

Quercus species differ in water and nutrient characteristics in a resource-limited fall-line sandhill habitat

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Summary We compared co-occurring mature *Quercus laevis* Walt. (turkey oak), *Q. margaretta* Ashe (sand post oak) and *Q. incana* Bartr. (bluejack oak) trees growing in resource-limited sandhill habitats of the southeastern United States for water and nutrient characteristics. The *Quercus* spp. differed in their distribution along soil water and nutrient gradients, and in their access to and use of water, even though the study year was wetter than average with no mid-season drought. *Quercus laevis* had the greatest access to soil water (least negative pre-dawn water potential, Ψ_{pd}) and the most conservative water-use strategy based on its relatively low stomatal conductance (g_s), high instantaneous water-use efficiency (WUE), least negative midday water potential (Ψ_{md}) and high leaf specific hydraulic conductance (K_L). *Quercus margaretta* had the least conservative water-use characteristics, exhibiting relatively high g_s , low instantaneous WUE, most negative Ψ_{md} , and low K_L . *Quercus margaretta* also had a low photosynthetic nitrogen-use efficiency (PNUE), but a high leaf phosphorus concentration. *Quercus incana* had the poorest access to soil water, but intermediate water-use characteristics and leaf nutrient characteristics more similar to those of *Q. laevis*. There were no species differences for photosynthesis (A), leaf nitrogen on an area basis, or seasonally integrated WUE ($\delta^{13}C$). Both A and g_s were positively correlated for each species, but A and g_s were generally not correlated with Ψ_{pd} , Ψ_{md} or $\Delta\Psi_{pd-md}$. Although we found differences in resource use and resource status among these sandhill *Quercus* spp., the results are consistent with the interpretation that they are generally drought avoiders. *Quercus laevis* may have an advantage on xeric ridges because of its greater ability to access soil water and use it more conservatively compared with the other *Quercus* spp.

Keywords: nitrogen, oak, photosynthesis, soil-to-leaf hydraulic conductance, water potential.

Introduction

The longleaf pine–oak (*Pinus palustris* Mill.–*Quercus* spp.) habitats of the southeastern United States are characterized by deep, sandy soils with low soil water and nutrient availability (Wells and Shunk 1931, Laessle 1958, Woods et al. 1959,

Christensen 1988, Jacqmain et al. 1999). These habitats vary with topography, ranging from xeric areas dominated by *Quercus laevis* Walt. (turkey oak) to more mesic areas dominated by other *Quercus* spp. (Wells and Shunk 1931, Weaver 1969, Christensen 1988, Peet and Allard 1993, Jacqmain et al. 1999). Differences in the distribution and dominance of *Quercus* spp. along the topographic gradient are attributed primarily to interspecific differences in response to the availability of soil water, soil nutrients and light (Wells and Shunk 1931, Weaver 1969, Christensen 1988, Myers 1990, Jacqmain et al. 1999). Although fires are common and generally reduce *Quercus* dominance (Christensen 1988, Rebertus et al. 1993), they do not appear to drive the distribution patterns of *Quercus* spp. because these patterns are similar in areas with and without frequent burning (Weaver 1969).

Quercus spp. are adapted to a wide range of soil water conditions (Abrams 1990, Dickson and Tomlinson 1996). These oak species can avoid the development of more negative plant water potentials by deep rooting and stomatal control of gas exchange, and can tolerate more negative water potentials through osmotic adjustment and other morphological and physiological features (Rambal 1984, Stringer et al. 1989, Abrams 1990, Stone and Kalisz 1991, Bréda et al. 1993, Hamerlynck and Knapp 1996). Interspecific and ecotypic differences in water relations and gas exchange characteristics have been associated with occupation of sites differing in soil water availability (Wuenscher and Kozlowski 1971, Bahari et al. 1985, Abrams 1990, Kubiske and Abrams 1992, Hamerlynck and Knapp 1996).

Drought tolerance has been inferred for some sandhill *Quercus* spp. based on the sandy nature of the substrate and the xeric appearance of the foliage (e.g., *Q. laevis* and *Q. marilandica* Muenchh.; Abrams 1990, Dickson and Tomlinson 1996). However, seasonal predawn water potential (Ψ_{pd}) values reported for these species do not indicate exposure to or tolerance of long periods of plant water stress (Mavity 1992, Vaitkus and McLeod 1995, Donovan and Pappert 1998). Mavity (1992) found that three deciduous species in a Georgia sandhill community (*Q. laevis*, *Q. margaretta* Ashe and *Q. incana* Bartr.) maintained Ψ_{pd} close to zero through most of the season and responded to a short drought with more negative

Ψ_{pd} values and reduced photosynthesis. There were differences among the *Quercus* spp., with *Q. incana* having a more negative Ψ_{pd} and lower stomatal conductance than *Q. laevis* and *Q. margaretta* (Mavity 1992). Interspecific differences have also been reported for sprout/juvenile responses to added nutrients and water, with *Q. laevis* showing less of a response (consistent with a stress-tolerant mechanism) than *Q. hemiphaerica* Bartr. ex Willd. (Vaitkus and McLeod 1995).

Based on observed differences in species distribution and potential differences in adaptation to soil water and nutrient availability, we expected the *Quercus* spp. in this study to differ in ecophysiological characteristics related to water and nutrient status. We compared co-occurring mature *Q. laevis*, *Q. margaretta* and *Q. incana* to determine differences in photosynthesis, stomatal conductance, intercellular CO₂ concentration, predawn water potential, midday water potential, leaf N and P, instantaneous and seasonally integrated water-use efficiency, photosynthetic nitrogen-use efficiency and leaf specific hydraulic conductance. We hypothesized (1) that the three species would differ in these characteristics where they co-occur, and (2) that *Q. laevis*, which dominates the most xeric sites, would have the most conservative water-use strategy among the species studied, even under conditions of high water availability.

Materials and methods

The study site is a sandhill habitat in the northeastern part of the Savannah River Site near Aiken, SC, located in the Department of Energy set-aside area No. 29: Scrub Oak Natural Area (Davis and Janecek 1997). The soils are Lakeland sands with 0–6% slope (Davis and Janecek 1997). Deciduous oaks (*Q. laevis*, with associated *Q. margaretta* and *Q. incana*) dominate the site canopy. *Pinus palustris* individuals are emergents. Selective logging of the larger pines may have occurred prior to land acquisition in 1951, because the oldest individuals are 81 years old (Davis and Janecek 1997). The site has not burned for at least 45 years and *Vaccinium* spp. dominate the understory. Precipitation and temperature data were collected for the 1997 growing season (Savannah River Site, Williston barricade, about 1 km from the study site) and compared with 33-year mean temperature and 45-year mean precipitation data (Area 773A, about 13 km from the study site). The study area is contiguous with sites previously used for ecophysiological studies of *Q. laevis* (Donovan and Pappert 1998) and spatial and genetic structure studies of *Q. laevis* and *Q. margaretta* (Berg and Hamrick 1993, 1994). The three winter deciduous *Quercus* spp. are all small trees 5–8 m in height, with relatively open canopies and no closed overstory of *P. palustris*. Leaves generally emerge in late March, reach complete expansion in early May and senesce in November. *Quercus laevis* and *Q. incana* are red oaks, whereas *Q. margaretta* is a white oak.

Within a 100 × 100 m plot, 12 locations were selected, each containing one suitably sized individual (> 2 cm DBH) of each of the three *Quercus* spp. Locations were far enough apart to ensure that individual trees of each species were unlikely to be

connected by intact roots. However, because of the prolific lateral extension of roots of these species, and the capacity for clonal growth, it is possible that independent ramets of the same clone were sampled (Berg and Hamrick 1994). The 12 individuals of each *Quercus* sp. were repeatedly sampled for ecophysiological characteristics three times during the 1997 growing season: June 9–10, July 13–15, and September 7–9. Plant water potentials were measured before dawn (Ψ_{pd}) and at midday (Ψ_{md}) on mature, fully expanded leaves from the lower canopy with a Scholander-type pressure chamber (PMS Instruments Co., Corvallis, OR). Net photosynthesis (A) and stomatal conductance to H₂O (g_s) were measured on mature, unshaded leaves (incident radiation > 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for June and Sept, > 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for July), with two LI-6200 portable photosynthesis systems equipped with 250-ml chambers (Li-Cor, Inc., Lincoln, NE). The two LI-6200s were consistently used at different locations, so that any minor difference attributable to the systems was accounted for as a block effect in the analyses. For each individual on each sampling date, gas exchange measurements were made three times during the day, between 1000 and 1700 h. No consistent diurnal trend for A or g_s was evident for any species on any date, so the mean of the three measurements on each tree was used in the analysis of subsequent time-of-season effects and correlations.

Photosynthetic nitrogen-use efficiency (PNUE) was calculated from A and leaf N (Field et al. 1983). Intercellular CO₂ concentration (c_i ; Farquhar and Sharkey 1982) was used as a comparative estimate of instantaneous water-use efficiency (WUE), because ambient CO₂ concentration, leaf temperature and leaf-to-air vapor pressure deficit (calculated from leaf temperature during measurements and air temperature and relative humidity from open chamber readings), Δw , were not significantly different among species on each sampling date (Donovan and Ehleringer 1994). A higher c_i reflects lower or less conservative instantaneous WUE.

Leaf specific hydraulic conductance from soil to leaf ($K_L = (g_{smd}\Delta w_{md})/(\Psi_{pd} - \Psi_{md})$) was calculated using Ψ_{pd} to approximate soil water potential, Ψ_{md} , and g_{smd} and Δw_{md} (g_s and Δw , respectively, measured at the same time as Ψ_{md}) (Thompson and Hinckley 1977, Pallardy et al. 1995, Hubbard et al. 1999). Leaf area was measured (Agvision leaf area meter, type AMS, Delta-T Devices, Cambridge, U.K.) and then leaves were dried and weighed for calculation of specific leaf area (SLA). Mature leaves were also collected, dried and ground for analysis of leaf N (micro-Dumas combustion, Carlo Erba, Milan, Italy) and leaf P (colorimetric analysis of a dry ash/acid extraction; Allen 1989).

Plant characteristics measured on three sampling dates were analyzed by multivariate, repeated measures analysis of variance (MANOVA; O'Brien and Kaiser 1985, von Ende 1993) on untransformed data using the SAS PROC GLM statistical software package (SAS Institute, Cary, NC) to test for seasonal trends and differences among species. Pillai's trace is the F -statistic that is reported for within-subject effects (time) (Olson 1976). Relationships among plant characteristics were

analyzed by determining significance of Pearson's product moment correlation coefficients.

Leaves collected in September were analyzed for $\delta^{13}\text{C}$ by continuous flow mass spectrometry (University of Georgia Stable Isotope/Soil Biology Laboratory) to estimate seasonally integrated c_i and WUE (Farquhar et al. 1989, Donovan and Ehleringer 1994). A more negative $\delta^{13}\text{C}$ reflects a lower or less conservative seasonally integrated WUE. A one-way analysis of variance (ANOVA) on inverse, natural log-transformed data was used to test for differences among species for $\delta^{13}\text{C}$ values.

At 20 locations within the 100 × 100 m study area, soil water and soil nutrient contents were measured to determine their association with woody plant nutrient concentration and *P. palustris* seedling abundance and survival (K.W. McLeod, J.B. West and L.A. Donovan, unpublished data). Although these locations did not correspond to the 12 *Quercus* study sites in a one-to-one fashion, they are representative of the overall site. Soil samples were taken in March 1997 at 15 and 60 cm depths for determination of gravimetric soil water content and nutrient content. Soils were weighed wet, dried at 60 °C, weighed again, and ground in a ball mill. Soil N and C were obtained from micro-Dumas combustion (Carlo Erba) and available soil P was obtained from colorimetric analysis of a double acid extraction (Olsen and Sommers 1982). For gravimetric soil water content, and soil N, P and C, the two depths were compared with a one-way ANOVA, with 20 replicates per depth (data were transformed as necessary to meet assumptions). Concurrent with gravimetric measurements of soil water in March and the *Quercus* ecophysiology sampling in June, July and September, soil water content was measured with a portable Time Domain Reflectometer (Soil Moisture Equipment, Santa Barbara, CA) for 0–15 and 0–60 cm depth intervals. On each sampling date, TDR soil water estimates at the two depths were compared with a one-way ANOVA, with 20 replicates per depth.

Results

Compared with long-term trends, precipitation was generally near average and air temperature generally below average during the study period (Figure 1). Major rain events (> 25 mm) occurred throughout the study period, and within a week immediately before the June and July measurement periods. Soil water content, estimated from TDR measurements, differed significantly between the 0–15 and 0–60 cm depths (Figure 1). The shallower soil had a significantly higher soil water content than the 0–60 cm depth in March, May, and September ($P \leq 0.01$), but the deeper soil was wetter in July ($P < 0.0001$). Gravimetric water contents for the March sampling date ($8.5 \% \pm 0.41$ and $5.5 \% \pm 0.41$ for 15 and 60 cm depths, respectively; $P = 0.03$) were consistent with the TDR measurements. The two methods differed in the absolute amount of soil water because gravimetric samples were taken at 15 and 60 cm depths, whereas TDR measurements yielded integrated results from surface to 15 or 60 cm depth. For soils sampled in March, total soil N was significantly higher at 15 cm ($0.043 \pm 0.002\%$) than at 60 cm depth ($0.026 \pm 0.003\%$; $P < 0.0001$).

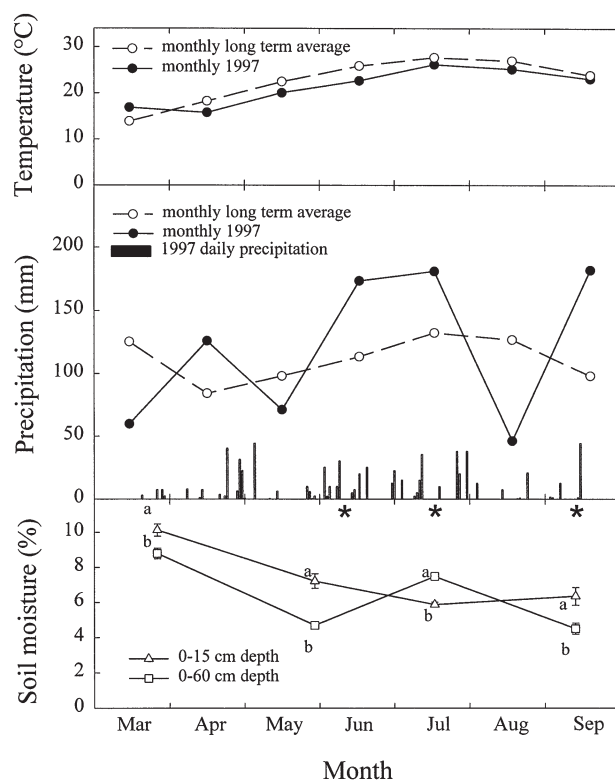


Figure 1. Monthly long-term means (33 years for temperature and 45 years for precipitation), and 1997 monthly mean temperature and monthly total precipitation for the study area. In addition, daily precipitation events for 1997 are indicated in bar graph form on the precipitation panel. Gravimetric soil water (mean \pm SE) from TDR measurements for 0–15 and 0–60 cm depths are presented. For soil water content (bottom panel), values associated with different letters are statistically significantly different within a date. Asterisks on the x-axis indicate sampling dates for ecophysiological characteristics of the *Quercus* spp.

Soil carbon was also higher at 15 cm depth ($0.76 \pm 0.07\%$) compared with 60 cm depth ($0.11 \pm 0.02\%$; $P < 0.0001$). In contrast, soil-extractable P tended to be lower at 15 cm depth (4.5 ± 3.0 ppm) compared with 60 cm depth (8.1 ± 0.6 ppm; $P = 0.07$).

There was a significant species effect for Ψ_{pd} , with *Q. laevis* consistently exhibiting the least negative values and *Q. incana* consistently exhibiting the most negative values (Figure 2A, Table 1). For all species, Ψ_{pd} declined through the season. Species also differed significantly for Ψ_{md} (Figure 2B, Table 1). *Quercus laevis* had the least negative values, and *Q. margaretta* had the most negative values. The significant time \times species interaction was most likely a result of the similar Ψ_{md} values of *Q. incana* and *Q. margaretta* in June. Seasonal means and maxima for $\Delta\Psi_{pd-md}$ were 1.71 and 2.05, 2.55 and 2.90, and 1.98 and 2.04 MPa for *Q. laevis*, *Q. margaretta* and *Q. incana*, respectively.

There was no significant species effect for A , which declined throughout the season for all species (Table 1, Figure 2C). Species differed significantly for g_s and c_i , with *Q. margaretta* having the highest values late in the season

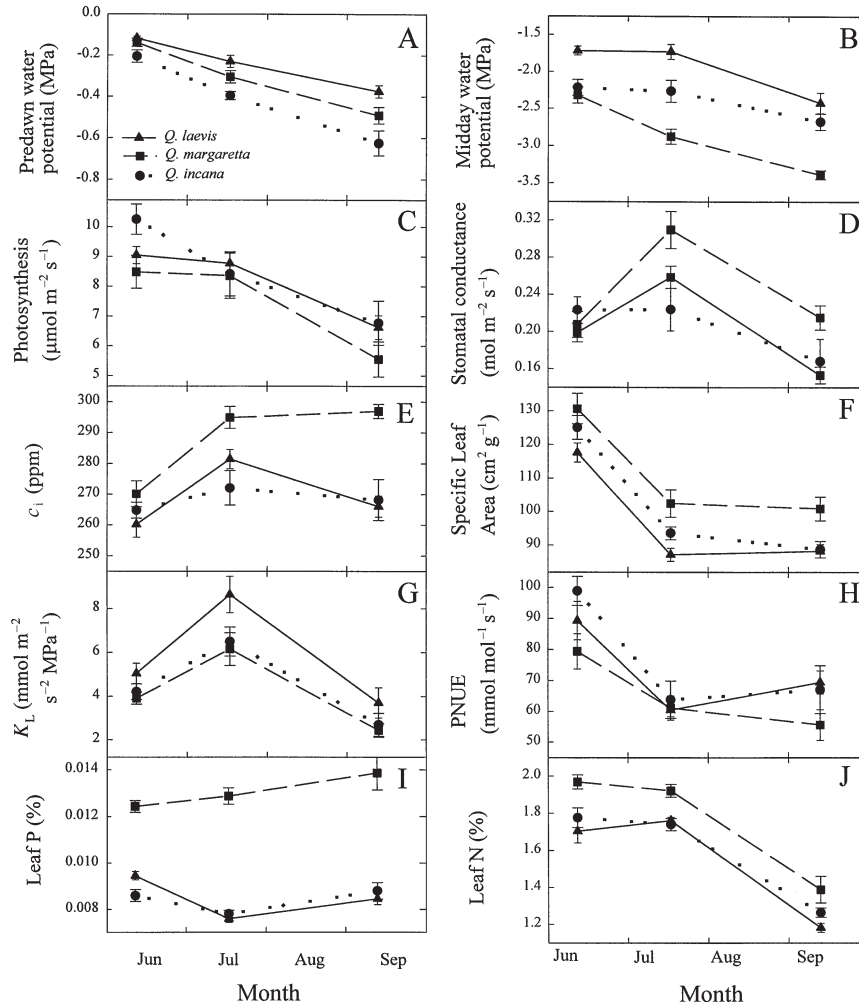


Figure 2. Ecophysiological characteristics of *Quercus laevis*, *Q. margaretta* and *Q. incana* (means \pm SE, $n = 12$ trees per species) sampled repeatedly during the 1997 growing season. (A) Plant predawn water potential, Ψ_{pd} , (B) plant midday water potential, Ψ_{md} , (C) photosynthesis, A , (D) stomatal conductance, g_s , (E) intercellular CO_2 concentration, c_i , (F) specific leaf area, SLA, (G) leaf-to-soil hydraulic conductance, K_L , (H) photosynthetic nitrogen use efficiency, PNUE, (I) leaf nitrogen, leaf N, and (J) leaf phosphorus, leaf P. See Table 1 for statistical results.

Table 1. Repeated measures ANOVA for seasonal characteristics for *Quercus laevis*, *Q. margaretta* and *Q. incana* trees. Abbreviations: plant predawn water potential, Ψ_{pd} ; plant midday water potential, Ψ_{md} ; photosynthesis, A ; stomatal conductance, g_s ; intercellular CO_2 concentration, c_i ; specific leaf area, SLA; leaf-to-soil hydraulic conductance, K_L ; photosynthetic nitrogen use efficiency, PNUE; leaf nitrogen, leaf N; and leaf phosphorus, leaf P. Degrees of freedom (numerator/denominator) are 2/44 for Time, 4/11 for Time \times Species and 2/22 for Species. Significance values are indicated as: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Source	F statistic		
	Time	Time \times Species	Species
Ψ_{pd} (MPa)	92.03***	1.73	16.74***
Ψ_{md} (MPa)	59.97***	4.35**	38.05***
A ($\text{mmol m}^{-2} \text{s}^{-1}$)	40.53***	1.45	1.87
g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	29.54***	3.89**	3.79*
c_i (ppm)	23.08***	5.12***	21.04***
K_L ($\text{mmol m}^{-2} \text{s}^{-1}$)	44.95***	0.6	5.51**
PNUE ($\text{mmol mol}^{-1} \text{s}^{-1}$)	40.22***	1.57	4.05*
Leaf P (%)	10.96***	6.87***	177.9***
Leaf N (%)	229.5***	0.97	15.35***
Leaf N (mg cm^{-2})	157.2***	2.58*	0.74
Leaf SLA ($\text{cm}^2 \text{g}^{-1}$)	354.5***	1.65	10.31***

(Figures 2D and 2E, Table 1). For g_s and c_i , the species \times time interactions were also significant. For each sampling date, there were no significant species effects for leaf temperature, irradiance and Δw ($P > 0.10$). Leaf temperature ($^{\circ}\text{C}$), PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and Δw (mmol mol^{-1}) were 31.3, 1472 and 35 for June, 35.9, 971 and 42 for July, and 32.3, 1181 and 42 for September, respectively.

In September, leaf $\delta^{13}\text{C}$ values were -29.49 ± 0.15 , -29.70 ± 0.24 , and -29.25 ± 0.19 for *Q. laevis*, *Q. margaretta* and *Q. incana*, respectively. There was no significant difference among species for $\delta^{13}\text{C}$ ($P = 0.249$). There was a significant species effect and time effect for K_L (Table 1, Figure 2G). Among species, *Q. laevis* had the highest K_L throughout the season.

There were significant species and time effects for SLA, leaf N and P on a weight basis, and PNUE (Table 1, Figures 2F and 2H–J). Among species, *Q. margaretta* had the highest leaf SLA and leaf N and P concentrations (weight basis). However, when leaf N was examined on an area basis, there was no significant species difference.

There were significant positive correlations between A and g_s for each species on each date and across dates (except

Q. laevis and *Q. margaretta* in July) (Table 2). There were few significant relationships between Ψ_{pd} and A or g_s , or between Ψ_{md} and A or g_s , or between $\Delta\Psi_{pd-md}$ and g_s . There was generally a significant positive relationship between midday g_s and K_L (data not presented).

Discussion

At a location where these three oak species co-occurred, they achieved the same photosynthetic carbon gain per unit leaf area despite differences among them in resource status and resource-use strategies. Their comparative strategies, with strategy denoting a set of traits acquired through natural selection, were related to their relative species distribution along soil water gradients in the sandhills.

Quercus laevis had the greatest access to soil water, based on having the least negative Ψ_{pd} of the three species throughout the season (Hinckley et al. 1978, Bréda et al. 1995). Greater access to soil water could be achieved by more extensive rooting—either greater extension of laterals or greater rooting depth. *Quercus laevis* has extensive lateral roots that can extend up to 15 m (Hough et al. 1965). Rooting depth profiles are less certain, with many roots observed in the upper 15 cm, and indications that there may be a few roots going deeper than 1 m (Woods 1957; L.A. Donovan and K.W. McLeod, unpublished observations). In addition to having greater access to soil water, *Q. laevis* also had a conservative water-use strategy, based on its low g_s and a high instantaneous WUE (indicated by lower c_i from gas exchange), even though it had the least negative Ψ_{md} values and a high K_L . The greater soil water access and more conservative water-use strategy of

Q. laevis is consistent with its dominance on xeric ridges where these features might allow it to avoid soil water limitations, whereas the avoidance capacity of the other species might be exceeded.

Quercus incana exhibited the most negative Ψ_{pd} values throughout the season, suggesting the least extensive root system. It had low g_s , c_i , and leaf N and P (%) values, similar to those of *Q. laevis*. Its Ψ_{md} was intermediate compared with the other species, and its K_L was similar to that of *Q. margaretta*. Thus, the water-use strategy of *Q. incana* appeared to be intermediate between those of the other study species.

Values of Ψ_{pd} in *Q. margaretta* were between those of *Q. laevis* and *Q. incana*, indicating intermediate access to soil water. However, *Q. margaretta* was less conservative in its water use than the other species. In *Q. margaretta*, mid- and late-season Ψ_{md} values were considerably more negative than those of the other species and were accompanied by relatively high values of g_s and c_i , indicating a relative lack of stomatal closure. This weak stomatal control at low Ψ_{md} could lead to excessive water loss, resulting in low A because of non-stomatal inhibition and xylem cavitation during drought (Pezeshki and Chambers 1986, Bragg et al. 1993, Sparks and Black 1999), and exclusion from xeric sites. This interpretation is supported by our observation that high g_s and high leaf N concentrations were not associated with high A . In addition, during an extended drought, *Q. margaretta* leaves have been observed to maintain a higher g_s , followed by leaf wilting and death before those of co-occurring *Q. laevis* (K.W. McLeod, unpublished data). Alternatively, the ability to maintain open stomata during a drought may be necessary to maintain carbon gain for species on xeric sites (Bahari et al. 1985, Abrams 1990, Bréda et al. 1993, Dickson and Tomlinson 1996). Comparisons of these species under drought conditions, and assessments of stem and root xylem vulnerability to cavitation, would help distinguish among these possibilities.

Among species, *Q. margaretta* had the highest leaf N and P concentrations (weight basis) and the lowest PNUE. However, the species differences in leaf N disappeared when N was expressed on an area basis. To compare our species with the published literature on general plant characteristics related to photosynthesis, we examined the June data for A , SLA and leaf N, all on a weight basis. June data were used because A was highest during this month. The species means for *Q. laevis*, *Q. margaretta* and *Q. incana* were as follows: leaf A of 106.0, 111.8 and 125.1 $\text{nmol g}^{-1} \text{s}^{-1}$; SLA of 117.6, 130.6 and 125.1 $\text{cm}^2 \text{g}^{-1}$; and leaf N of 17.0, 19.7 and 17.8 mg g^{-1} , respectively. These values are similar to those reported for broad-leaved deciduous species (Reich et al. 1997). In our study species, leaf SLA and N interacted to maintain a relatively constant photosynthetic rate per unit leaf area across species.

The $\delta^{13}\text{C}$ values, which estimate seasonally integrated c_i and thus water-use efficiency (Farquhar et al. 1989, Donovan and Ehleringer 1994), did not differ among species, even though instantaneous c_i was higher for *Q. margaretta*. There are several possible explanations for this finding. First, there may be a scaling problem, because instantaneous c_i measurements

Table 2. Relationships among parameters. Abbreviations: plant pre-dawn water potential, Ψ_{pd} ; plant midday water potential, Ψ_{md} ; photosynthesis, A ; and stomatal conductance, g_s . Values of A and g_s are means of 2–3 measurements for each tree on each date. For each species, $n = 11$ –12 for each month, and $n = 35$ –36 for all months combined. Significance values are indicated as: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, and ns = non-significant.

Dependent Independent	A g_s	A Ψ_{pd}	A Ψ_{md}	g_s Ψ_{pd}	g_s Ψ_{md}	g_s Ψ_{pd-md}
<i>Q. laevis</i>						
June	**	ns	ns	ns	ns	ns
July	ns	ns	ns	ns	ns	ns
September	**	ns	ns	ns	ns	ns
All months	**	**	ns	ns	ns	ns
<i>Q. margaretta</i>						
June	**	ns	ns	ns	ns	ns
July	ns	ns	ns	ns	ns	ns
September	**	ns	ns	ns	ns	ns
All months	**	**	ns	ns	ns	ns
<i>Q. incana</i>						
June	**	ns	ns	ns	ns	ns
July	*	ns	ns	ns	ns	ns
September	**	ns	ns	ns	ns	ns
All months	**	*	ns	*	ns	ns

made on three sunny days during the season may not agree well with an integrated estimate for the whole season (e.g., Picon et al. 1996). Second, the $\delta^{13}\text{C}$ values may disproportionately reflect conditions during maximum carbon gain early in the season when instantaneous c_i values were most similar (Hansen and Steig 1993, Damesin et al. 1997). In addition, the $\delta^{13}\text{C}$ values may partly reflect carbon remobilization of photosynthate acquired at the end of the previous growing season (Smedley et al. 1991). Additional studies are needed to distinguish among these and other possibilities (Picon et al. 1996) and thus evaluate the usefulness of $\delta^{13}\text{C}$ values for estimating seasonally integrated gas exchange characteristics of these oak species.

Our values of Ψ_{pd} , Ψ_{md} , A , g_s , c_i and leaf N concentration for *Q. laevis*, *Q. margaretta* and *Q. incana* were similar to those previously reported for these species (Mavity 1992, Vaitkus and McLeod 1995, Donovan and Pappert 1998). In addition, the species rankings for Ψ_{pd} , Ψ_{md} , A and g_s were comparable to those found for these species at a Georgia sandhill site (Mavity 1992). Where these *Quercus* spp. co-occur, they rarely achieve Ψ_{pd} below -1 MPa except during extreme droughts (Mavity 1992, Vaitkus and McLeod 1995, Donovan and Pappert 1998, K.W. McLeod, unpublished data). Similar findings have been reported for other eastern North American *Quercus* spp. (Stringer et al. 1989, Abrams 1990, Kubiske and Abrams 1992, Bragg et al. 1993, Kloeppe et al. 1993, but see Parker et al. 1982). In contrast, *Quercus* spp. in Mediterranean climates routinely achieve Ψ_{pd} below -1.5 MPa (Sala and Tenhunen 1994, Goulden 1996, Damesin et al. 1997). Based on the Ψ_{pd} values, we conclude that *Quercus* spp. in sandhill habitats do not routinely experience severe limitations of soil water availability even though the habitats are xeric in appearance. The complex deep sands and intermittent clay layers may serve to store soil water (Oliver 1978).

The *Quercus* spp. in our study were unusual in achieving high $\Delta\Psi_{\text{pd-md}}$. Values of $\Delta\Psi_{\text{pd-md}}$ are generally less than 1.5 MPa for other eastern North American *Quercus* spp. (Bahari et al. 1985, Abrams and Knapp 1986, Abrams et al. 1990, Kubiske and Abrams 1992, Kloeppe et al. 1993). In contrast, some oaks in Mediterranean climates achieve $\Delta\Psi_{\text{pd-md}}$ of approximately 2.0 MPa (Gallego et al. 1994, Sala and Tenhunen 1994), approaching the values for the sandhill oaks. The large $\Delta\Psi_{\text{pd-md}}$ values that we found, up to 2.1 MPa for *Q. laevis* and *Q. incana*, and 2.9 MPa for *Q. margaretta*, are similar to the values of 2.6 MPa for *Q. laevis* and *Q. incana*, and 3.2 MPa for *Q. margaretta*, reported by Mavity (1992). The relationship of gas exchange parameters to these large daily fluctuations in leaf water potential warrants further investigation.

Examination of the relationships among parameters revealed a strong correlation between A and g_s for each species, as has been previously documented for these (Mavity 1992, Vaitkus and McLeod 1995) and many other species. However, A and g_s were not generally correlated with either Ψ_{pd} or Ψ_{md} on any sampling date or across dates (data combined). This is contrary to the strong relationship found between g_s and Ψ_{pd} for *Quercus marilandica* and *Q. rubra* L. under field conditions (Reich and Hinckley 1989) and for other oaks under con-

trolled drought conditions (Acherar and Rambal 1992). In the non-drought year of our study, soil water limitations (estimated by Ψ_{pd}) may not have been sufficient to affect maximum rates of gas exchange. Reich and Hinckley (1989) also found a strong correlation between g_s and K_L , suggesting a possible controlling effect of K_L on g_s . Although our data also support this relationship (data not shown), the fact that K_L is not mathematically independent of g_s (see equation in Methods) suggests that these correlations should be interpreted cautiously. Contrary to the findings of Reich and Hinckley (1989), K_L was not significantly correlated with Ψ_{md} for our data (results not shown). The relationship of K_L to threshold water potentials for stomatal closure may provide more insight into stomatal control for these species (Bond and Kavanagh 1999).

Our data, collected in a relatively wet year, are consistent with the interpretation that sandhill *Quercus* spp. are largely drought avoiders, and that *Q. laevis* is found on xeric ridges because of its greater capacity for access to, and conservative use of, soil water. Under severely dry conditions, the lack of stomatal response to drought in *Q. margaretta* might result in earlier depletion of water available to its roots, with deleterious consequences as the season progresses. Also, the apparent inability of *Q. incana* to explore the wetter portion of the soil profile may limit its survival at the driest sites. Although other adaptations of *Quercus* spp. and environmental factors may also be important, the interaction of the resource-use strategies of these species and water availability is a strong determinant of their performance and distribution patterns in the sandhills.

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