

CARBON ISOTOPE DISCRIMINATION AND WATER RELATIONS OF OAK HYBRID POPULATIONS IN SOUTHWESTERN UTAH

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ABSTRACT.—The evergreen oak *Quercus turbinella* and the deciduous *Q. gambelii* form natural hybrids in southwestern Utah and northern Arizona. Hybrid individuals also are found in northern Utah in a region where only *Q. gambelii* currently exists, indicating that *Q. turbinella* has recently retreated southward. Our objectives were to (1) examine the ecophysiology of parental taxa and hybrids under natural conditions in southeastern Utah, and (2) investigate the level of integration between leaf carbon isotope discrimination (a synthetic gas exchange trait) and structural and chemical traits of leaves in morphologically variable hybrid populations. Leaf length, width, mass-to-area ratio (LMA, g m^{-2}), and nitrogen concentration (N, g g^{-1}) within 2 hybrid populations near New Harmony, Utah, were highly intercorrelated. Variation within the hybrid populations spanned mean values for these traits observed in parental taxa from adjacent “pure” populations of each species. Carbon isotope discrimination (Δ), an integrated measure of the ratio of intercellular to ambient CO_2 concentration, ranged from 16.1‰ to 19.6‰ within the 2 hybrid populations and was positively correlated with leaf nitrogen concentration and negatively correlated with LMA; individuals in hybrid populations with leaves resembling *Q. gambelii* had the highest leaf Δ and N concentrations and lowest LMA compared with leaves from plants that resembled *Q. turbinella*. CO_2 uptake is limited by stomatal conductance and possibly by mesophyll resistance to a greater extent in *Q. turbinella* phenotypes than in intermediate or *Q. gambelii* phenotypes. δD of stem xylem water (an indication of active rooting depth) and predawn water potential during the peak monsoon period in August were not correlated to leaf Δ values within the hybrid populations. Several individuals that were morphologically similar to *Q. turbinella* in the hybrid populations maintained high predawn water potentials and derived moisture from winter recharge that presumably was taken from deep soil layers. Apparently, a few adult individuals of the *Q. turbinella* phenotype in hybrid populations accessed water from deep in the soil profile, which enabled them to avoid summer drought. Reduced monsoonal activity may have been an important, but not the single, determinant of *Q. turbinella*’s retreat from northern Utah during the recent Holocene.

Key words: oak hybrids, *Quercus turbinella*, *Quercus gambelii*, leaf structure, leaf nitrogen, carbon isotope discrimination, $\delta^{13}\text{C}$, δD , water potential.

Fossil records reveal dramatic shifts in woody species’ distributions during the late Pleistocene through the recent Holocene in the American Southwest (Van Devender and Spaulding 1979, Spaulding and Graumlich 1986, Betancourt et al. 1990, Miller and Wigand 1994). One such migration involves the southward retreat of *Quercus turbinella* Greene, an evergreen diffuse-porous oak, from northern Utah. This species hybridizes with *Quercus gambelii* Nutt., a deciduous ring-porous oak, in contact zones in southwestern Utah and northwestern Arizona (Cottam et al. 1959). Relict hybrid clones occur in northern Utah along the western front of the Wasatch Mountain Range almost 400 km north of the current contact zone (Fig. 1). Cottam et al. (1959) argued that hypsithermal warming was

responsible for the northward migration of both species through the Arizona-Utah region, and more recent cooling has resulted in extirpation of the evergreen *Q. turbinella* from northern Utah, leaving behind the more cold-tolerant hybrid individuals. Neilson and Wullstein (1983, 1985), however, found that successful seedling establishment in both *Q. turbinella* and *Q. gambelii* depends on summer moisture and argued that the northern range limits for both species are controlled synergistically by 2 distinct air mass boundaries: the polar front that controls the probability of late spring frost, and the summer “monsoon” that controls summer moisture availability. Biogeographic implications of seedling stress tolerance and demography, however, do not reveal why hybrid individuals have persisted and

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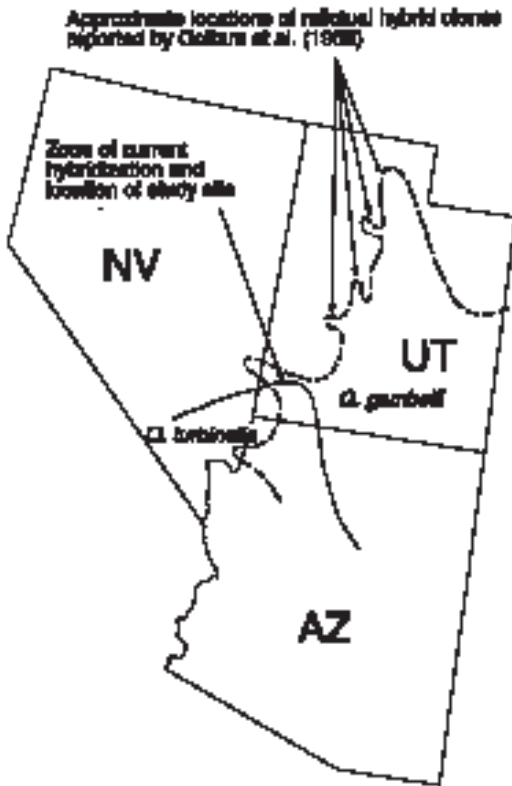


Fig. 1. Map of current northern boundaries of *Quercus gambelii* and *Q. turbinella* in the Intermountain region and location of relict hybrid clones in north central Utah. Map is based on information in Cottam et al. (1959) and Little (1971).

adult *Q. turbinella* individuals have disappeared from northern Utah in spite of the fact that clones of these oaks have long life spans.

The present northern limit of *Q. turbinella* is geographically more closely related to the sharp summer moisture gradient in the Southwest than is that of *Q. gambelii*. Ecophysiological studies conducted in natural populations and in common gardens reveal that adult individuals of *Q. gambelii* do not take up summer precipitation but instead use winter moisture stored in deep soil layers during the growing season (Phillips and Ehleringer 1994). Ehleringer and Phillips (1996) demonstrated that adult *Q. turbinella* in a common garden near Salt Lake City, far north of *Q. turbinella*'s present northern boundary, took up water from shallow soil layers following summer rains. The tradeoff associated with having roots deployed in shallow soil layers is that

plants experience very low and potentially damaging soil water potentials during the summer months in the absence of significant monsoon storms. Hybrid individuals between these 2 oaks appear to have an intermediate rooting depth that allows them to persist in the summer-dry region of northern Utah, where the intensity of the summer monsoon has apparently declined over the recent Holocene. Greater drought tolerance and higher water-use efficiency are commonly found among species or populations that extract water only from shallow soil layers compared to taxa that have access to a stable water source deep in the soil profile (Knapp and Fahenstock 1990, Flanagan et al. 1992, Williams and Ehleringer 1996). Ehleringer and Phillips (1996) and Ehleringer and Smedly (1988) showed that stomatal conductance is lower and carbon isotope discrimination (Δ) is higher in the drought-tolerant *Q. turbinella* compared to that in the moisture-requiring *Q. gambelii*. In C_3 plants, Δ depends upon c_i/c_a , the ratio of internal to ambient CO_2 concentration (Evans et al. 1986, Farquhar et al. 1989) and thus records the tradeoff between biochemical demand for CO_2 by photosynthetic enzymes in the chloroplasts and CO_2 supply through the stomata. Flanagan et al. (1992) found that leaf Δ and depth of water extraction from the soil (inferred from δD values of xylem water) were positively correlated among 4 woody species of the pinyon-juniper ecosystem in southern Utah. Since Δ is often correlated with stomatal conductance and water-use efficiency, it is an important parameter for unraveling the potential effects of hybridization on the water balance of woody perennials such as oak.

Hybrid oak populations in southern Utah also are useful for examining leaf structural and physiological controls on photosynthesis. The dependence of carbon isotope discrimination (Δ) on leaf structural and chemical traits is typically studied at the interspecific and interpopulation level (Vitousek et al. 1990, Meinzer et al. 1992, Sparks and Ehleringer 1997). Generally, Δ has been shown to decrease with leaf mass-to-area ratio and leaf nitrogen content. The *Q. gambelii* \times *Q. turbinella* hybrid zones are intriguing because these species represent extreme leaf morphological types; small, thick-leaved *Q. turbinella* grade into large, thin-leaved *Q. gambelii* types in these extremely

variable hybrid populations. Integration between leaf structural and chemical traits and carbon isotope discrimination should be retained in these hybrid populations if c_i/c_a is strongly controlled by these characters.

This study evaluated plant water relations, leaf Δ , and leaf structural and chemical traits in *Q. gambelii*, *Q. turbinella*, and their natural hybrids in southwestern Utah. We predicted that these 2 oaks would show differential capacities to take up summer rains in this natural setting and that hybrids would have intermediate water use and leaf gas exchange characteristics, similar to patterns observed in F1 hybrids in common gardens in Salt Lake City (Ehleringer and Phillips 1996). Of interest also was whether leaf structural and chemical traits that are often linked to Δ also would be correlated to Δ in hybrid populations, where there is a high potential for loss of trait integration because of recombination and back crossing.

MATERIALS AND METHODS

The study was conducted in southeastern Utah in Washington County near the town of New Harmony within a large area of hybridization between *Quercus gambelii* and *Q. turbinella* (Fig. 1). Hybridization between these 2 oak species contributes to substantial leaf morphological variation in this area (Cottam et al. 1959, Tucker et al. 1961). Two hybrid populations were selected for study. Hybrid population 1 (HP1; 37°30'N, 113°19'W, 1707 m), located on a broad alluvial terrace above an ephemeral drainage (Pace Draw), is approximately 5 km north of the town of New Harmony. Hybrid population 2 (HP2; 37°30'N, 113°19'W, 1713 m) is 2 km northwest of HP1 near the same drainage. Vegetation at both sites is open scrub-oak woodland.

Twelve plants were selected from within each of these 2 hybrid populations for detailed morphological and physiological measurements. All plants used in the study were multi-stemmed adult plants and were 2–4 m in height. Plants were selected haphazardly with the intent of including the full range of leaf morphological variation that distinguishes the 2 oak species. Between 8 and 10 leaves were collected for morphological analysis on 24 August 1994 from each selected plant in the 2 hybrid populations and also from 5 plants from 1 nonhybrid population of each *Quercus*

species. The “pure” stand of *Q. gambelii* (37°31'N, 113°20'W, 1798 m) was 3 km northwest of HP2 at the mouth of a mesic canyon feeding the drainage that passes near HP1 and HP2. The nonhybrid population of *Q. turbinella* was approximately 18 km south of New Harmony (37°20'N, 113°18'W, 1340 m).

Blade length, width, 1-sided area, and dry mass were determined for each leaf collected from the populations and averaged for each plant. Leaf mass-to-area ratio (LMA, g m^{-2}) was calculated from average mass and 1-sided area values from the leaves collected from each plant. These same leaves were analyzed for stable isotope ratios of carbon ($\delta^{13}\text{C}$) and total nitrogen concentration (N , g g^{-1}). $\delta^{13}\text{C}$ was determined on finely ground, oven-dried (70°C for 48 h) blade tissue using an isotope ratio mass spectrometer (Delta S, Finnigan MAT, San Jose, CA) attached on-line to a CHN combustion furnace at the University of Utah Stable Isotope Facility for Environmental Research (SIRFER). $\delta^{13}\text{C}$ was converted to carbon isotope discrimination values (Δ) using an atmospheric $\delta^{13}\text{C}$ value of -8‰ (Ehleringer and Osmond 1989, Farquhar et al. 1989). Nitrogen concentration was measured on these same samples using a Perkin-Elmer 2400 CHN analyzer (Norwalk, CN).

Predawn leaf water potential (Ψ_{pd}) was determined for the same plants sampled above from all populations on 25 August 1994 using a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR). Ψ_{pd} was measured between 0300 and 0530 h local time within 1 to 2 min after twigs were cut from the plants to minimize changes in Ψ due to water loss.

Plant water sources (winter recharge or summer monsoon-derived soil moisture) were inferred from δD values of plant xylem water. Although we did not measure isotopic values of soil, precipitation, or groundwater, it has been shown repeatedly for this region that winter moisture stored in deep soil layers is depleted in deuterium compared to water from surface soil layers that has been subjected to evaporative enrichment and mixed with isotopically heavy summer precipitation (Ehleringer et al. 1991, Flanagan et al. 1992, Phillips and Ehleringer 1994). Our interest here was simply to evaluate the covariation of δD with other physiological measurements rather than to identify the exact depth of water extraction by these trees or the proportion of water

obtained from different sources. We cut 3–4 suberized twigs at midday from different locations on a tree canopy the same day that Ψ_{pd} measurements were taken. Cut twigs were immediately enclosed and sealed in screw-cap glass vials using Parafilm and kept frozen in the lab until water was extracted using a cryogenic vacuum distillation technique (Ehleringer and Osmond 1989). Samples were then prepared for hydrogen isotope analysis by reacting 3 μL of the extracted water with 100 mg of zinc at 500°C for 1 h in sealed Pyrex tubes (method modified from Coleman et al. 1982). Zinc was obtained from J.M. Hayes, Departments of Chemistry and Geology, Indiana University. Hydrogen gas was analyzed for δD in the same manner as for $\delta^{13}\text{C}$ at SIRFER. Standard lab waters were calibrated against samples of the international standards GISP and V-SMOW and were used in linear corrections of raw values obtained from the mass spectrometer.

Correlation, linear regression, and t tests were used to evaluate leaf morphological variation within and between oak populations and the associations between plant ecophysiological characteristics, leaf morphology, and chemistry. All analyses were performed using the JMP statistical software for Macintosh (Version 3.1, SAS Institute Inc. 1995).

RESULTS

Data for leaf structural and chemical traits were pooled between the 2 hybrid populations to examine broad trends for these characteristics. Blade length, width, LMA, and N concentration within the 2 hybrid populations were highly intercorrelated (Table 1). As expected, blade length, width, and area were all positively correlated. LMA was negatively correlated to length, width, and area, indicat-

ing that larger leaves were also thinner and likely contained less mesophyll tissue per unit leaf surface area. Conversely, leaf N concentration was positively correlated to leaf size. Because LMA declined with leaf size and N concentration increased in these hybrid populations, leaf N content (mmol N m^{-2}) was constant over the range of leaf sizes (Table 1).

Leaf structural and chemical traits for plants in hybrid populations (HP1 and HP2) had values that spanned the range found in leaves from the 2 nonhybrid populations (Table 2). Leaves differed significantly between nonhybrid populations of *Q. gambelii* and *Q. turbinella* for all morphological traits and for leaf N concentration (Table 2). Larger leaves of *Q. gambelii* had lower LMA, higher N, but did not differ from leaves of *Q. turbinella* for leaf N content. Plants in the 2 hybrid populations, because of the high degree of trait variation, did not differ significantly from each other for any leaf morphological or chemical trait (Table 2).

Dependence of carbon isotope discrimination (Δ) on leaf structural and chemical traits and plant water relations traits in the 2 hybrid populations were evaluated by regression (Figs. 2, 3). Variation in Δ was related significantly to leaf N concentration and LMA, but not to leaf nitrogen content (Fig. 2). Δ ranged almost 4‰ within these hybrid populations, with plants resembling *Q. turbinella* (high LMA and low leaf N concentration) having the lowest Δ values (near 16‰), and plants with leaves resembling those of *Q. gambelii* (low LMA and high N concentration) having the highest Δ values of up to 20‰.

Several rain events that preceded our sampling provided necessary conditions to evaluate water source variation within hybrid populations. Ψ_{pd} and δD were highly variable

TABLE 1. Pearson correlation coefficients for leaf morpho-physiological traits within a *Quercus gambelii* \times *Q. turbinella* hybrid zone. Data for the correlations were from average per leaf values from each plant and are pooled from 2 hybrid populations near New Harmony, Utah. Correlation coefficients in italics are significant ($P < 0.05$) after sequential Bonferroni corrections for multiple comparisons (Rice 1989).

	Leaf length	Leaf width	Leaf area	LMA	N (%)
Leaf width	<i>0.98</i>				
Leaf area	<i>0.97</i>	<i>0.97</i>			
LMA	<i>-0.83</i>	<i>-0.81</i>	<i>-0.80</i>		
N (%)	<i>0.81</i>	<i>0.83</i>	<i>0.75</i>	<i>-0.77</i>	
N (mmol m^{-2})	<i>-0.29</i>	<i>-0.23</i>	<i>-0.32</i>	<i>0.52</i>	0.11

TABLE 2. Mean ($\pm s_{\bar{x}}$), range (min, max), and significance levels (t tests) of leaf structural and chemical traits for nonhybrid and hybrid populations of *Quercus turbinella* and *Q. gambelii* near New Harmony, Utah, in August 1994. Parameters and hybrid populations are as in Figure 2.

Leaf trait	Nonhybrid populations			Hybrid populations		
	<i>Q. turbinella</i>	<i>Q. gambelii</i>	t test	HP1	HP2	t test
Length (mm)	26.9 (1.6) (23.1, 31.9)	80.8 (3.1) (70.3, 83.5)	***	57.0 (8.1) (27.2, 103.5)	47.6 (6.2) (25.0, 88.7)	n.s.
Width (mm)	19.3 (0.7) (17.7, 22.0)	53.2 (1.6) (48.4, 58.6)	***	36.7 (5.8) (16.2, 66.1)	33.2 (4.5) (15.4, 58.8)	n.s.
Area (cm ²)	24.9 (8.2) (15.1, 36.1)	138.2 (24.4) (108.8, 173.4)	***	65.5 (18.9) (22.3, 215.1)	56.4 (17.0) (20.8, 172.3)	n.s.
LMA (g m ⁻²)	199 (4) (188, 210)	115 (2) (110, 123)	***	143 (9) (100, 185)	160 (7) (111, 206)	n.s.
N (%)	1.2 (0.1) (1.0, 1.3)	2.0 (0.1) (1.8, 2.1)	***	1.8 (0.1) (1.4, 2.3)	1.7 (0.1) (1.2, 1.9)	n.s.
N (mmol m ⁻²)	173 (9) (140, 189)	161 (7) (143, 175)	n.s.	174 (7) (123, 207)	189 (7) (145, 226)	n.s.

*** $p < 0.001$

within hybrid populations; Ψ_{pd} ranged from -1.5 to -0.2 MPa and δD ranged from -90% to -58% . Groundwater and integrated summer precipitation collected from a site in Zion National Park, approximately 50 km to the east of our hybrid population site and at a similar elevation, were 95% and 30%, respectively. Surprisingly, the regression of leaf Δ on plant δD or Ψ_{pd} was not significant when hybrid populations were analyzed separately or together (Fig. 3). Although these water relations traits were not correlated with Δ , Ψ_{pd} was strongly correlated with δD (Fig. 4). Ψ_{pd} declined as δD increased across the 2 hybrid populations.

Although leaf N concentration differed significantly between the 2 nonhybrid populations (Table 2), Δ did not (Table 3). Leaf carbon isotope discrimination, furthermore, was substantially higher in the pure *Q. turbinella* population than would be predicted from relationships found in hybrid populations (Fig. 2). Δ was high in the nonhybrid population of *Q. turbinella* even though Ψ_{pd} was low. δD values for individuals within the nonhybrid *Q. turbinella* population were higher than for *Q. gambelii*, but these were not significantly different (Table 3).

DISCUSSION

Reduced monsoonal activity over the recent Holocene may have contributed to the extinc-

tion of *Quercus turbinella* from northern Utah, but other climatic factors cannot be eliminated as possible causes. Although the present study was limited in scope, we found few differences among intermediate and parental phenotypes of *Q. gambelii* and *Q. turbinella* for summer precipitation use in hybrid populations in southwestern Utah. A few individuals that morphologically resembled *Q. turbinella* within the hybrid populations had δD values that were identical to that of winter precipitation, and these same individuals had high predawn water potentials. Presumably, these *Q. turbinella* phenotypes avoid drought through the summer because of their access to water stored in deep soil layers. However, more detailed isotopic and root profile studies would be needed to verify this hypothesis. If our water relations measurements represent general patterns for the entire growing season, then at least some *Quercus turbinella* phenotypes have the potential to persist and maintain high physiological activity despite limited access to summer rainfall. Hybrid populations that occurred in northern Utah some time in the past presumably had comparable levels and patterns of variation for these water relations traits. Consequently, loss of monsoonal storms from the region would not have resulted in complete extirpation of *Q. turbinella* or morphologically similar individuals of hybrid origin. Although our conclusions are based on only a single sampling event during 1 yr, both

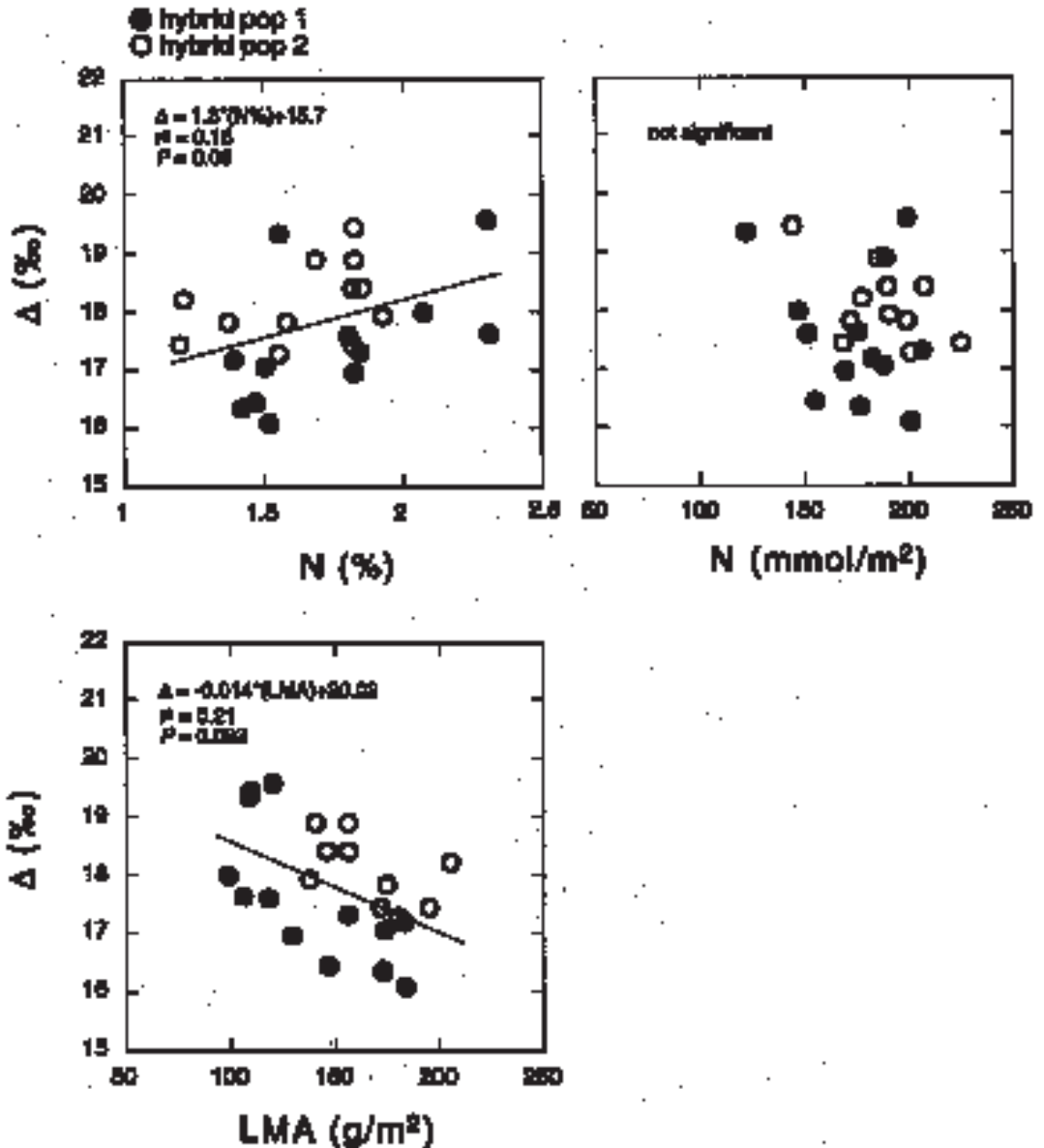


Fig. 2. Dependence of leaf carbon isotope discrimination (Δ) on leaf mass per unit area (LMA, g m⁻²), nitrogen concentration (% g⁻¹), and nitrogen content (mmol N m⁻²) for plants selected within hybrid populations (HP1 and HP2) near the town of New Harmony in southwestern Utah. Regressions were fit to the pooled data for the 2 populations.

hybrid populations in our study yielded similar results.

Based on biogeographic analysis and seedling stress studies, Neilson and Wullstein (1983, 1985) concluded that the northern limit of *Q. gambelii* in Utah is constrained by the summer monsoon gradient and the probability of late spring frost determined by the polar front gra-

dient. In addition to monsoon dynamics, the influence of freeze-thaw cycles may be exceptionally important in controlling the present northern limit of adult *Q. turbinella*. Hydraulic dysfunction caused by frost-induced xylem cavitation can be catastrophic for a diffuse-porous evergreen species (Sperry and Sullivan 1992, Sperry et al. 1994, Pockman and Sperry

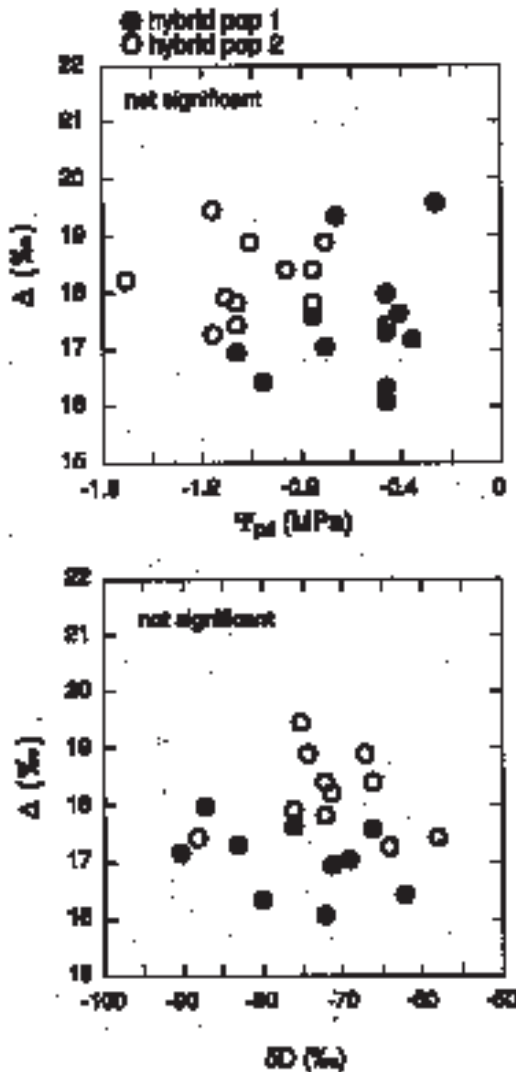


Fig. 3. Dependence of leaf carbon isotope discrimination (Δ) on plant predawn water potential (Ψ_{pd} , MPa) and xylem water isotopic composition (δD , ‰) for plants selected within hybrid populations (HP1 and HP2) near the town of New Harmony in southwestern Utah. Regressions were fit to the pooled data for the 2 populations.

1997). Apparently, the ring-porous *Quercus gambelii* will tolerate >90% loss of hydraulic conducting efficiency during winter and rely on new xylem production prior to leaf-out in spring to sustain high rates of transpiration (Sperry et al. 1994). Hybrid oak clones found in northern Utah are deciduous and potentially cope with freeze-thaw cycles in a manner similar to that in *Q. gambelii*. Neither the refilling of cavitated vessels with positive root

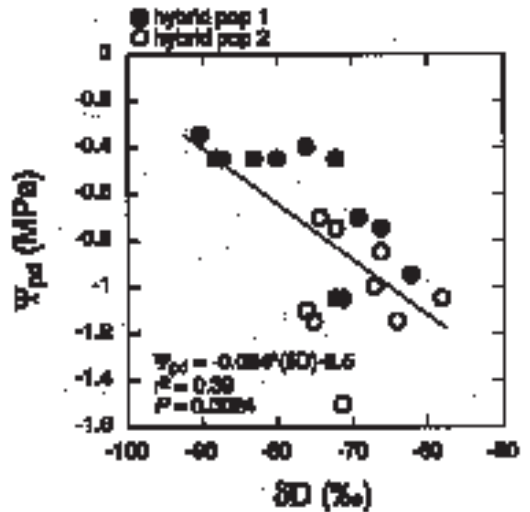


Fig. 4. Dependence of plant predawn water potential (Ψ_{pd}) on δD of xylem water for plants selected within hybrid populations (HP1 and HP2) near the town of New Harmony in southwestern Utah. Regressions were fit to the pooled data for the 2 populations.

pressure nor the ability to avoid freeze-thaw cavitation by having very small conducting elements seems like a plausible mechanism allowing the diffuse-porous and evergreen *Q. turbinella* to sustain significant hydraulic conducting efficiency in the cold climate presently characterizing northern Utah (Sperry et al. 1994). This diffuse-porous species likely experiences significant and nonreversible xylem dysfunction on an annual basis.

Carbon isotope discrimination in this study provides indirect evidence that hydraulic efficiency is reduced in *Q. turbinella* phenotypes in hybrid populations growing naturally near New Harmony in southwestern Utah and in an experimental garden at Salt Lake City studied by Ehleringer and Phillips (1996). Variation in Δ can be attributed directly to changes in stomatal conductance affecting c_i/c_a . Adjustments in stomatal conductance, furthermore, accompany changes in hydraulic conducting efficiency following hydraulic dysfunction in *Quercus* (Cochard et al. 1996). Low carbon isotope discrimination values measured in the common garden by Ehleringer and Phillips (1996) in northern Utah and at the northern limits of *Q. turbinella*'s range in the hybrid populations studied here may therefore reflect stomatal responses to reduced xylem conducting efficiency caused by frost. Notably, Δ in

TABLE 3. Mean leaf carbon isotope discrimination (Δ), δD of xylem water, and predawn water potential (Ψ_{pd}) for nonhybrid populations of *Quercus turbinella* and *Q. gambelii* near New Harmony, Utah, in August 1994. Data include $1 \pm s_{\bar{x}}$ (in parentheses) and significance levels from *t* tests (***, $P < 0.001$).

Plant trait	<i>Q. turbinella</i>	<i>Q. gambelii</i>	<i>t</i> test
Δ (‰)	18.0 (0.2)	18.2 (0.2)	n.s.
Ψ_{pd} (MPa)	-2.0 (0.1)	-0.4 (0.1)	***
δD (‰)	-82 (4)	-94 (6)	n.s.

the nonhybrid population of *Q. turbinella* at lower elevation and on a drier microsite south of New Harmony (18.0‰) was not different from that of *Q. gambelii* found in a common garden in northern Utah (18.8‰) or that of *Q. gambelii* in pure stands near New Harmony (18.0‰). Δ in *Q. turbinella* phenotypes was much reduced in the hybrid populations and in the common garden in Salt Lake City. It is likely that frost, in addition to reduced monsoonal activity, played a role in the loss of adult *Q. turbinella* from northern Utah, but the combination of these climatic effects on this migration requires further study.

Leaf nitrogen concentration was almost twice as high for *Q. gambelii* as it was for *Q. turbinella* in pure and hybrid populations. Bulk leaf N concentration often reflects concentrations of photosynthetic enzymes, pigments, and electron transport components in leaves and is positively correlated with maximum photosynthetic rate within and among species of C_3 plants (Evans 1989) and oaks (Reich et al. 1995). Plants morphologically similar to *Q. gambelii* in the hybrid populations maintained higher Δ (hence higher c_i/c_a) and leaf N concentration compared to *Q. turbinella* phenotypes. The positive relationship between Δ and N concentration in this study is opposite of what is expected if nitrogen forms a suitable proxy for photosynthetic capacity. Higher N (greater photosynthetic capacity) should cause c_i/c_a and Δ to decline, not rise. Furthermore, we found no correlation between Δ and nitrogen content per unit leaf area, and a negative relationship between Δ and LMA. Vitousek et al. (1990) observed similar correlations between leaf $\delta^{13}C$ and LMA for *Metrosideros polymorpha* across an elevational gradient in Hawaii, and attributed $\delta^{13}C$ variation to variation in leaf internal resistance.

High internal resistance reduces CO_2 concentration at sites of carboxylation in the chloroplast and potentially lessens discrimination against $^{13}CO_2$ (Evans et al. 1986). Although we found patterns of leaf carbon isotope variation and LMA in oak hybrid populations that were similar to that reported by Vitousek et al. (1990) for *Metrosideros*, we have no direct estimates of c_i/c_a from instantaneous gas exchange measurements to demonstrate conclusively the magnitude of internal resistance. In any event, some combination of high internal resistance and low c_i/c_a produced the relatively high discrimination values in *Q. turbinella* phenotypes in our study.

Carbon isotope discrimination in the oak hybrid populations was not related to water source (δD) or plant water potential (Ψ_{pd}) during our August sampling period. Tucker et al. (1961) noted that these oak populations apparently have undergone repeated hybridization and backcrossing. Hybridization and further recombination in these populations may have reduced the level of integration between traits that control rooting depth and leaf Δ . Leaf gas exchange traits and rooting patterns appear to be functionally integrated among parental and F1 hybrids in the artificially maintained common garden populations near Salt Lake City (Ehleringer and Phillips 1996), but these traits are not functionally integrated in natural hybrid populations in southwestern Utah. We found no correlation between either predawn water potential or δD and Δ within our hybrid populations (Fig. 3). Introgression of genes into populations of *Q. turbinella* that control development of a deep root system remains a possibility and would explain the high levels of variation in δD among *Q. turbinella* phenotypes in hybrid populations.

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LITERATURE CITED

- BETANCOURT, J.L., T.R. VAN DEVENDER, AND P.S. MARTIN. 1990. Packrat middens: the last 40,000 years of biotic change. University of Arizona Press, Tucson.

- COCHARD, H., N. BRÉDA, AND A. GRANIER. 1996. Whole tree hydraulic conductance and water loss regulation in *Quercus* during drought: evidence for stomatal control of embolism? *Annales des Sciences Forestières* 53:197–206.
- COLEMAN, M.L., T.J. SHEPARD, J.J. DURHAM, J.E. ROUSE, AND G.R. MOORE. 1982. Reduction of water with zinc for hydrogen isotope analysis. *Analytical Chemistry* 54:993–995.
- COTTAM, W.P., J.M. TUCKER, AND R. DROBNICK. 1959. Some clues to Great Basin postpluvial climates provided by oak distributions. *Ecology* 40:361–377.
- EHLERINGER, J.R., AND C.B. OSMOND. 1989. Stable isotopes. Pages 281–300 in R.W. Pearcy, J. Ehleringer, H.A. Mooney, and P.W. Rundel, editors, *Plant physiological ecology: field methods and instrumentation*. Chapman and Hall, London, UK.
- EHLERINGER, J.R., AND S.L. PHILLIPS. 1996. Ecophysiological factors contributing to the distributions of several *Quercus* species in the Intermountain West. *Annales des Sciences Forestières* 53:291–302.
- EHLERINGER, J.R., S.L. PHILLIPS, W.S.F. SCHUSTER, AND D.R. SANDQUIST. 1991. Differential utilization of summer rains by desert plants. *Oecologia* 88:430–434.
- EHLERINGER, J.R., AND M.P. SMEDLY. 1988. Stomatal sensitivity and water-use efficiency in oaks and their hybrids. Pages 98–102 in A. Wallace, E.D. McArthur, and M.R. Haferkamp, editors, *Symposium on shrub ecophysiology and biotechnology*. USDA Forest Service, Technical Report INT-256, Ogden, UT.
- EVANS, J.R. 1989. Photosynthesis and nitrogen relationships in leaves of C₃ plants. *Oecologia* 78: 9–19.
- EVANS, J.R., T.D. SHARKEY, J.A. BERRY, AND G.D. FARQUHAR. 1986. Carbon isotope discrimination measured concurrently with gas exchange to investigate CO₂ diffusion in leaves of higher plants. *Australian Journal of Plant Physiology* 13:281–292.
- FARQUHAR, G.D., J.R. EHLERINGER, AND K.T. HUBICK. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* 40:503–537.
- FLANAGAN, L.B., J.R. EHLERINGER, AND J.D. MARSHALL. 1992. Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland. *Plant, Cell and Environment* 15:831–836.
- KNAPP, A.K., AND J.T. FAHNESTOCK. 1990. Influence of plant size on the carbon and water relations of *Cucurbita foetidissima* HBK. *Functional Ecology* 4:789–797.
- LITTLE, E.L., JR. 1971. *Atlas of United States trees*. Volume 1. Conifers and important hardwoods. U.S. Department of Agriculture, Miscellaneous Publication 1146. Washington, DC.
- MEINZER, F.C., P.W. RUNDEL, G. GOLDSTEIN, AND M.R. SHARIFI. 1992. Carbon isotope composition in relation to leaf gas exchange and environmental conditions in Hawaiian *Metrosideros polymorpha* populations. *Oecologia* 91:305–311.
- MILLER, R.F., AND P.E. WIGAND. 1994. Holocene changes in semiarid pinyon-juniper woodlands. *BioScience* 44:465–474.
- NEILSON, R.P., AND L.H. WULLSTEIN. 1983. Biogeography of two southwest American oaks in relation to atmospheric dynamics. *Journal of Biogeography* 10:275–297.
- _____. 1985. Comparative drought physiology and biogeography of *Quercus gambelii* and *Quercus turbinella*. *American Midland Naturalist* 114:259–271.
- PHILLIPS, S.L., AND J.R. EHLERINGER. 1994. Limited uptake of summer precipitation by bigtooth maple (*Acer grandidentatum* Nutt) and Gambel's oak (*Quercus gambelii* Nutt). *Trees* 9:214–219.
- POCKMAN, W.T., AND J.S. SPERRY. 1997. Freezing-induced xylem cavitation and the northern limit of *Larrea tridentata*. *Oecologia* 109:19–27.
- REICH, P.B., B.D. KLOEPEL, D.S. ELLSWORTH, AND M.B. WALTERS. 1995. Different photosynthesis nitrogen relations in deciduous hardwood and evergreen coniferous tree species. *Oecologia* 104:24–30.
- RICE, W.R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- SAS INSTITUTE, INC. 1995. *JMP user's guide*, version 3.1. JMP. SAS Institute, Inc., Cary, NC.
- SPARKS, J.P., AND J.R. EHLERINGER. 1997. Leaf carbon isotope discrimination and nitrogen content of riparian trees along an elevational gradient. *Oecologia* 109: 362–367.
- SPAULDING, W.G., AND L.J. GRAUMLICH. 1986. The last pluvial climatic episodes in the deserts of southwestern North America. *Nature* 320:441–444.
- SPERRY, J.S., AND E.M. SULLIVAN. 1992. Xylem embolism in response to freeze-thaw cycles and water stress in ring-porous, diffuse porous, and conifer species. *Plant Physiology* 100:605–613.
- SPERRY, J.S., K.L. NICHOLS, J.E.M. SULLIVAN, AND S.E. EASTLICK. 1994. Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. *Ecology* 75:1736–1752.
- TUCKER, J.M., W.P. COTTAM, AND R. DROBNICK. 1961. Studies in the *Quercus undulata* complex. II. The contribution of *Quercus turbinella*. *American Journal of Botany* 48:329–339.
- VAN DEVENDER, T.R., AND W.G. SPAULDING. 1979. Development of vegetation and climate in the southwestern United States. *Science* 204:701–710.
- VITOUSEK, P.M., C.B. FIELD, AND P.A. MATSON. 1990. Variation in foliar δ¹³C in Hawaiian *Metrosideros polymorpha*: a case of internal resistance. *Oecologia* 84: 362–370.
- WILLIAMS, D.G., AND J.R. EHLERINGER. 1996. Carbon isotope discrimination in three semi-arid woodland species along a monsoon gradient. *Oecologia* 106: 455–460.

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