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Research paper

Physiological strategies of co-occurring oaks in a water- and nutrient-limited ecosystem

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Oak species are well suited to water-limited conditions by either avoiding water stress through deep rooting or tolerating water stress through tight stomatal control. In co-occurring species where resources are limited, species may either partition resources in space and/or time or exhibit differing efficiencies in the use of limited resources. Therefore, this study seeks to determine whether two co-occurring oak species (*Quercus prinus* L. and *Quercus velutina* Lam.) differ in physiological parameters including photosynthesis, stomatal conductance, water-use (WUE) and nitrogen-use efficiency (NUE), as well as to characterize transpiration and average canopy stomatal responses to climatic variables in a sandy, well-drained and nutrient-limited ecosystem. The study was conducted in the New Jersey Pinelands and we measured sap flux over a 3-year period, as well as leaf gas exchange, leaf nitrogen and carbon isotope concentrations. Both oak species showed relatively steep increases in leaf-specific transpiration at low vapor pressure deficit (VPD) values before maximum transpiration rates were achieved, which were sustained over a broad range in VPD. This suggests tight stomatal control over transpiration in both species, although *Q. velutina* showed significantly higher leaf-level and canopy-level stomatal conductance than *Q. prinus*. Average daytime stomatal conductance was positively correlated with soil moisture and both oak species maintained at least 75% of their maximum canopy stomatal conductance at soil moistures in the upper soil layer (0–0.3 m) as low as 0.03 $m^3\ m^{-3}$. *Quercus velutina* had significantly higher photosynthetic rates, maximum Rubisco-limited and electron-transport-limited carboxylation rates, dark respiration rates and nitrogen concentration per unit leaf area than *Q. prinus*. However, both species exhibited similar WUEs and NUEs. Therefore, *Q. prinus* has a more conservative resource-use strategy, while *Q. velutina* may need to exploit niches that are locally higher in nutrients and water. Likewise, both species appear to tap deep, stable water sources, highlighting the importance of rooting depth in modeling transpiration and stomatal conductance in many oak ecosystems.

Keywords: nitrogen-use efficiency, photosynthesis, *Quercus*, sap flow, water-use efficiency.

Introduction

Oak species tend to display contrasting strategies of either avoiding drought through deep rooting and access to the water table (Griffin 1973, Abrams 1990, Jackson et al. 1999, Cavender-Bares and Bazzaz 2000) or tolerating drought by tight control of stomatal conductance (Damesin and Rambal 1995, Dickson and Tomlinson 1996). Under conditions of water stress, oaks have been shown to maintain higher photosynthetic rates compared with co-occurring tree species (Bahari et al. 1985, Abrams 1990, Kubiske and Abrams 1992, Turnbull et al. 2002). Oaks are a prevalent tree group in many North American forests as well as forests around the world (Dickson and Tomlinson 1996) and are particularly well adapted to many drought-prone areas including the Mediterranean (Acherar and

Rambal 1992, Sala and Tenhunen 1994, Damesin and Rambal 1995, Goulden 1996, Valladares et al. 2000) and California (Griffin 1973, Field et al. 1983, Xu and Baldocchi 2003), as well as tropical forests with a prominent dry season (Brodribb et al. 2003, Brodribb and Holbrook 2005).

In regions like the Atlantic Coastal Plain in the Northeastern USA, species composition favoring drought-adapted trees like oaks is driven primarily by the deep, sandy soils of the region which have limited water retention and nutrient-holding capacity (Webb et al. 2000). This differs from other regions including those with a more Mediterranean climate in which oaks are prevalent due to a strong seasonality in precipitation and high evaporative demand. Therefore, although water stress conditions due to the sandy, well-drained soils are prevalent in many Atlantic Coastal forests, the atmospheric conditions and seasonality in temperature are much different than forests with a Mediterranean climate and may lead to differing physiological adaptations between oaks in each location. Likewise, forested systems with limited soil surface water and nutrient retention are important to study because they give interesting insights into species adaptations to these conditions (Craine et al. 2012).

In ecosystems where both water and nutrients may limit growth, co-occurring species may exhibit partitioning of these resources either spatially or temporally (Moreno-Gutiérrez et al. 2012) or may use either water or nutrients more efficiently in order to compete effectively. For example, several studies have found that co-occurring oaks have differing rooting depths and extract water from different soil layers (Bréda et al. 1995, Goulden 1996, Donovan et al. 2000). In terms of using resources efficiently, several studies have identified a trade-off between using water and using nitrogen (N) efficiently (Field et al. 1983, Turnbull et al. 2002, Ferrio et al. 2003, Xu and Baldocchi 2003). Water-use efficiency (WUE) can be described as carbon (C) assimilation per unit water lost. Instantaneous values of WUE are obtained from gas exchange measurements, while integrated measures of WUE are obtained from the C isotopic ratio of plant tissues (Farquhar et al. 1989). Nitrogen-use efficiency (NUE; Peñuelas et al. 2000) can be determined either at the individual level based on the amount of plant growth per N in the plant (Boerner 1984, Berendse and Aerts 1987) or at the leaf level based on the C assimilated per unit leaf N (Field et al. 1983, Valladares et al. 2000). Since water in sandy soils is found mainly near the water table, but nutrients are located primarily in the organic (OM) layer, there may exist a trade-off for trees between acquiring water or N optimally (Ferrio et al. 2003). Likewise, at the leaf level, greater stomatal conductance should lead to higher NUE, but may decrease the WUE of these leaves (Field et al. 1983).

The objectives of this study were to (i) compare patterns of transpiration and stomatal conductance in response to photosynthetically active radiation, vapor pressure deficit (VPD) and shallow soil moisture content between two co-occurring oak species, chestnut oak (*Quercus prinus* L.) and black oak (*Quercus velutina* Lam.), and (ii) compare WUE and NUE between oak species to determine whether either are conserved or divergent between co-occurring oaks in a resource-limited forest. The study was conducted within the 650,000 ha New Jersey Pinelands National Reserve, which has been designated a United Nations International Biosphere Reserve. Upland forests are comprised of ~46% oak-dominated forests, 31% oak–pine mixed forests and 23% pine-dominated forests (Clark et al. 2010). The Pinelands are characterized by excessively sandy soils with little water- and nutrient-holding capacity. Because both water and nutrients can be limiting in this system, we hypothesize that *Q. prinus* and *Q. velutina* will differ in WUE and NUE by either optimizing water or N use throughout the growing season. These data give insights into the controls and drivers of transpiration in sandy, well-drained ecosystems, which will aid in more accurate modeling of water and C fluxes from these systems (Medvigy et al. 2012) and lead to a better understanding of how co-occurring species compete in resource-limited systems. Likewise, these data can be compared with data from oaks growing in differing ecosystems to better understand the physiology of this widely distributed genus.

Materials and methods

Site description

This study was conducted at the Rutgers Pinelands Research Station (USFS Silas Little Experimental Forest; 39° 51′ 57″ N, 74° 35′ 46″ W) in Burlington County, NJ, USA. This site is an oak-dominated forest located within the New Jersey Pinelands. The dominant species in this site are chestnut oak (*Q. prinus*) and black oak (*Q. velutina*) with scattered scarlet oak (*Quercus coccinea* Muenchh.), white oak (*Quercus alba* L.), post oak (*Quercus stellata* Wangenh.), pitch pine (*Pinus rigida* Mill.) and shortleaf pine (*Pinus echinata* Mill.). The understory is composed of mainly huckleberry and blueberry (*Vaccinium* and *Gaylussacia* sp.) shrubs (Skowronski et al. 2007). The site receives, on average, 1123 ± 182 mm of precipitation per year. Average summer temperatures are ~22.7 °C (29.6 °C average daytime high and 16.8 °C average nighttime low) and winter temperatures are around 1.3 °C (5.4 °C average daytime high and −5.9 °C average nighttime low; www.ameriflux.ornl.gov; Clark et al. 2012). The oak species in the area tend to leaf out around early May and leaves senesce around late October. Soils in the area are excessively sandy (95–97% sand) with low nutrient- and water-holding capacity. The water table at the site occurs at ~6–7 m depth and is generally highest in the spring then decreases as the growing season progresses (United States Geological Survey http://waterdata.usgs.gov/nwis/).

Within the larger Pinelands landscape, depth to groundwater varies from a maximum of ~18 m decreasing to a few centimeters in the vicinity of surface waters (Rhodehamel 1998).

Within the site, measurements of sap flux, leaf area, photosynthesis and stable isotopes were made on two stands of oaks that contained a similar distribution of species and were located ~600 m from one another. Overstory leaf area index (LAI) and basal areas for each stand are shown in Table 1. Samples of the organic layer (~10 mm thick) and the first 0–50 mm of mineral soil were collected from both stands in February 2012 and nutrient analysis was performed (University of Massachusetts Amherst Soil and Plant Tissue Testing Laboratory, Amherst, MA, USA; Table 2). Notably, N concentration was ~10 times higher in the OM layer than the mineral soil and phosphorus was approximately three times higher.

Throughout the study period, atmospheric and edaphic parameters were measured in Stand 1. Temperature and relative humidity were measured with a Vaisala HMP45C sensor (Campbell Scientific Inc., Logan, UT, USA) located in the mid-canopy, ~6 m aboveground. Photosynthetic photon flux density (PPFD) was measured with an LI-190SB quantum sensor (LI-COR Biosciences Inc., Lincoln, NE, USA) located 18 m aboveground on a canopy tower. Throughfall was measured with a Texas Electronics TE525M tipping bucket (Campbell Scientific Inc.), and soil moisture content in the upper 0.3 m of the soil was measured in four locations using CS616 sensors (Campbell Scientific Inc.). Each sensor was attached to a CR3000 datalogger (Campbell Scientific Inc.), which collected data every 30 s and averaged data every 30 min.

Table 1. Stand-level characteristics including overstory LAI and basal area of the dominant tree species for the two measured stands within the site.

	Stand 1	Stand 2
Overstory LAI	1.40 (0.06)	1.96 (0.08)
Basal area (m^2 ha^{-1})		
Q. prinus	10.6	2.6
Q. velutina	3.7	5.6
Q. coccinea	0.2	0
Q. alba	0.4	3.2
Q. stellata	0.2	0
Pinus sp.	0.04	8.6

Table 2. Means and standard errors ($n = 4$ for the OM layer and $n = 7$ for mineral soil) from the chemical analysis of soil samples collected from the study site in February and March 2012. The OM layer (0.02–0.03 m thick) is defined as the soil layer directly below the leaf litter and containing a mix of partially decomposed organic matter and sand. The 0–0.05-m layer is defined as the top of the mineral soil, which is comprised of mainly sand.

	OM layer	0–0.05-m mineral soil
pH	3.9 (0.08)	4.2 (0.2)
OM (%)	19.1 (2.7)	2.3 (0.3)
CEC (meq + /100 g)	38.4 (6.4)	8.2 (1.8)
N (%)	0.57 (0.09)	0.05 (0.006)
P (ppm)	9.25 (1.4)	2.7 (1.4)
K (ppm)	118 (18)	11 (1.6)
Ca (ppm)	182 (37.1)	31.1 (14.6)
Mg (ppm)	61 (9.3)	7.3 (0.9)

CEC, cation exchange capacity.

Sap flux density measurements

In 2011, sap flux densities were measured in seven *Q. prinus* and five *Q. velutina* individuals in Stand 1 ranging in size from 0.15 to 0.33 m diameter at breast height (DBH) using 20-mm-long Granier-type heat dissipation sensors. In 2012, 20-mm-long sensors were replaced with 10-mm-long sensors and four more *Q. velutina* individuals were measured in Stand 1 and four *Q. prinus* and four *Q. velutina* individuals were added in Stand 2. All individuals measured in 2012 were also measured in 2013. Individuals exhibited a wide range in leaf area to sapwood area ratios at a given DBH likely due to a severe gypsy moth defoliation that had occurred in the site in 2007. Nevertheless, *Q. prinus* and *Q. velutina* sap flow trees covered a similar range in leaf area to sapwood area ratios (Table 3).

Heat dissipation sensors consisted of a pair of hypodermic needles with a thermocouple inside each. One of the needles was constantly heated (200 mW for 20-mm-long sensors and 100 mW for 10-mm-long sensors) and the other acted as a reference. Each sensor was radially inserted into the sapwood with the heated sensor located ~0.1 m above the reference sensor. Aluminum shields were placed over the sensor pairs to protect against sunflecks. As transpiration and sap flow began, the heated sensor was cooled relative to conditions when sap was not flowing (i.e., nighttime). Therefore, a temperature difference between the heated and reference sensors is correlated with sap flow rates (Eq. 1). The sensor pairs were connected to a CR3000 datalogger and AM16/32 multiplexer (Campbell Scientific Inc.) that measured the millivolt output of the sensor pairs (proportional to the temperature difference between the heated and reference sensors) every 30 s and averaged data every 30 min. These millivolt values were converted to sap flux densities (J_S; kg m^{-2} s^{-1}) using an empirical equation developed by Granier (1987) as follows:

$$J_s = 0.119 \times \left[\frac{\Delta T_{max}}{\Delta T} - 1\right]^{1.23} \quad (1)$$

where ΔT_{max} is the temperature difference between sensors when no water is flowing and ΔT is the temperature difference when sap flow is occurring. To confirm that ΔT_{max} values were chosen when sap flow rates were truly zero, ΔT_{max} values were chosen when VPD < 0.05 kPa over a 2-h period (to avoid periods of nocturnal transpiration) and ΔT_{max} values were stable over a 2-h period (to avoid periods of nocturnal stem water

Table 3. Biometric parameters and years of measurement for the *Q. prinus* and *Q. velutina* trees in which sap flux rates were measured.

Species	Height (m)	DBH (mm)	Sapwood depth (mm)	Average sapwood area (m^2)	2012 leaf area (m^2)	Average leaf area/ sapwood area (m^2 m^{-2})	Years sensored
Q. prinus	13.2	170	20	0.0086	2.2	253	2011, 2012, 2013
	12.8	172	14	0.0073	2.4	345	2011, 2012, 2013
	11.3	188	12	0.0065	4.5	699	2011, 2012, 2013
	13.2	192	11	0.0073	7.9	1100	2011, 2012, 2013
	10.9	153	10	0.0063	3.5	540	2011, 2012, 2013
	18.1	246	25	0.0117	7.7	694	2011, 2012, 2013
	17.5	333	19	0.0140	13.7	986	2011, 2012, 2013
	13.5	180	15	0.0124	13.6	1096	2012, 2013
	12.2	137	10	0.0161	11.0	685	2012, 2013
	13.5	163	12	0.0141	25.3	1798	2012, 2013
	12.8	186	11	0.0117	15.2	1294	2012, 2013
Q. velutina	8.6	272	20	0.0146	2.0	139	2011, 2012, 2013
	13.2	198	15	0.0058	8.2	1437	2011, 2012, 2013
	9.3	180	13	0.0033	1.5	452	2011, 2012, 2013
	9.1	200	11	0.0068	1.0	147	2011, 2012, 2013
	9.5	195	12	0.0047	6.1	1307	2011, 2012, 2013
	14.9	213	20	0.0086	14.6	1691	2012, 2013
	12.8	212	15	0.0053	5.5	1053	2012, 2013
	15	185	15	0.0047	6.1	1284	2012, 2013
	14.4	290	19	0.0153	17.8	1174	2012, 2013
	13.9	188	11	0.0104	3.2	306	2012, 2013
	14.2	209	13	0.0087	8.4	964	2012, 2013
	14.4	156	9	0.0127	1.6	127	2012, 2013
	15.1	215	18	0.0082	4.7	575	2012, 2013

recharge; Oishi et al. 2008). Because Granier-style heat dissipation sensors have been shown to underestimate sap flux in ring-porous individuals like oaks (Taneda and Sperry 2008, Bush et al. 2010, Hultine et al. 2010), another correction was applied to the sap flux half-hourly data based on equations derived from the comparison of sap flux measured with tissue heat balance sensors (Čermák et al. 1973) and heat dissipation sensors located in the same individuals (Renninger and Schäfer 2012). For times when sensors were malfunctioning, half-hourly data were gap-filled for each sensor using multiple linear regressions in R version 2.5.1 (The R Foundation for Statistical Computing, http://www.R-project.org). To gap-fill periods of sensor malfunction, log-transformed sap flux data were modeled using year, month, soil moisture, log-transformed VPD and log-transformed PPFD, and the interaction between year or month and the continuous environmental variables as explanatory variables. These models had r^2 values between 0.37 and 0.68 depending on the individual.

Individual transpiration rates were calculated by multiplying half-hourly sap flux rates by the sapwood area (A_S, m^2) of the individual. Sapwood areas for all sap flow trees were calculated by coring individuals in June 2013 and determining sapwood depth via a color change between sapwood and heartwood. We then determined the number of growth rings making up the total sapwood area in 2013 and used this ring count and measurements of the previous six to 10 growth rings to estimate sapwood area for 2012 and 2011. Leaf-specific daily transpiration rates (E_L; kg m^{-2} day^{-1}) were calculated by dividing sap flow per unit sapwood area by the leaf area of each individual (methods in the Leaf area estimation section). Leaf areas were measured in the summer of 2012 and leaf area to sapwood area ratios were assumed to be constant for each individual throughout the study period (Rogers and Hinckley 1979). Therefore, estimated sapwood areas based on growth ring widths were used to estimate leaf areas in 2011 and 2013. Half-hourly data were integrated to daily values for the summer growing season (June, July, August) for each study year.

Mean canopy stomatal conductance to water vapor (canopy G_s; m s^{-1}) was also estimated from the half-hourly E_L data as follows (Köstner et al. 1992, Ewers et al. 2001):

$$\text{canopy}\, G_s = \frac{K_G \times E_L}{\text{VPD}} \quad (2)$$

where K_G is a conductance coefficient ($115.8 + 0.4236 \times$ air temp in °C; Phillips and Oren 1998). In order to convert canopy G_s in m s^{-1} to mol H_2O m^{-2} s^{-1}, canopy G_s was divided by the density of water vapor (m^3/mol, $0.0224 \times$ air temp (K) / 27.3). These equations require that boundary layer conductance is high, VPD is constant throughout the canopy and there is negligible use of stored bole water. Forests in the Pinelands are relatively open and individual tree crowns have low leaf area densities; therefore, individual leaves should be well coupled with the surrounding atmosphere. VPD calculated from a temperature and humidity sensor located in the lower canopy

differed by ~0.3 kPa compared with a sensor located above the canopy. Therefore, variation in VPD throughout the canopy is typically low. Likewise, sapwood volumes in oaks are relatively small, and therefore bole water should contribute little to daily sap flux. Lag analysis showed that r^2 values were on average 15% lower when VPD was lagged with sap flux by 30 min compared with non-lagged values; thus there is no statistically detectable use of significant amounts of stored water for transpiration.

Once half-hourly canopy G_s was calculated, average daytime values were obtained from values corresponding to half-hourly VPD > 0.5 kPa (Ewers et al. 2001). An overall average across all individuals of each species was then calculated to compare with average daily soil moisture, average daytime VPD and daily PPFD. Equations for linear relationships between average daytime canopy G_s and environmental parameters were computed using *R* with between-year variation accounted for in the model. Residuals were found to have constant variance across the range of predictor variables.

Leaf area estimation

In August 2012, individual leaf areas were estimated for the same 11 *Q. prinus* and 13 *Q. velutina* individuals that were measured for sap flux from both stands within the study site. An LAI 2000 Plant Canopy Analyzer (LI-COR Biosciences Inc.) was used and measurements were made at dawn to avoid shadows caused when the foliage is lit from directly above. Two analyzers were used: one remained in a canopy gap and measured overstory sky conditions and the other was used to take light transmittance measurements at four locations around the trunks of each oak individual. Ninety degree caps were placed on each light sensor to block the effect of the tree trunk and care was taken to hold each sensor as level as possible. Comparison of light transmittance between the two sensors provided a measure of the leaf density (m^2 leaf area per m^3 canopy volume) of each canopy calculated using FV2000 version 1.2.1 software (LI-COR Biosciences Inc.).

Canopy volumes were estimated from the canopy profiles of each individual. To begin, the width of the canopy at its widest point was measured. At the trunk, a measurement of vertical distance to the bottom of the canopy and vertical distance to the top of the canopy was made using a hypsometer (Haglof VL400, Haglof Sweden AB, Langsele, Sweden). At the horizontal mid-point of the canopy, measurements of vertical distance to the bottom and top of the canopy were performed. A final vertical distance to the mid-canopy was measured at the widest part of the canopy. This was done in two planes for each individual, and an average canopy profile was obtained by graphing both planes and manually fitting a line between both profiles.

Gas exchange measurements

In July 2012, light response and net assimilation to internal CO_2 concentration (A/C_i) response curves were measured using an LI-COR 6400 photosynthesis system (LI-COR Biosciences Inc.) with a red/blue light source attached for six *Q. prinus* and nine *Q. velutina* individuals from both stands within the study site. Measurements were made in the late morning to early afternoon after the dew had evaporated from leaves but before stomata began closing due to mid day water deficits. We did not have access to the canopies directly, so small branches were cut from trees with a pole pruner and immediately transferred to a bucket of water and the branch recut under water to remove embolisms. Measurements were made in sunny canopy gaps and relatively quickly before leaves on cut branches closed their stomata. Stomatal conductances were monitored to ensure that measured photosynthetic rates were not limited by stomatal closure.

Light response curves were produced by holding CO_2 concentrations in the leaf chamber constant at 400 ppm and varying light levels from 1500 to 0 μmol photons m^{-2} s^{-1}. Curves were graphed in Sigmaplot (SPSS Inc., Chicago, IL, USA) and exponential curves fitted to estimate maximum assimilation at saturating light levels (A_{max}), light compensation points (*x*-intercept) and dark respiration rates (*y*-intercept). Linear regressions were also fitted to data corresponding to light levels between 0 and 200 μmol m^{-2} s^{-1} and the slope of this line was used to estimate quantum yield. To produce A/C_i curves, light levels were held constant at 1500 μmol m^{-2} s^{-1} and CO_2 concentrations in the leaf chamber began at 400 ppm, were progressively dropped to 50 ppm, then returned to 400 ppm and raised by 200 ppm increments until photosynthetic rates saturated. Data from A/C_i curves were used to calculate maximum Rubisco-limited carboxylation rates (V_{cmax}), maximum electron-transport-limited carboxylation rates (J_{max}) and carboxylation rates limited by triose phosphate utilization (TPU). Non-linear regression was used based on theory and equations from Farquhar et al. (1980), Sharkey (1985) and Harley and Sharkey (1991) whereby best-fit models that minimized the sums of squares difference between measured values and modeled data for the Rubisco-limited portion of the curve (to estimate V_{cmax}), the electron-transport-limited portion of the curve (to estimate J_{max}) and the TPU-limited portion of the curve (to estimate TPU) were calculated. V_{cmax}, J_{max} and TPU values were then scaled to a common reference leaf temperature of 25 °C by fitting a temperature response curve for each parameter and scaling estimated values using these curves.

Data from A/C_i curves were also used to estimate the Ball–Berry parameter (Leuning 1990, Collatz et al. 1991), which is the slope (*m*) of the following equation:

$$g_s = m \times \frac{A \times rh_s}{C_S - \Gamma} + g_o \quad (3)$$

where g_s (mol H_2O m^{-2} s^{-1}) is leaf-level stomatal conductance to water vapor, *A* is net photosynthetic assimilation (μmol CO_2

m^{-2} s^{-1}), rh_s is relative humidity at the leaf surface, C_s is CO_2 concentration at the leaf surface (μmol mol^{-1}), Γ is the CO_2 compensation point (μmol mol^{-1}) of the corresponding A/C_i curve and g_o is minimum conductance (mol H_2O m^{-2} s^{-1}).

Leaf-level stomatal conductances were estimated from data used to create the light response and A/C_i curves during conditions when light levels were saturating (1500 μmol m^{-2} s^{-1}) and CO_2 levels in the leaf chamber were approximately ambient (400 ppm). Likewise, WUEs (μmol CO_2 $mmol^{-1}$ H_2O), calculated as assimilation divided by transpiration, and intrinsic WUEs (iWUEs; μmol CO_2 mol^{-1} H_2O), calculated as assimilation divided by stomatal conductance, were estimated under conditions of saturating light and ambient CO_2. To determine whether any of the photosynthetic parameters, stomatal conductances or calculated WUEs differed significantly between *Q. prinus* and *Q. velutina*, analysis of variance (ANOVA) was performed in R with between-stand variation accounted for in each model.

Leaf nutrient and isotopic composition

To estimate leaf C and N concentrations and stable isotope ratios, one or two leaf samples (corresponding to leaves used to create light response and A/C_i curves) were collected from six *Q. prinus* and nine *Q. velutina* individuals from both stands within the study site. Leaf samples were dried, finely ground using a ball mill and sealed in aluminum capsules for determination of C isotopic ratios ($\delta^{13}C$, ‰) and C and N concentrations (University of California, Davis Stable Isotope facility, Davis, CA, USA). In order to scale N concentrations per unit leaf area (N_{area}), N concentrations were multiplied by the leaf mass per area (LMA) obtained for leaves taken from each individual. Additional leaves for LMA analysis were also collected for *Q. prinus* and *Q. velutina* individuals monitored for sap flow. In September 2012, two leaves from the lower canopy of seven *Q. prinus* and 12 *Q. velutina* were cut, scanned with a scaling factor using a flatbed scanner (Hewlett Packard ScanJet 5200C, Palo Alto, CA, USA) and their areas determined using Image J software (Scion Image, Frederick, MD, USA). Then, leaves were dried at 70 °C for 3 days and their dry weights were measured. Nitrogen-use efficiency (μmol CO_2 g^{-1} N s^{-1}) was calculated by dividing net photosynthetic assimilation rates at ambient CO_2 and saturating light conditions by the N concentration (expressed on a unit area basis) for each measured leaf. To determine whether LMA, N_{area} and NUE differed significantly between *Q. prinus* and *Q. velutina*, ANOVAs were performed in R with between-stand variation accounted for in the models.

Carbon isotope discrimination (Δ; ‰) was calculated from the C stable isotope data using the following equation (Farquhar et al. 1989):

$$\Delta = \left(\frac{\delta^{13}a - \delta^{13}C}{1000 + \delta^{13}C}\right) \times 1000 \quad (4)$$

where $\delta^{13}a$ is the isotopic concentration of the source air (measured in January 2010 at the study site as –12.9‰). Intrinsic WUE ($iWUE_{isotope}$) was also estimated from the isotope data as follows (Farquhar et al. 1989):

$$iWUE_{isotope} = \frac{C_a}{1.6} \times \left(\frac{27 - \Delta}{27 - 4.4}\right) \quad (5)$$

where C_a is the ambient CO_2 concentration (400 ppm), 1.6 is the ratio of water vapor to CO_2 diffusivity, 27 is the discrimination of Rubisco to C^{13} and 4.4 is the diffusive discrimination of C^{13} in air through the stomata. To determine whether leaf nutrient or isotopic parameters differed significantly between *Q. prinus* and *Q. velutina* leaves, ANOVAs were performed in R with the variation associated with stand location accounted for in the models.

Results

Transpiration and canopy stomatal conductance

Air temperature, VPD and PPFD were consistent over the three measured growing seasons, and soil moisture in the top 0.3 m varied between 0.03 and 0.12 m m^{-3} (Figure 1). Whole-tree leaf areas and leaf area to sapwood area ratios of study trees did not differ significantly ($P = 0.16$ and 0.78, respectively) between *Q. velutina* and *Q. prinus* after accounting for DBH; thus any observed patterns in E_L also translate to canopy transpiration. Over the 3-year study period, daily E_L increased at low average daytime VPD, then remained relatively constant over a wide range of values from 0.75 to 3 kPa (Figure 2). When combined over a 3-year period, both *Q. prinus* and *Q. velutina* maintained similarly shaped curves for the relationship between average daytime VPD and daily E_L (*Q. prinus*: $y = 1.56(1 - e^{-2.79x})$, $r^2 = 0.37$; *Q. velutina*: $y = 2.34(1 - e^{-2.14x})$, $r^2 = 0.39$), with *Q. velutina* having ~50% higher daily E_L than *Q. prinus*. Over a range of soil moistures, daily E_L remained relatively constant (in 2011), increased with increasing soil moisture (*Q. velutina* in 2012) or, in the case of *Q. prinus* in 2012 and 2013, decreased slightly at higher soil moistures (Figure 3). When combined over a 3-year period, *Q. velutina* showed no relationship between shallow soil moisture content and daily E_L (linear regression slope $P = 0.68$), whereas *Q. prinus* showed a slightly negative relationship between shallow soil moisture and daily E_L ($y = -4.15x + 1.69$, $r^2 = 0.08$, slope $P < 0.01$). For both species, daily E_L increased non-linearly with increasing daily overstory PPFD (*Q. prinus*: $y = 1.61(1 - e^{-0.058x})$, $r^2 = 0.30$; *Q. velutina*: $y = 2.43(1 - e^{-0.048x})$, $r^2 = 0.33$; Figure 4).

The daytime canopy G_s was ~38% higher in *Q. velutina* compared with *Q. prinus*. Canopy G_s for both species tended to decrease non-linearly with increasing average daytime VPD, increase with increasing shallow layer soil moisture content

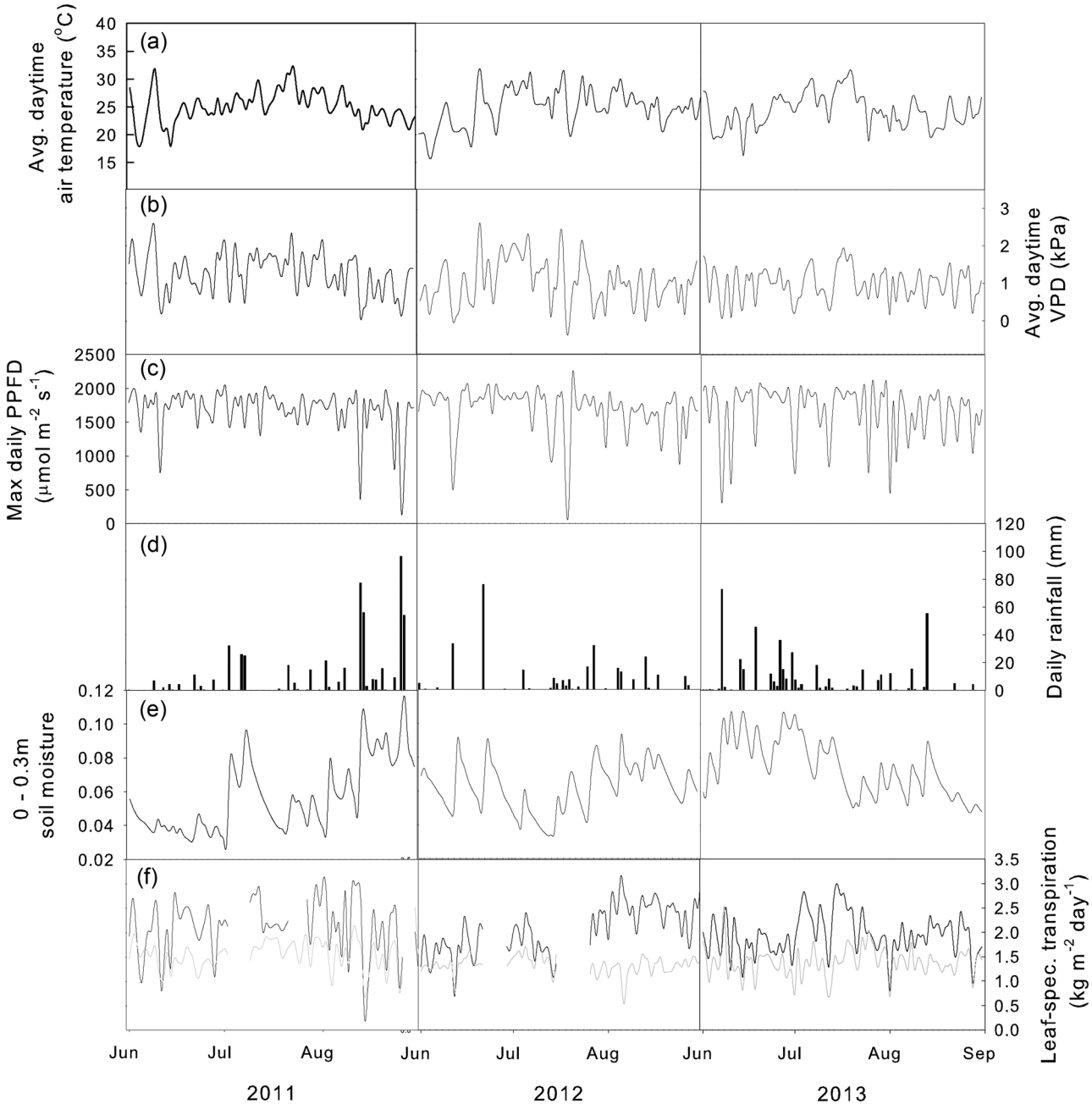

Figure 1. Environmental variables including (a) average daytime air temperature (°C), (b) average daytime VPD (kPa), (c) maximum daytime PPFD (µmol m^{-2} s^{-1}), (d) daily rainfall (mm), (e) soil moisture content (m m^{-3}) measured in the upper 0–0.3 m of the soil and (f) E_L (kg m^{-2} $_{leaf\ area}$ day^{-1}) for *Q. velutina* (black line) and *Q. prinus* (gray line) measured during the study period (2011–2013).

and decrease with increasing daily overstory PPFD over all measurement years (Figure 5). When all three parameters were included in a model, both species had statistically different relationships between canopy G_s and average daytime VPD ($P = 0.04$), soil moisture ($P < 0.001$) and daily PPFD ($P = 0.05$). Models for daily canopy G_s for each species were as follows:

$$\text{canopy}\,G_s = 0.18 - 0.19\log(\text{VPD}) - 0.26 \times \text{soil moisture} - 5.9 \times 10^{-5} \times \text{PPFD for } Q.\ prinus \quad (7)$$

$$\text{canopy}\,G_s = 0.18 - 0.12\log(\text{VPD}) + 0.53 \times \text{soil moisture} - 1.2 \times 10^{-3} \times \text{PPFD for } Q.\ velutina \quad (8)$$

and the full model had an adjusted r^2 value of 0.59. Based on these models, daytime canopy G_s remained relatively stable in both species across a wide range of shallow soil moisture contents. Canopy G_s increased by ~17% in *Q. prinus* and decreased by ~27% in *Q. velutina* when soil moistures in the upper 0–0.3 m decreased from 0.12 to 0.03 m m^{-3} (at average VPD = 1.5 kPa and average PPFD = 40 mol m^{-2} day^{-1}). On the other hand,

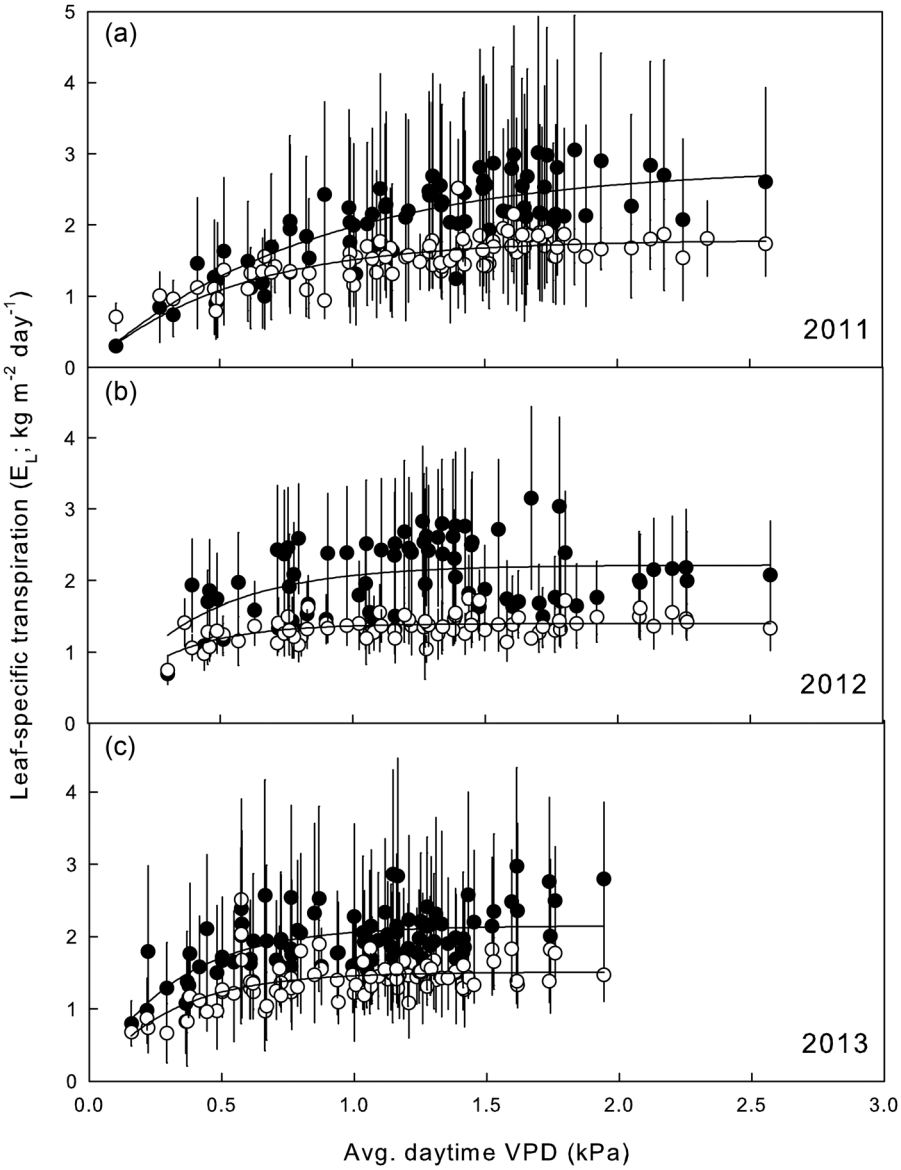

Figure 2. Leaf-specific daily transpiration (kg m^{-2} $_{\text{leaf area}}$ day^{-1}) vs average daytime VPD (kPa) during (a) 2011 for *Q. velutina* (closed circles; $y = 2.82\ (1 - e^{-1.20x})$; $r^2 = 0.67$) and *Q. prinus* (open circles; $y = 1.79\ (1 - e^{-1.86x})$; $r^2 = 0.56$), (b) 2012 for *Q. velutina* ($y = 2.22\ (1 - e^{-2.71x})$; $r^2 = 0.20$) and *Q. prinus* ($y = 1.40\ (1 - e^{-3.75x})$; $r^2 = 0.29$) and (c) 2013 for *Q. velutina* ($y = 2.15\ (1 - e^{-3.18x})$; $r^2 = 0.34$) and *Q. prinus* ($y = 1.51\ (1 - e^{-3.39x})$; $r^2 = 0.36$).

canopy G_s in both species responded significantly to increases in VPD, with *Q. velutina* showing a reduction of ~44% of canopy G_s when VPD increased from 0.5 to 3 kPa (at average soil moisture = 0.08 and average PPFD = 40 mol m^{-2} day^{-1}) and *Q. prinus* showing a reduction of ~69% over the same range. Canopy G_s in *Q. prinus* responded only slightly to increases in daily PPFD decreasing by ~2% when PPFD increased from 20 to 60 mol m^{-2} day^{-1} (at average VPD = 1.5 kPa and average soil moisture = 0.08), whereas canopy G_s in *Q. velutina* decreased by ~26% over the same range.

Gas exchange, leaf isotopes and leaf N

Based on the light response and A/C_i curves, leaves of *Q. velutina* had higher photosynthetic rates than leaves of *Q. prinus* (Figure 6). *Quercus velutina* had ~16% higher A_{max} and quantum yield was ~29% higher in *Q. velutina* than in *Q. prinus* (Table 4). Light compensation points did not differ significantly between the two oak species with an average (and standard error) of 28.7 ± 4.4 µmol m^{-2} s^{-1}, but dark respiration rates were about twice as large in *Q. velutina* as in *Q. prinus* (Table 4). The V_{cmax} was ~90% higher in *Q. velutina* than in *Q. prinus* and J_{max} in *Q. velutina* was more than three times higher than in *Q. prinus* (Table 4). Likewise, TPU-limited carboxylation rates in *Q. velutina* were more than twice that of *Q. prinus* (Table 4).

Leaf-level stomatal conductance estimates at ambient CO_2 and saturating light levels were significantly larger, by ~47%, in *Q. velutina* compared with *Q. prinus* (Table 5). The Ball–Berry

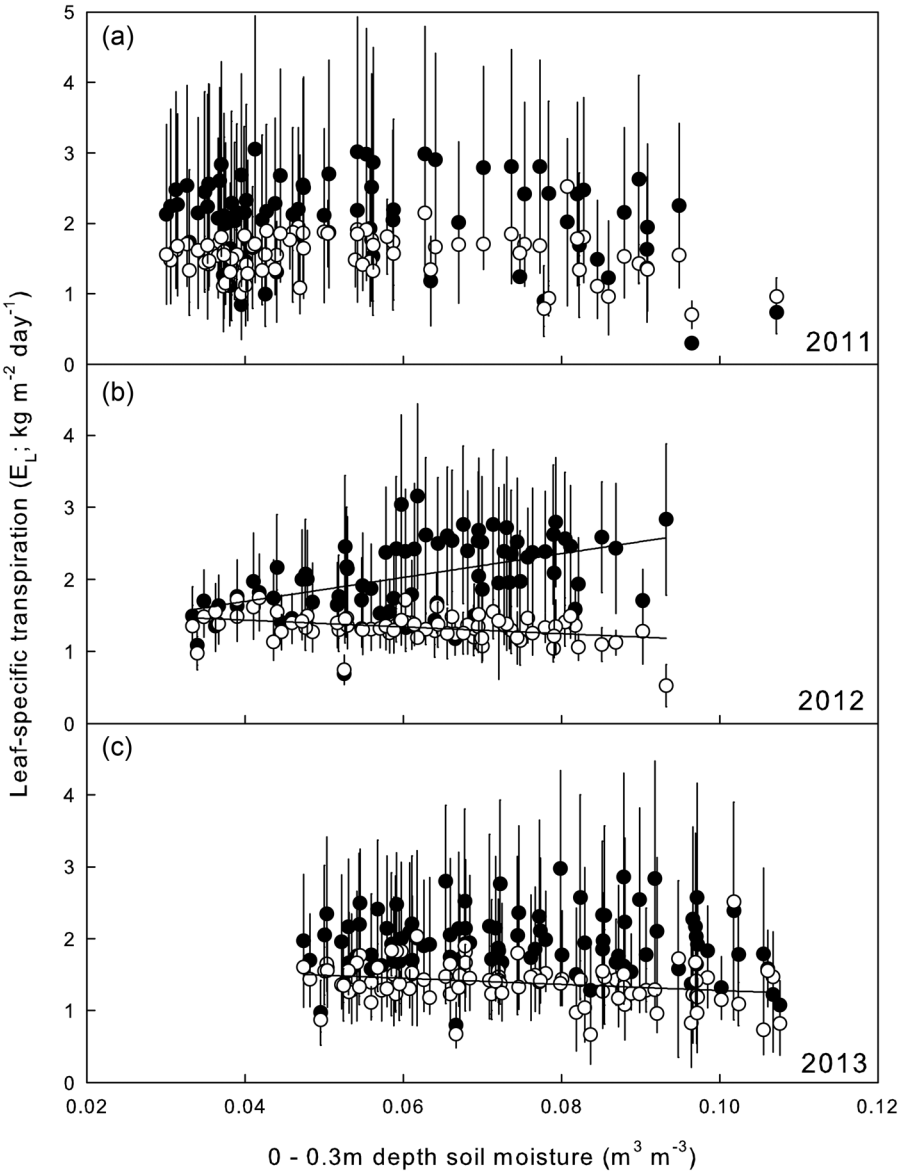

Figure 3. Leaf-specific daily transpiration (kg m^{-2} $_{leaf\ area}$ day^{-1}) vs daily average soil moisture content (m m^{-3}) measured in the top 0.3 m of soil during (a) 2011 for *Q. velutina* (closed circles) and *Q. prinus* (open circles), (b) 2012 for *Q. velutina* ($y = 16.6x + 1.0$; $r^2 = 0.23$) and *Q. prinus* ($y = -4.7x + 1.6$; $r^2 = 0.13$) and (c) 2013 for *Q. velutina* and *Q. prinus* ($y = -4.2x + 1.7$; $r^2 = 0.06$). Only equations with statistically significant slopes are reported.

parameter was similar between both species and averaged ~8. Water-use efficiencies (A/E) were not significantly different between the two oak species and averaged 2.2 ± 0.13 μmol CO_2 $mmol^{-1}$ H_2O. Likewise, iWUEs (A/g_s) did not differ significantly between the two oak species both when measured instantaneously via gas exchange (60.5 ± 3.2 μmol CO_2 mol^{-1} H_2O) and when estimated from C isotope ratios (107 ± 1.8 μmol CO_2 mol^{-1} H_2O; Table 5). Leaf-level N and C concentrations did not differ significantly between the two oak species and were 2.1 ± 0.08 and 46.8 ± 1.6%, respectively (Table 5). Likewise, LMA did not differ significantly between the two oak species and averaged 94.4 ± 1.8 g m^{-2}. However, when N in leaves was expressed on a per unit leaf area basis, values in *Q. velutina* were significantly higher than in *Q. prinus* by ~27% (Table 5). Calculated NUEs did not differ significantly between *Q. prinus* and *Q. velutina* and averaged 7.1 ± 0.33 μmol CO_2 g^{-1} N s^{-1} (Table 5).

Discussion

In a comparison of two co-occurring oak species growing on sandy soils of the Atlantic Coastal Plain, *Q. velutina* was found to have higher stomatal conductances when measured at both the leaf and the canopy level, higher photosynthetic rates and higher N per unit leaf area than *Q. prinus*. However, both species were statistically similar in terms of WUE and NUE.

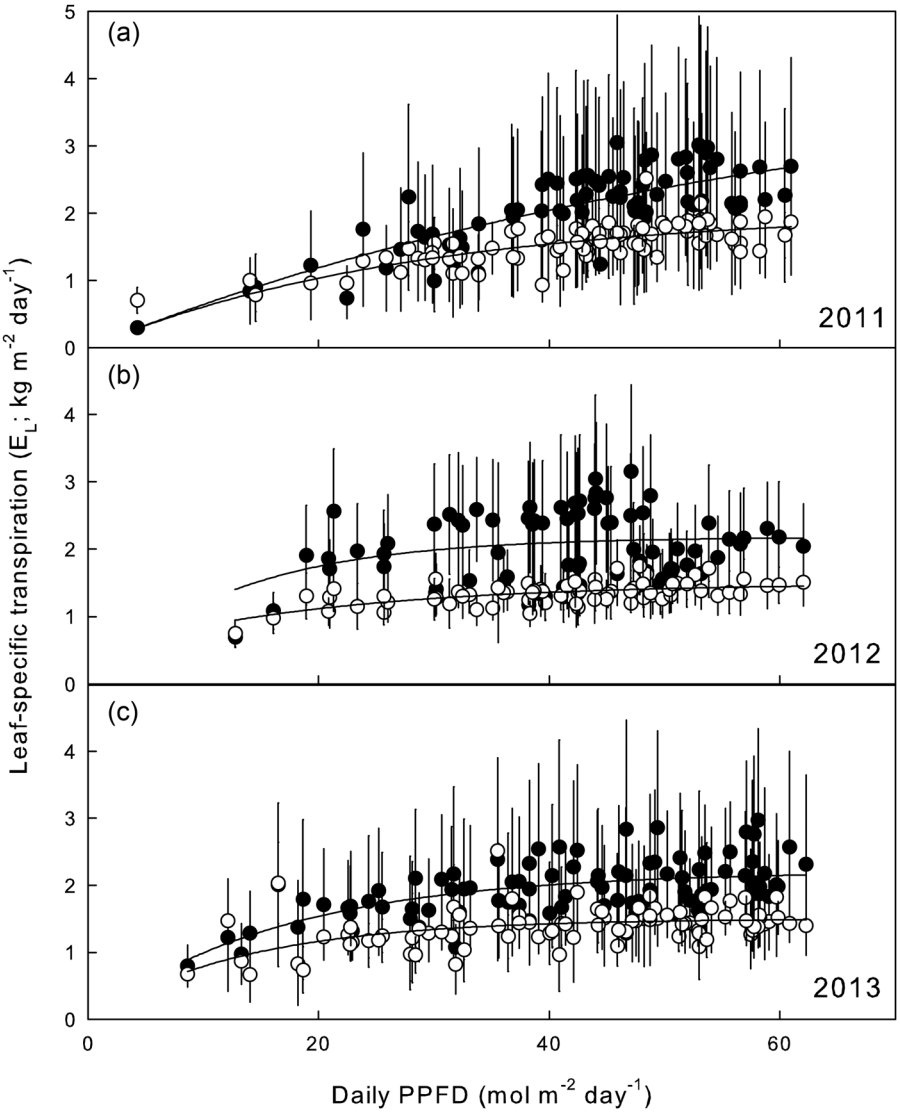

Figure 4. Leaf-specific daily transpiration (kg m^{-2} $_{\text{leaf area}}$ day^{-1}) vs integrated daily PPFD (mol m^{-2} day^{-1}) during (a) 2011 for *Q. velutina* (closed circles; $y = 4.24\ (1 - e^{-0.017x})$; $r^2 = 0.63$) and *Q. prinus* (open circles; $y = 2.03\ (1 - e^{-0.036x})$; $r^2 = 0.53$), (b) 2012 for *Q. velutina* ($y = 2.18\ (1 - e^{-0.081x})$; $r^2 = 0.11$) and *Q. prinus* ($y = 1.44\ (1 - e^{-0.074x})$; $r^2 = 0.35$) and (c) 2013 for *Q. velutina* ($y = 2.21\ (1 - e^{-0.060x})$; $r^2 = 0.36$) and *Q. prinus* ($y = 1.50\ (1 - e^{-0.075x})$; $r^2 = 0.21$).

Based on these data, *Q. velutina* should be outcompeting *Q. prinus* in this ecosystem given its higher photosynthetic rates and similar resource-use efficiencies, although other factors may also affect species competition in this ecosystem. *Quercus velutina* also requires more water and more N per unit leaf area to achieve its higher photosynthetic rates, and therefore may specialize in niches that have locally higher quantities of water and N. *Quercus velutina* also exhibits a larger decrease in canopy stomatal conductance than *Q. prinus* as upper layer soil moisture decreases. Likewise, *Q. velutina* pays a cost for its higher photosynthetic rates with leaf respiration rates that are approximately twice as high as *Q. prinus*. It is interesting to note that *Q. velutina* was much more hard-hit by a recent gypsy moth defoliation occurring in 2007 and 2008 in this forest, with ~50% mortality of *Q. velutina* individuals compared with 17% mortality in *Q. prinus* (Schäfer 2011). This could be because *Q. prinus* has more chemical defenses against herbivory (Kleiner et al. 1989) than *Q. velutina*, although both species were completely defoliated at the height of the gypsy moth defoliation. Differences in survival between the two species after defoliation may also be attributed to changes in N cycling that occurred after the gypsy moth disturbance. Gypsy moths completely defoliated trees in June 2007 removing all leaf N before it could be reabsorbed, which likely affected *Q. velutina* more than *Q. prinus* since leaves have more N per unit leaf area.

Quercus velutina had, on average, ~50% higher canopy E_L, 47% higher g_S and 38% higher daytime canopy G_s compared

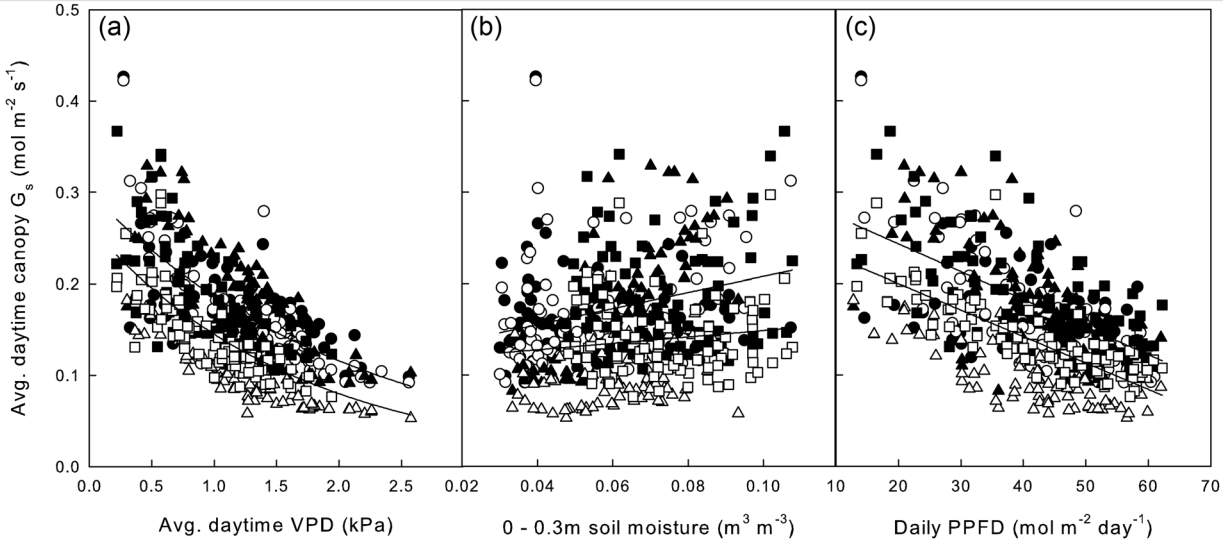

Figure 5. Daytime canopy G_s (mol m^{-2} $_{\text{leaf area}}$ s^{-1}) vs (a) average daytime VPD (kPa) for *Q. velutina* (closed symbols; $y = 0.30 \times e^{-0.48x}$; $r^2 = 0.47$) and *Q. prinus* (open symbols; $y = 0.26 \times e^{-0.60x}$; $r^2 = 0.47$), (b) daily average soil moisture content (m m^{-3}) measured in the top 0.3 m of soil for *Q. velutina* ($y = 0.88x + 0.12$; $r^2 = 0.08$) and *Q. prinus* ($y = 0.35x + 0.11$; $r^2 = 0.01$) and (c) integrated daily PPFD (mol m^{-2} day^{-1}) for *Q. velutina* ($y = -0.003x + 0.30$; $r^2 = 0.37$) and *Q. prinus* ($y = -0.003x + 0.26$; $r^2 = 0.37$) during 2011 (circles), 2012 (triangles) and 2013 (squares).

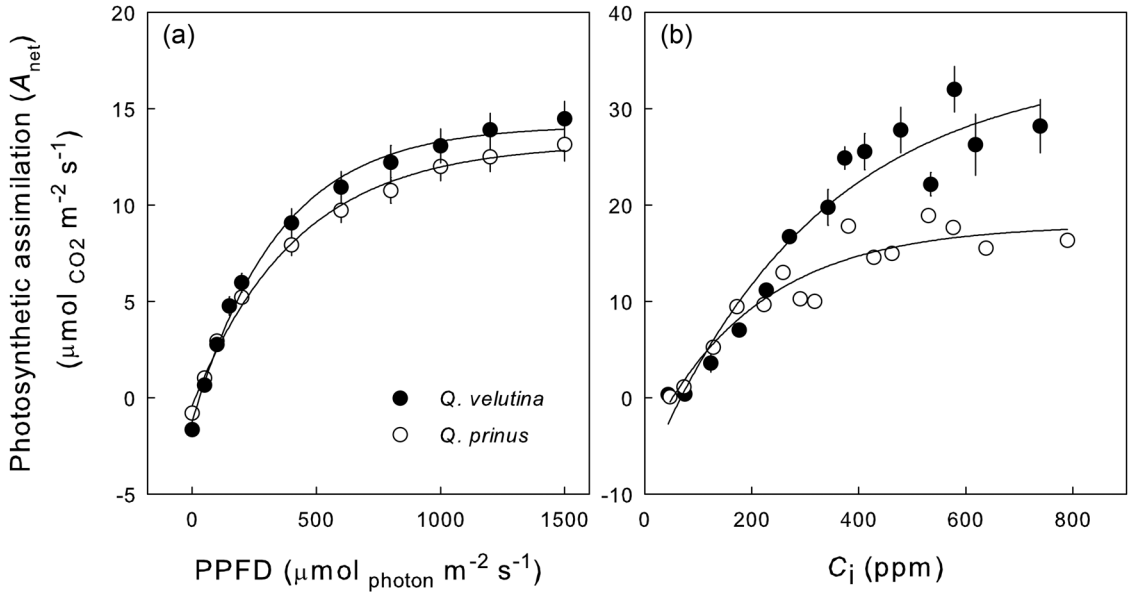

Figure 6. (a) Light response curves for *Q. velutina* (closed circles; $y = -1.27 + 15.41(1 - e - ^{0.0029x})$; $r^2 = 0.995$) and *Q. prinus* (open circles; $y = -0.42 + 13.62\ (1 - e^{-0.0024x})$; $r^2 = 0.996$) and (b) A/C_i curves for *Q. velutina* ($y = -8.14 + 42.80\ (1 - e^{-0.0031x})$; $r^2 = 0.93$) and *Q. prinus* ($y = -5.26 + 23.21\ (1 - e^{-0.0049x})$; $r^2 = 0.91$).

with *Q. prinus*. However, canopy G_s decreased to a larger degree with decreasing soil moisture and increasing PPFD in *Q. velutina* than in *Q. prinus* but canopy G_s in *Q. prinus* decreased more substantially with increasing VPD than *Q. velutina*. Canopy G_s in *Q. prinus* may be more responsive to atmospheric VPD due to its lower abundance of trichomes compared with *Q. velutina* (Hardin 1979). Interestingly, leaf-specific transpiration in both species remained relatively constant over a broad range of average daytime VPD values ranging from 0.75 to 3 kPa, suggesting that daily water use is held fairly constant regardless of evaporative demand through tight stomatal control. This stomatal closure is illustrated by the curvature parameter (b) in the exponential fits ($y = a(1 - e^{-bx})$) for the relationship between canopy E_L vs average daytime VPD, which is ~2.79 for *Q. prinus* and 2.14 for *Q. velutina*. These curvature parameters are higher than those of reported trees growing in more mesic environments (Phillips et al. 1999, Pataki et al. 2000, Wilson et al. 2001, Wullschleger and Norby 2001, Moore et al. 2004) but

Table 4. Means and standard errors of photosynthetic parameters and gas exchange derived from light response and A/C_i curves (Figure 6) for *Q. prinus* ($n = 6$) and *Q. velutina* ($n = 9$).

	Q. prinus	*Q. velutina*	*P*-value
A_{max} (μmol m^{-2} s^{-1})	13.9 (0.9)	16.1 (0.8)	**0.02**
Light compensation points (μmol$_{photon}$ m^{-2} s^{-1})	20.9 (5.7)	34.3 (5.9)	0.08
Quantum yield (μmol CO_2 μmol^{-1}_{photon})	0.034 (0.003)	0.044 (0.002)	**0.02**
Dark respiration rate (μmol CO_2 m^{-2} s^{-1})	0.78 (0.3)	1.6 (0.2)	**0.01**
V_{cmax} (μmol m^{-2} s^{-1})	22.6 (2.4)	43.8 (7.6)	**0.02**
J_{max} (μmol m^{-2} s^{-1})	47.5 (4.5)	161.9 (47)	**0.04**
TPU (μmol m^{-2} s^{-1})	3.8 (0.26)	9.0 (1.8)	**0.01**
Ball–Berry parameter (m; unitless)	8.72 (1.1)	7.11 (1.3)	0.37

P-values for differences between the *Quercus* species are based on ANOVAs for each parameter with species and stand as explanatory variables. Bold denotes significant differences at $\alpha = 0.05$.

Table 5. Means and standard errors of gas exchange, C isotopes and leaf nutrient compositions for *Q. prinus* and *Q. velutina*.

	Q. prinus	*Q. velutina*	*P*-value
g_s (mol H_2O m^{-2} s^{-1})	0.19 (0.02)	0.28 (0.03)	**0.04**
C_i/C_a (instantaneous)	0.66 (0.04)	0.68 (0.02)	0.48
WUE (A/E; μmol CO_2 $mmol^{-1}$ H_2O)	2.3 (0.3)	2.2 (0.1)	0.69
iWUE (A/g_s; μmol CO_2 mol^{-1} H_2O)	60 (4.0)	62 (5.6)	0.39
$\delta^{13}C$ (‰)	–29.6 (0.3)	–29.4 (0.1)	0.30
Δ (‰)	17.2 (0.3)	16.9 (0.1)	0.30
C_i/C_a (isotope)	0.57 (0.01)	0.56 (0.01)	0.30
$iWUE_i$ (isotope; μmol CO_2 mol^{-1} H_2O)	105.4 (3.2)	108.4 (1.6)	0.30
N concentration (%)	2.1 (0.1)	2.2 (0.1)	0.46
C concentration (%)	46.4 (2.2)	47.2 (2.4)	0.82
C/N	22.6 (0.5)	21.8 (0.5)	0.22
LMA (g m^{-2})	90.8 (3.0)	96.7 (2.1)	0.1
N_{area} (g m^{-2})	1.61 (0.08)	2.05 (0.12)	**0.009**
NUE (μmol CO_2 g^{-1} N s^{-1})	6.8 (0.5)	7.5 (0.5)	0.34

Stomatal conductance, WUE and iWUE were derived from instantaneous gas exchange measurements. $\delta^{13}C$, N and C concentrations were derived from analysis of leaf tissue ($n = 16$ and 17 for *Q. prinus* and *Q. velutina*, respectively). *P*-values for differences between the *Quercus* species are based on ANOVAs for each parameter with species and stand as explanatory variables. Bold denotes significant differences at $\alpha = 0.05$.

similar to Australian forests during drought (Zeppel et al. 2008), trees measured in the US Great Lakes region and Canadian boreal forest (Ewers et al. 2006, 2008; Table 6). Therefore, E_L in *Q. prinus* and *Q. velutina* growing on the mid-Atlantic Coastal Plain increase steeply at low VPD and reach a maximum that is maintained over a wide range of VPD values. This pattern makes water use in oak-dominated forests fairly constant across a broad range of soil moisture and atmospheric conditions, which has also been corroborated on a larger scale using eddy covariance measurements at this site (Clark et al. 2012).

Quercus velutina retained ~75% of its daytime canopy G_s at soil moistures as low as 0.03 m^3 m^{-3} in the upper soil (0–0.3 m) and canopy G_s in *Q. prinus* increased slightly with decreasing shallow soil moisture. Maintenance of stomatal conductance during drought has been seen in other oak species (Epron and Dreyer 1993a, 1993*b*) and suggests that *Q. prinus* and *Q. velutina* in this study have access to a relatively stable water source. It has been shown that many other oak species tap groundwater (Griffin 1973, Abrams 1990, Jackson et al. 1999, Cavender-Bares and Bazzaz 2000) and therefore avoid the drought conditions that are prevalent at the soil surface. However, we have shown that nutrients are most heavily concentrated at the soil surface, and therefore may not be available for much of the growing season when this layer becomes too dry. To withstand nutrient limitations, a significant amount of N (>50%) has been shown to be reabsorbed in oaks at this site before leaf drop (Schäfer et al. 2010). Also, these oaks may be relying on the groundwater as a source of N as suggested by Ferrio et al. (2003). In this scenario, easily leached N compounds like NO_3^- may be found in appreciable concentrations in the groundwater and trees that tap groundwater could bring this N back into the biotic system, although nitrification rates are relatively low in the Pinelands (Poovarodom et al. 1988). Robinson et al. (2012) also found evidence for hydraulic lift in this ecosystem, which may allow oaks to alter the soil hydraulic conductivity in the direct vicinity of their roots to enhance nutrient acquisition.

Comparison of measured water use, assimilation, C isotope concentrations and leaf nutrient content of these two oak species

Table 6. Comparison of curvature parameters (b in the equation: daily transpiration = $a(1 - e^{-b * \text{avg. daytime VPD}})$) from this study and values reported in the literature. Curvature parameters from the literature were either obtained from reported values or calculated by re-graphing reported daily transpiration and VPD data.

Species	Location	Curvature parameter 'b'	Reference
Q. prinus	NJ Pinelands, USA	2.79	This study
Q. velutina		2.14	
Liquidambar styraciflua (L.)	Southeastern USA	1.02	Wullschleger and Norby (2001)
Various sp.	Panamanian tropical moist forest	1.02	Phillips et al. (1999)
Q. prinus, *Q. alba*	Southeastern USA non-drought	0.98	Wilson et al. (2001)
N. sylvatica (Marsh.), *Acer rubrum* (L.)	Southeastern USA drought	1.09	
Aspen and conifer mixed	Western USA	1.15	Pataki et al. (2000)
Aspen or conifer dominated		1.26	
Pseudotsuga menziesi ((Mirb.) Franco) and *Tsuga heterophylla* ((Raf.) Sarg.)	Pacific Northwest	1.7	Moore et al. (2004)
Eucalyptus crebra (F. Muell)	Australian remnant forest non-drought	1.61	Zeppel et al. (2008)
Eucalyptus crebra (F. Muell)	Australian remnant forest drought	2.36	
Tilia americana (L.)	Great Lakes region, USA	1.38	Ewers et al. (2008)
Acer saccharum (Marsh.)		2.26	
Tsuga canadensis ((L.) Carr.)		2.66	
Betula allenghaniensis (Britton)		3.88	
Populus tremuloides (Michx.)	Canadian boreal forest	2.44	Ewers et al. (2006)
Pinus banksiana (Lamb.)		2.45	
Betula papyrifera (Marshall)		2.79	

can also give insight into how conserved each of these parameters are within the oak genus. *Quercus prinus* and *Q. velutina* had similar Ball–Berry parameters, which describe the relationship between stomatal conductance and net assimilation, leaf surface humidity and surface CO_2 concentration. Mean values of $\delta^{13}C$ of around –29.5‰ seen in our oaks are similar to those seen by Donovan et al. (2000) for three oak species (*Quercus laevis* (Walter), *Quercus margaretta* ((Ashe) Small) and *Quercus incana* (Bartram)) growing on sandy soils in the Southeastern USA and slightly more negative than the most negative values seen in *Quercus ilex* (L.) and *Quercus pubescens* (Willd.) growing in the Mediterranean (Damesin et al. 1997). Values of Δ of ~17‰ are also within the range seen in *Q. ilex* growing in the Mediterranean measured by Ferrio et al. (2003) but slightly lower than the values measured by Fleck et al. (1996) for *Q. ilex*. The A_{max} values measured in *Q. prinus* and *Q. velutina* were within the range seen in *Q. pubescens* growing in the Mediterranean (Damesin and Rambal 1995) and in *Quercus robur* (L.) and *Quercus petraea* ((Mattuschka) Liebl.) growing near Nancy, France (Epron and Dreyer 1993*a*, *1993b*) but higher than *Quercus rubra* (L.) and *Q. prinus* growing at Black Rock forest, NY, USA (Turnbull et al. 2002). Values of N concentration per leaf area were similar to *Q. ilex* growing in the Mediterranean (Fleck et al. 1996) and within the survey of literature values for oaks carried out by Xu and Baldocchi (2003). The V_{cmax} values for *Q. velutina* in our study were on the low end of values reported for *Q. rubra* and *Q. prinus* growing in Black Rock forest in NY, USA (Turnbull et al. 2002), *Q. alba* and *Q. prinus* growing in Oak Ridge, TN, USA (Wilson et al. 2000) and *Quercus douglasii* (Hook & Arn.) growing in the Sierra Nevada foothills of CA, USA (Xu and Baldocchi 2003). However, our *Q. prinus* growing on the Atlantic Coastal plain had much lower V_{cmax} rates than reported values for oaks growing in other regions (Wilson et al. 2000, Turnbull et al. 2002, Xu and Baldocchi 2003). Likewise, J_{max} values for *Q. velutina* in this study were similar to published values from other studies (Turnbull et al. 2002, Xu and Baldocchi 2003), but *Q. prinus* generally had lower J_{max} rates than oaks in the previously published studies. Therefore, *Q. prinus* and *Q. velutina* in this study fall within similar ranges of values in terms of gas exchange, leaf N and WUE as oaks across a range of species and growing conditions including a Mediterranean climate and temperate US forests.

We have found that two co-occurring oak species growing in a sandy, well-drained and nutrient-limited ecosystem have similar WUEs and NUEs even though *Q. velutina* uses more water and has more N per unit leaf area than *Q. prinus*. Therefore, *Q. prinus* exhibits a more conservative strategy in terms of nutrients and water use while *Q. velutina* maintains higher photosynthetic rates but requires more water and N per unit leaf area. The conservative strategy of *Q. prinus* may put it at a disadvantage under optimal growing conditions; however, it was shown to endure a gypsy moth defoliation more successfully than *Q. velutina* (Schäfer 2011), highlighting the importance of disturbance in forest species composition. Both species appear to tap a stable water source such as groundwater showing relatively little variation in leaf-specific transpiration over a range of VPD and soil moisture contents in the upper soil layer. This differs from many other ecosystems where trees are more responsive to decreases in soil moisture

in the shallow soil layers and highlights the importance of considering rooting depth when making predictions about how transpiration and species composition will be altered by climate change.

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