions of *Q. alba*, *Q. falcata*, and *Q. palustris*. 1a: Distribution of the three oak species across SERC's Big Tree Plot (BTP), 700 m by 700 m. with elevation (m above sea level). 1b The climatic envelopes of the North American ranges of the three study species. Wetness 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.

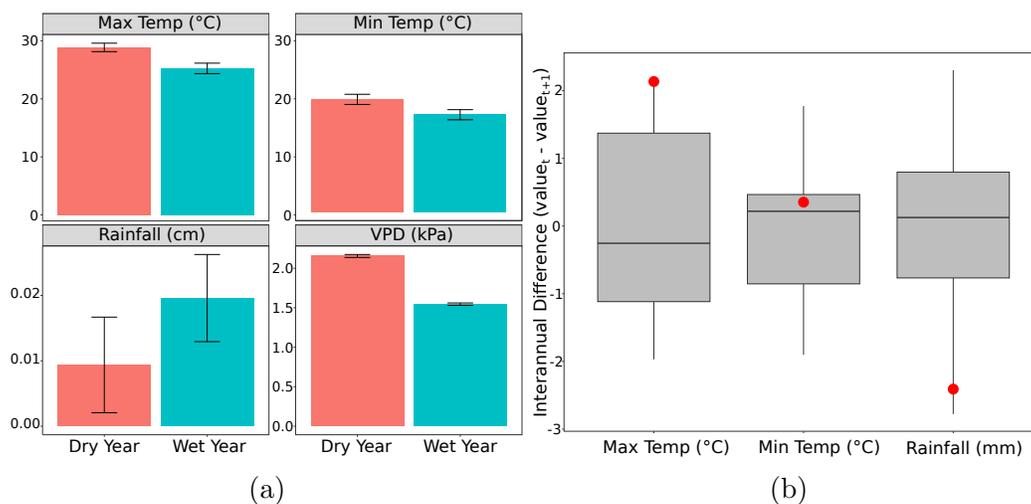


Figure 2: 2a: Mean total daily rainfall, minimum and maximum daily temperatures, and VPD for each summer during which data was collected, showing that dry summer was significantly warmer and drier than the wet summer. Error bars are $2 \times SE$. 2b: Year-to-year difference in average summer minimum 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.

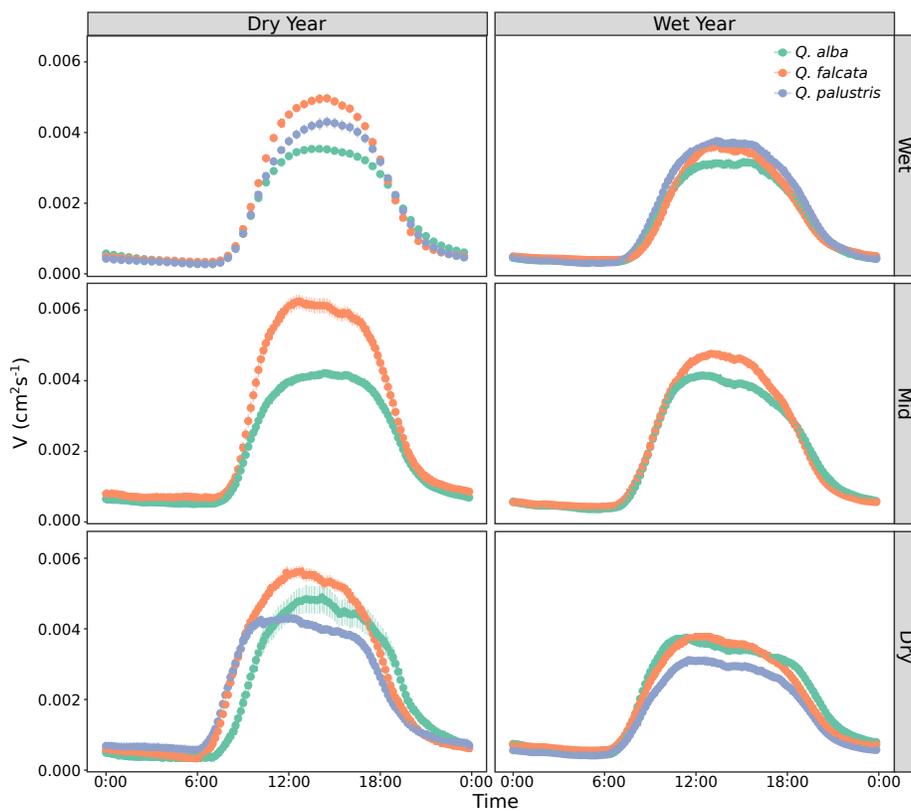


Figure 3: Average daily sap flow patterns for each species at each elevation and in the wet (July-September) and dry (August-October) year; the error bars are standard error. Daily maximum velocity is more variable in the dry year (SD in wet year = 0.00194, SD in dry year = 0.00239; $p = 0.0008$, Welch's 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).

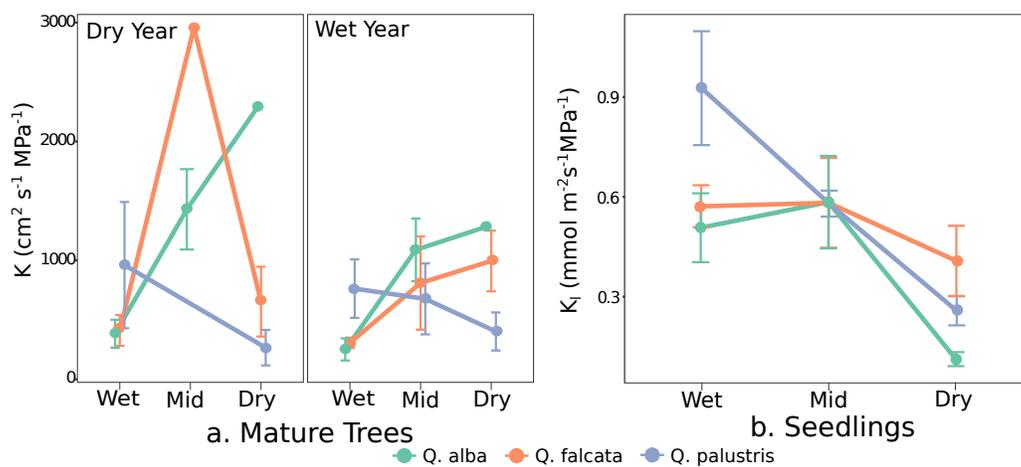


Figure 4: Differences in hydraulic conductance with water availability in mature trees (a) and seedlings (b). In mature trees, K ($\text{cm}^2\text{s}^{-1}\text{MPa}^{-1}$) differed significantly by site-based water availability (ANOVA, $p = 0.00225$); interactions between water availability and species (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.

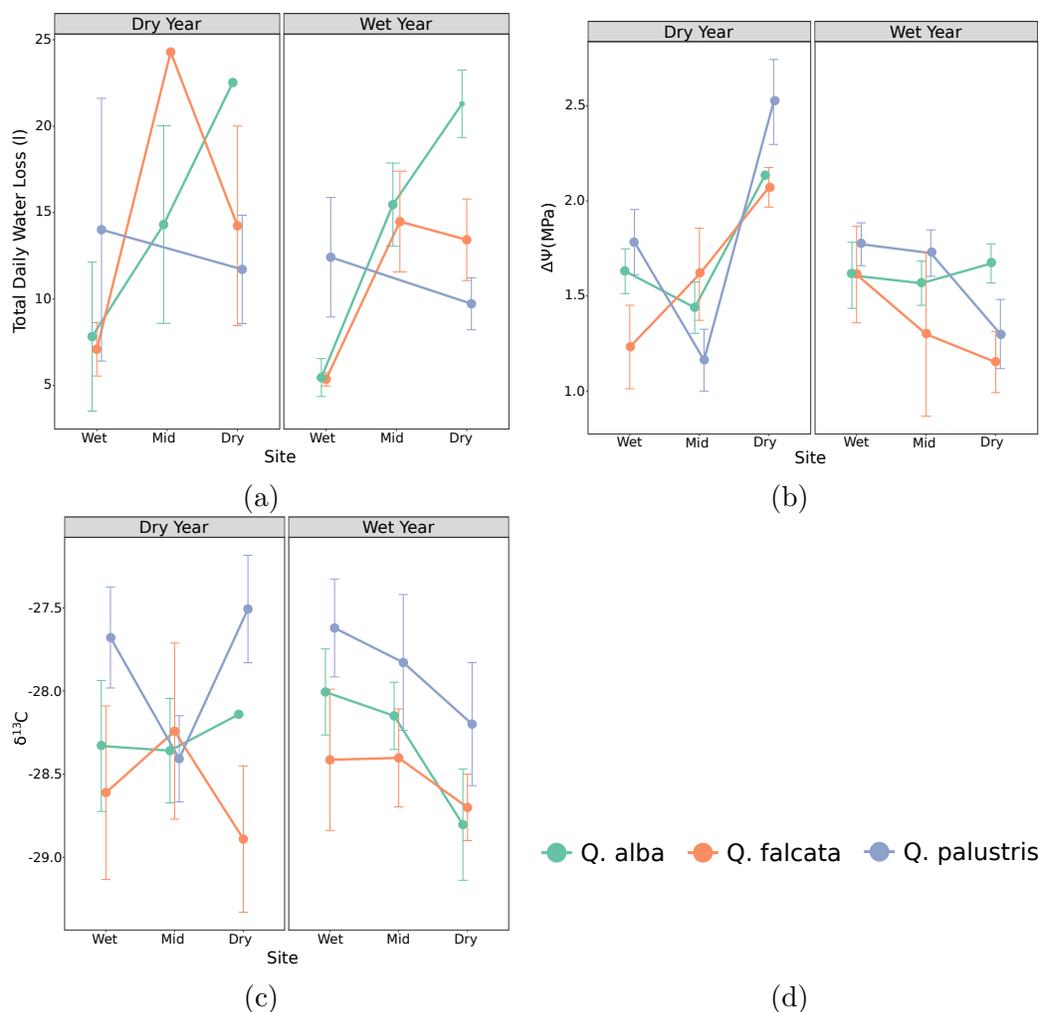


Figure 5: Differences by species, year, and elevation in four water-use traits measured in mature trees. 5a There were significant differences in total daily water loss (l) by elevation (ANOVA, $p = 0.009$), as well as a significant interaction between elevation and species (ANOVA, $p = 0.024$). 5b $\Delta\Psi$ 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.

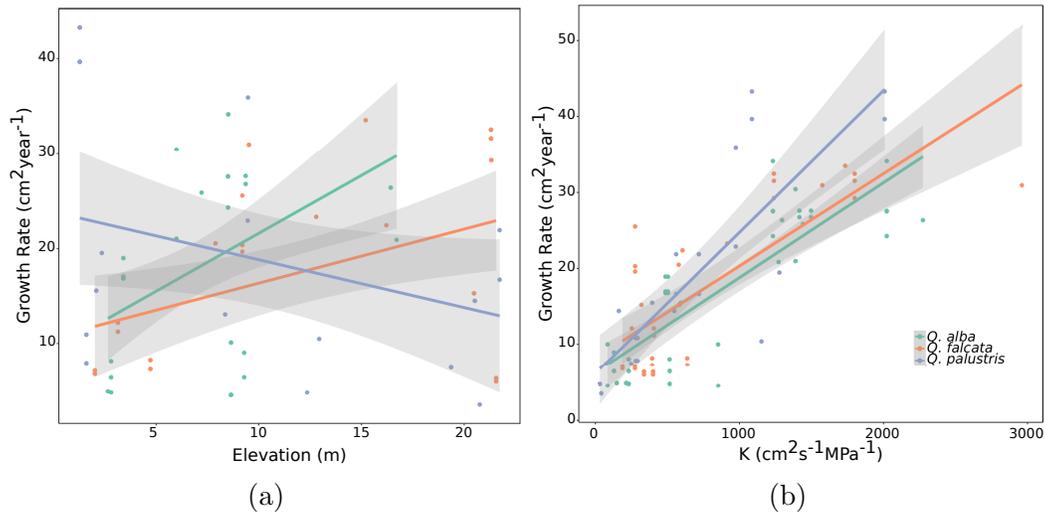


Figure 6: Growth rate (basal area increment, cm^2/year) versus 6a: elevation (m) and 6b: hydraulic conductance (K , $\text{cm}^2\text{s}^{-1}\text{MPa}^{-1}$), measured in mature trees. There is a strong, positive linear relationship between growth rate and hydraulic conductance (Multiple $R^2 = 0.67$), 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.

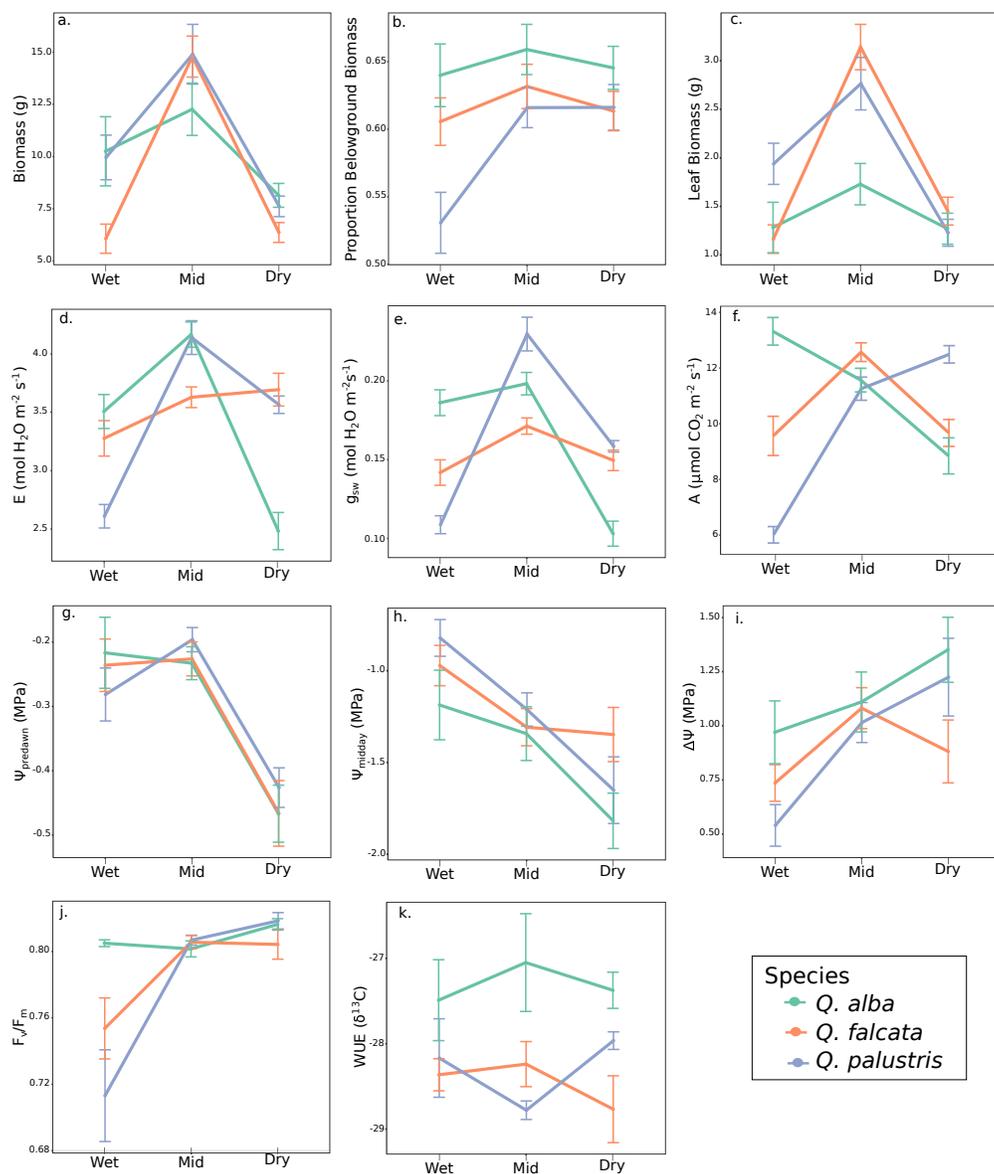


Figure 7: Seedling traits demonstrating (from top to bottom): growth (a. total biomass, b. proportion belowground biomass, and c. leaf biomass), gas exchange (c. transpiration rate, d. stomatal conductance, and e. photosynthesis), stress response and water status (g. $\Psi_{predawn}$, h. Ψ_{midday} ,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