

## Ecophysiological factors contributing to the distributions of several *Quercus* species in the intermountain west

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**Summary** — Aspects of the water relations of three oak species (*Quercus gambelii*, *Q. turbinella* and *Q. macrocarpa*) and their hybrids (*Q. gambelii* x *Q. turbinella*, *Q. gambelii* x *Q. macrocarpa*) were observed under common garden conditions in northern Utah, USA. In the absence of summer moisture inputs, *Q. macrocarpa* and *Q. turbinella* were unable to maintain active gas exchange through the day; following an early morning peak, leaf conductances to water vapor remained very low through the remainder of the day. In contrast, *Q. gambelii* and the hybrids were able to maintain high leaf conductances throughout this period. Consistent with these observations, *Q. gambelii* is thought to have a root system penetrating to the deeper, winter-recharged layers, a feature apparently absent in both *Q. macrocarpa* or *Q. turbinella*. Based on current hybrid distributions, both *Q. turbinella* and *Q. macrocarpa* once extended into drier more northerly regions than they occupy at present. When these parents retreated, they left behind hybrids with *Q. gambelii*, which do not depend on monsoonal moisture input. Leaf size, leaf longevity, carbon isotope ratio, and minimum winter temperatures appear not to be correlated with the absence of *Q. macrocarpa* and *Q. turbinella* from summer-dry habitats. Instead it appears that reliance on summer monsoon events is one of the critical factors influencing loss of these oaks from summer-dry sites in the intermountain west.

**leaf conductance / monsoon / carbon isotope ratio / oak / *Quercus***

**Résumé** — Facteurs écophysologiques contribuant à la distribution de différentes espèces de chênes dans l'Ouest américain. Les caractéristiques hydriques de trois espèces de chênes (*Quercus gambelii*, *Q. turbinella* et *Q. macrocarpa*) et de leurs hybrides (*Q. gambelii* x *Q. turbinella*, *Q. gambelii* x *Q. macrocarpa*) ont été analysées sur des arbres en plantations comparatives dans le nord de l'Utah (États-Unis). En l'absence d'irrigation pendant les mois d'été, *Q. turbinella* et *Q. macrocarpa* étaient incapables de maintenir des échanges gazeux actifs en cours de journée ; après un pic matinal, la conductance stomatique restait très faible pendant le reste du temps. En revanche, *Q. gambelii* et les hybrides ont maintenu des conductances stomatiques élevées pendant toute cette période. Ces observations sont à mettre en relation avec la présence sur les individus de *Q. gambelii* d'un système racinaire capable d'atteindre les couches du sol plus profondes et rechargées en humidité en cours de l'hi-

ver, alors que ni *Q turbinella* ni *Q macrocarpa* ne présentent cette caractéristique. En se basant sur la distribution actuelle des deux hybrides, on peut supposer que *Q turbinella* et *Q macrocarpa* occupaient autrefois des régions plus septentrionales et plus sèches que leur aire actuelle. Lors du retrait des deux espèces parentes, les hybrides avec l'espèce *Q turbinella*, qui dépend moins des pluies estivales, sont restés en place. La dimension et la longévité des feuilles, le rapport de composition isotopique du carbone, et les températures hivernales minimales ne sont pas corrélés avec l'absence de *Q macrocarpa* et de *Q turbinella* des habitats à sécheresse estivale. En revanche, la dépendance aux pluies estivales semble être le facteur critique contribuant à la disparition progressive de ces espèces des sites à sécheresse estivale de la zone des plateaux de l'ouest américain.

**conductance stomatique / pluies estivales / composition isotopique en carbone / chêne / sécheresse**

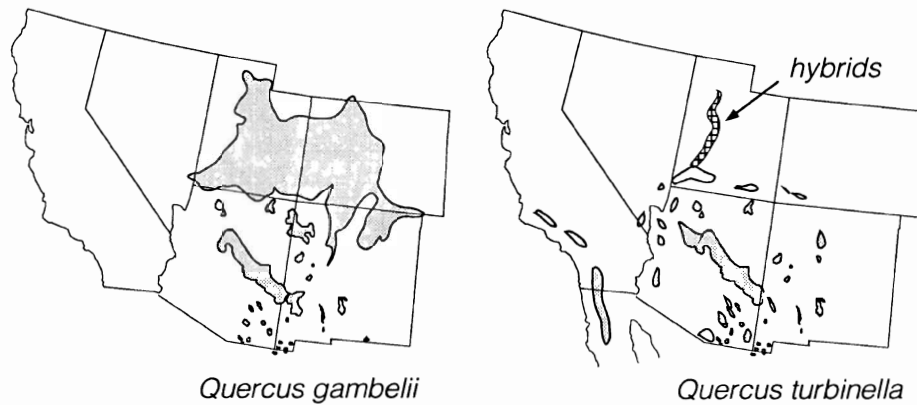
## INTRODUCTION

Oak distributions have been influenced by numerous abiotic and biotic factors over the millenia. Since the last glacial–interglacial cycle, there is substantial evidence from pollen analyses of lake sediments indicating significant oak migrations in eastern portions of North America. In the Rocky Mountain and intermountain west portions of the western United States, pack rat midden records have recorded the migration of oaks and other woody species (Betancourt et al, 1990; Cole, 1990). While general aspects of the factors contributing to a species' migration may be derived from either pollen or midden analyses, specifics on the environmental factor(s) influencing the capacity of a species to invade or persist in a specific habitat may be more elusive.

Relictual natural hybrids of oak species may provide some insight for elucidating why one particular oak has migrated away from a geographic region that once was occupied by two or more oak species. In the western United States, numerous relict oak hybrid populations have been described, where one of the parents has retreated some 200–500 km from its original location. Such is the case for naturally occurring hybrids involving 1) *Quercus gambelii* and *Q turbinella*, and 2) *Q gambelii* and *Q macrocarpa*. Drobnik (1958) described *Q gambelii* x *turbinella* hybrids occurring at the lower

elevation limits of *Q gambelii* all along the western range of *Q gambelii* (fig 1). Cottam et al (1959) noted that these hybrids had arisen since post-glacial periods and thought that these hybrids represented long-lived remnants from former periods when the two species had overlapping distributions, perhaps as long as several thousands of years ago. Since Drobnik's original observations, hybrids between these two oaks have been collected from additional locations in central Utah, but there have been no firm age estimates for any of these hybrid clones.

The two most common oak species in the Rocky Mountain and intermountain west portions of the western United States are *Q gambelii* and *Q turbinella*. While there is species overlap and frequent hybridization at the southern portions of the distribution of *Q gambelii*, the occurrence of long-lived hybrids between *Q gambelii* and *Q turbinella* 300 km north of the northernmost *Q turbinella* is unusual and has been the focus of paleoecological interest (Drobnik, 1958). Cottam et al (1959) proposed that cold winter temperatures were the primary factor restricting the distribution of *Q turbinella* to the southerly latitudes and that these hybrids were remnants of a warmer postpluvial climate. While not focusing specifically on the remnant oak hybrids, Neilson and Wullstein (1983) concluded that a combination of spring freezes and summer moisture stress restricted the northerly distributions of both *Q gambelii* and



**Fig 1.** Distribution of *Q. gambelii*, *Q. turbinella*, and natural hybrids. Based on information in Drobnik (1958) and Miller and Lamb (1985).

*Q. turbinella*. In related studies, Neilson and Wullstein (1985, 1986) showed that both oak species exhibited nearly identical water relations and drought tolerance characteristics and the oak seedling establishment occurred only in the southern locations where summer rains were frequent.

A third oak species, common to habitats with abundant summer precipitation, has also left behind hybrids, possibly also indicative of a previous wetter climate. *Q. macrocarpa* is common throughout the eastern portions of the Great Plains of North America. However, remnant hybrid populations of *Q. gambelii*  $\times$  *macrocarpa* occur in eastern parts of both New Mexico and Wyoming, at or beyond the driest portions of the current western limits of *Q. macrocarpa*'s distribution (Tucker and Maze, 1966; Maze, 1968).

The focus of this paper is to examine aspects of the water relations of these three oak species native to the intermountain west and of their hybrids under common growth environments in order to evaluate characteristics that might have been important in restricting the distribution of one parent and yet allowing the hybrids to persist as one of the parents retreated from its former distribution.

### **Q GAMBELII, Q TURBINELLA, Q MACROCARPA, AND HYBRID DISTRIBUTIONS**

*Q. gambelii* is widely distributed through the Rocky Mountain region of North America from northern Utah and Colorado in the north to southern Arizona and New Mexico in the south (fig 1). It is a dwarf tree, ranging in height from 2 to 10 m. Ecologically, in its northern distribution range this species occupies the scrub-brush zone between the lower boundary of the white fir forest and the upper limits of the sagebrush steppe, while in the south its distribution is between the juniper woodland and pine forest communities. Nielsen and Wullstein (1983, 1985) characterized the biogeographic factors limiting the distribution of *Q. gambelii*; they concluded that cold winter temperatures and spring freezes determined the northern distribution limits of this species and that summer water stress was a contributing factor limiting this oak's distribution.

*Q. turbinella* has narrower and more southerly distribution compared to *Q. gambelii* (fig 1). This oak is also a scrub oak, ranging in height from 2 to 5 m. Ecologically, its distribution is very similar to that of *Q.*

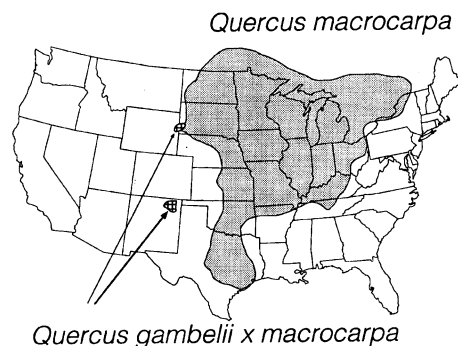
*gambelii*, being a dominant component of the transition between arid zone scrub and coniferous woodland. *Q turbinella* tends to grow in habitats with lower overall precipitation amounts than *Q gambelii*. Hybrids commonly occur where the distributions overlap in southern Utah and northern Arizona. Nielsen and Wullstein (1983, 1985) concluded that both cold winter temperatures and the northern extent of the Arizona summer monsoon limited the northern distribution of *Q turbinella*.

*Q macrocarpa* is widely distributed throughout the central states region of the United States and on into southern Canada (fig 2). This oak is common along riparian regions and forms a tree that reaches a maximum height of 7 to 10 m. Its distribution is bounded on the east by the eastern deciduous forest and on the west by the semi-arid grasslands of the Great Plains.

## MATERIALS AND METHODS

### Study site

Measurements were collected on parents and F<sub>1</sub> hybrids of oaks established in the Cottam Oak



**Fig 2.** Distribution of *Q gambelii*, *Q macrocarpa*, and natural hybrids. Based on information in Tucker and Maze (1966), Maze (1968), and Miller and Lamb (1985).

Grove at the University of Utah (lat 40°46', long 110°50', 1 515 m). Soil at the site is alluvial and occurs to a depth of 2–3 m. *Q gambelii*, *Q macrocarpa*, and *Q turbinella* were planted into the Cottam Oak Grove in the mid-1960s (Cottam et al, 1982). Hybrids were produced by hand pollination and acorns planted into the same experimental garden. All plants had been irrigated to get them established, but then watered sparingly in later years.

During the two summers of our investigations (1985 and 1994), these trees received very limited summer precipitation and no irrigation because of irrigation-system failures; 1993 was a wetter and cooler year throughout the growing season. Oaks were also sampled at the Shields Grove Arboretum of the University of California at Davis (lat 38°33'N, long 121°44'W, 15 m elev), where Cottam and colleagues had also planted parents and hybrids from the same crosses (Tucker and Bogert, 1973; Cottam et al, 1982).

### Leaf conductance and transpiration

Leaf conductance and transpiration rates were measured with a steady state porometer (model 1600, Licor Instr, Lincoln, NE, USA). Each value represents the mean of five individual leaves measured on a single tree. The data presented represent the means of three trees.

### Leaf water potential

Predawn water potentials were measured on cut twigs of oak parents and hybrids using a pressure chamber (PMS Instr, Corvallis, OR, USA).

### Isotope ratio analyses

For carbon isotope ratios ( $\delta^{13}\text{C}$ ), five sunlit leaves per tree were collected, combined to form a single sample, oven-dried and finely ground. These samples were prepared, combusted, and analyzed using an isotope ratio mass spectrometer (model delta S, Finnigan MAT, San Jose, CA, USA) following procedures outlined in Ehleringer (1991). Leaf carbon isotope ratios ( $\delta^{13}\text{C}$ ) are expressed relative to the PDB standard; the over-

all analysis precision was  $\pm 0.11\%$ . Water source utilization was estimated by measuring the hydrogen isotope ratio of water in the xylem sap (Ehleringer and Dawson, 1992). A single suberized stem from each tree was collected and water from this stem was extracted cryogenically under vacuum (Dawson and Ehleringer, 1993). For hydrogen isotope ratios ( $\delta D$ ) of xylem sap, water was converted to diatomic hydrogen using a zinc-mediated reaction (Coleman et al., 1982). Analyses were then made using the same mass spectrometer as above with an overall analysis precision for hydrogen of  $\pm 1\%$  and are expressed relative to the SMOW standard.

## RESULTS

Parents and their  $F_1$  hybrids growing in the experimental garden were first compared for differences in leaf size (table I). While this morphological parameter has been used historically as a reliable means of distinguishing among parents and hybrids, its significance may be of adaptive value and influence plant distribution if leaf boundary layer considerations are important in influencing water relations, leaf temperature, or other aspects of leaf metabolism and if the character has limited variability. The deciduous-leaved *Q gambelii* leaves were significantly larger than those of either the evergreen-leaved *Q turbinella* or the tardily deciduous *Q gambelii* x *turbinella* hybrids. Such leaf size differences would contribute to a larger boundary layer in both *Q gambelii* and the hybrids, possibly a disadvantage for plants if transpirational evaporative cooling was not possible to help reduce leaf temperatures. Yet, countering this is that it is the smaller-leaved *Q turbinella* which is the species now absent from this summer-dry northern habitat; the larger-leaved *Q gambelii* and hybrids persisted in the north even though summer rain is very limited. Differences in leaf size were maintained throughout the growing season, despite the observation that the leaf size of the second flush of *Q gambelii* leaves was reduced by

41%. Leaf mass-to-area ratios showed differences similar to the leaf size data (table I). The evergreen-leaved *Q turbinella* had thicker leaves than the deciduous-leaved *Q gambelii* and the hybrids were consistently intermediate. Leaves of parents and hybrids tended to become thicker as the season progressed.

Similar significant differences in leaf size and leaf mass-to-area ratios were also observed between *Q gambelii*, *Q macrocarpa*, and their hybrids (table I). *Q gambelii* x *macrocarpa* hybrid leaf sizes and leaf mass-to-area ratios were similar to *Q gambelii* early in the growing season and to *Q macrocarpa* later in the season. In this comparison, the larger-leaved species (*Q macrocarpa*) would be expected to have higher leaf boundary layer (contributing to a higher leaf temperature) and this is the species that occurs in habitats with summer rains to relieve possible moisture stress. These more traditional approaches provided limited insight into the factors which might be contributing to distribution differences between parents and the hybrids, even though comparisons were made under uniform environmental conditions.

Based on the previous suggestion by Nielsen and Wullstein (1983, 1985) that summer rain was critical to *Q turbinella*, we hypothesized that *Q turbinella*, which is absent from the northern habitats, should be more water stressed during the summer in the experimental garden than either *Q gambelii* or the hybrids. Under uniform soil conditions on nonirrigated plants in the experimental garden, we evaluated water stress in parents and their hybrids. Counter to our initial expectations, midday leaf water potentials during dry summers were more positive in *Q turbinella* than in *Q gambelii* (fig 3) in 1985 and again in 1993 (data not shown). However, predawn leaf water potentials in both summers were more positive in *Q gambelii* than in *Q turbinella*, suggesting that differences in midday water

**Table 1.** Leaf area and leaf mass-to-area ratios of *Q gambelii*, *Q macrocarpa*, *Q turbinella*, and their hybrids from mature plants growing in the Cottam Oak Grove at the University of Utah.

	June 4	August 1	September 11
Leaf area (cm <sup>2</sup> )			
<i>Q gambelii</i>	34.3 <sup>a</sup>	28.5 <sup>a</sup>	20.2 <sup>a</sup>
<i>Q gambelii</i> x <i>turbinella</i>	9.3 <sup>b</sup>	9.7 <sup>b</sup>	9.4 <sup>b</sup>
<i>Q turbinella</i>	2.6 <sup>c</sup>	3.1 <sup>c</sup>	3.3 <sup>c</sup>
<i>Q gambelii</i>			
<i>Q gambelii</i>	34.3 <sup>a</sup>	28.5 <sup>a</sup>	20.2 <sup>a</sup>
<i>Q gambelii</i> x <i>macrocarpa</i>	35.5 <sup>a</sup>	36.7 <sup>d</sup>	44.4 <sup>d</sup>
<i>Q macrocarpa</i> x <i>gambelii</i>	43.6 <sup>d</sup>	44.5 <sup>d</sup>	51.2 <sup>e</sup>
<i>Q macrocarpa</i>	50.4 <sup>e</sup>	60.7 <sup>e</sup>	52.4 <sup>e</sup>
Leaf mass-to-area ratio (g m <sup>-2</sup> )			
<i>Q gambelii</i>	101 <sup>a</sup>	127 <sup>a</sup>	144 <sup>a</sup>
<i>Q gambelii</i> x <i>turbinella</i>	133 <sup>b</sup>	168 <sup>b</sup>	173 <sup>b</sup>
<i>Q turbinella</i>	151 <sup>c</sup>	185 <sup>c</sup>	209 <sup>c</sup>
<i>Q gambelii</i>			
<i>Q gambelii</i>	101 <sup>a</sup>	127 <sup>a</sup>	144 <sup>a</sup>
<i>Q gambelii</i> x <i>macrocarpa</i>	96 <sup>a</sup>	144 <sup>a</sup>	149 <sup>a</sup>
<i>Q macrocarpa</i> x <i>gambelii</i>	91 <sup>a</sup>	138 <sup>a</sup>	132 <sup>a</sup>
<i>Q macrocarpa</i>	73 <sup>d</sup>	156 <sup>b</sup>	164 <sup>b</sup>

Data are means and different letters indicate a statistical difference ( $P < 0.05$ ) among values within a column.

potentials could have been the result of stomatal closure. That is, stomatal closure in *Q turbinella* could have resulted in higher midday water potentials than in *Q gambelii* and *Q gambelii* x *turbinella*, which may have continued to transpire and maintain steeper water potential gradients between soil and leaf tissues.

Diurnal leaf conductance measurements on *Q gambelii*, *Q turbinella*, and the hybrids revealed that *Q gambelii* and *Q gambelii* x *turbinella* maintained substantially higher rates of gas exchange through the day than did leaves of *Q turbinella* (fig 4). Gas exchange in *Q gambelii* and *Q gambelii* x *turbinella* leaves reached peak values shortly before midday and then declined as temperatures increased through the day. Leaf conductance in both *Q gambelii* and *Q gambelii* x *turbinella* was significantly correlated with vapor pressure deficit (*Q gam-*

*belii*:  $r = -0.881$ ,  $P < 0.01$ , *Q gambelii* x *turbinella*:  $r = -0.688$ ,  $P < 0.02$ ). On the other hand, following a peak value shortly after sunrise, leaf conductances in *Q turbinella* remained low throughout the day; however, these conductance values were still related to vapor pressure deficit ( $r = -0.529$ ,  $P < 0.07$ ).

Similar to *Q turbinella*, *Q macrocarpa* naturally occurs in habitats with frequent summer precipitation. On a separate date, the diurnal courses of leaf water potential and leaf conductance were also measured in *Q gambelii*, *Q macrocarpa* and *Q gambelii* x *macrocarpa* to determine if the absence of summer moisture inputs would result in suppressed gas exchange and "apparently reduced" water stress patterns similar to that observed for *Q turbinella* and its hybrids. Predawn leaf water potentials in *Q gambelii*, *Q macrocarpa* and *Q gam-*

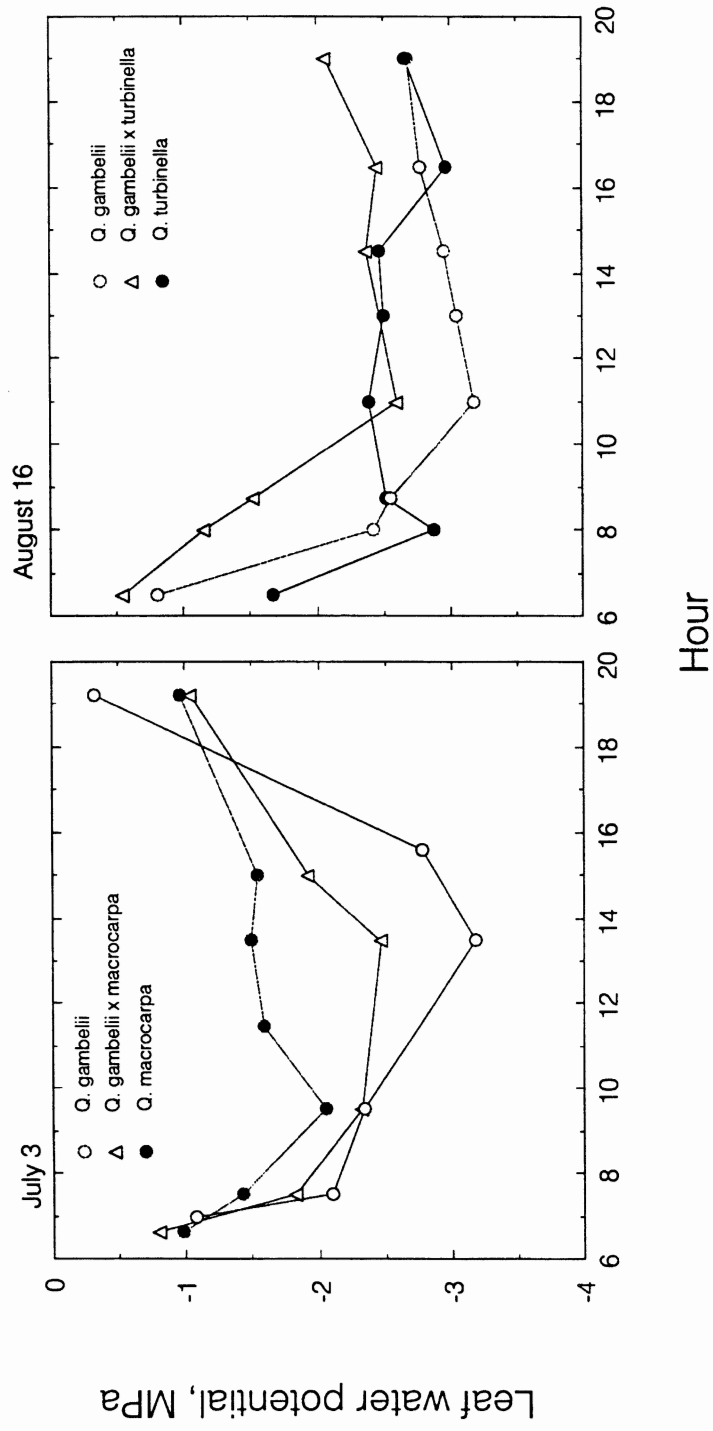


Fig 3. The diurnal course of leaf water potentials for mature plants of oak parents and their hybrids growing in the Cottam Oak Grove at the University of Utah. Left: *Q. gambelii* (○), *Q. macrocarpa* (●), and *F<sub>1</sub>* hybrids (△). Individual data are means of three observations. Right: *Q. gambelii* (○), *Q. turbinella* (●), and *F<sub>1</sub>* hybrids (△).

*belii* x *macrocarpa* were approximately the same, but midday values were substantially more positive in *Q macrocarpa* than in either *Q gambelii* or *Q gambelii* x *macrocarpa* in 1985 (fig 3) and again for both parents in 1993 (data not shown). The suppressed diurnal courses of leaf gas exchange provided an explanation for the apparent midday reduction of water stress in *Q macrocarpa*. Higher rates of gas exchange occurred in *Q gambelii* and *Q gambelii* x *macrocarpa* than in *Q macrocarpa*, which had very much reduced leaf conductances after attaining peak values in the early morning (fig 4). Leaf conductances in all three were significantly correlated with leaf vapor pressure deficits: *Q gambelii* ( $r = -0.903$ ,  $P < 0.01$ ), *Q macrocarpa* ( $r = -0.873$ ,  $P < 0.01$ ), and *Q gambelii* x *macrocarpa* ( $r = -0.883$ ,  $P < 0.01$ ).

Together these gas exchange data indicated that both species native to habitats with summer precipitation were not able to maintain gas exchange through the day in the experimental garden, which had received no precipitation inputs since the late spring. In contrast, the native species, *Q gambelii*, and the *Q gambelii* hybrids were able to maintain higher rates of gas exchange during this summer drought period. These data are consistent with the idea that *Q macrocarpa* and *Q turbinella* were more shallow rooted than *Q gambelii* and that the  $F_1$  hybrids had rooting distributions similar to that of the *Q gambelii* parent.

To evaluate the possibility that oaks might be utilizing moisture from different soil depths during the summer months, water potentials and water sources of *Q gambelii*, *Q turbinella*, and hybrids growing in the Cotnam garden were examined approximately 1 week following a summer rain event in late summer 1994. Predawn water potentials in *Q gambelii* were lower than in either *Q turbinella* ( $-1.06$  MPa vs  $-0.80$  MPa,  $P < 0.10$ ) or *Q gambelii* x *turbinella* ( $-1.06$  MPa vs

$-0.74$  MPa,  $P < 0.04$ ). However, the *Q turbinella* and *Q gambelii* x *turbinella* shrubs did not differ in their predawn water potentials ( $-0.80$  MPa vs  $-0.74$  MPa,  $P = 0.36$ ). At midday, leaf water potentials in *Q gambelii* ( $-3.03$  MPa) were still more negative than in *Q turbinella* ( $-2.72$  MPa) at the  $P = 0.06$  level.

Consistent with this pattern, the hydrogen isotope ratios ( $\delta D$ ) of xylem sap in these oaks showed a tendency for *Q gambelii* (mean value of  $-130.1\%$ , range of  $-128$  to  $131\%$ ) to be using a more deuterium-depleted water source than *Q turbinella* (mean value of  $-123.5\%$ , range of  $-94$  to  $-130\%$ ); however, this difference was only significant at the  $P = 0.14$  level because of greater variability in the responses of different *Q turbinella* shrubs. Although  $\delta D$  values of soil moisture throughout the soil profile were not measured to correlate with xylem sap values, we would expect that the surface soil layers would have a more positive  $\delta D$  value than deeper soil layers, because of evaporative enrichment and because summer precipitation has more positive  $\delta D$  values than the winter precipitation that charges the deeper soil layers (Phillips and Ehleringer, 1995).

Leaf carbon isotope ratio data were consistent with a pattern of functional rooting-depth differences among taxa. The spring and summer of 1993 were among the wettest and coolest periods in recent history. Precipitation was well above long-term averages at the Utah experimental garden. Leaf carbon isotope ratios measured on leaf materials produced that year averaged near  $-27\%$  and no significant differences were detectable among parental and hybrid materials (table II). When these leaf carbon isotope ratio values were compared to values from parental and hybrid materials growing in an irrigated experimental garden at the University of California at Davis, there were no significant differences among taxa or between sites (table II). These results con-



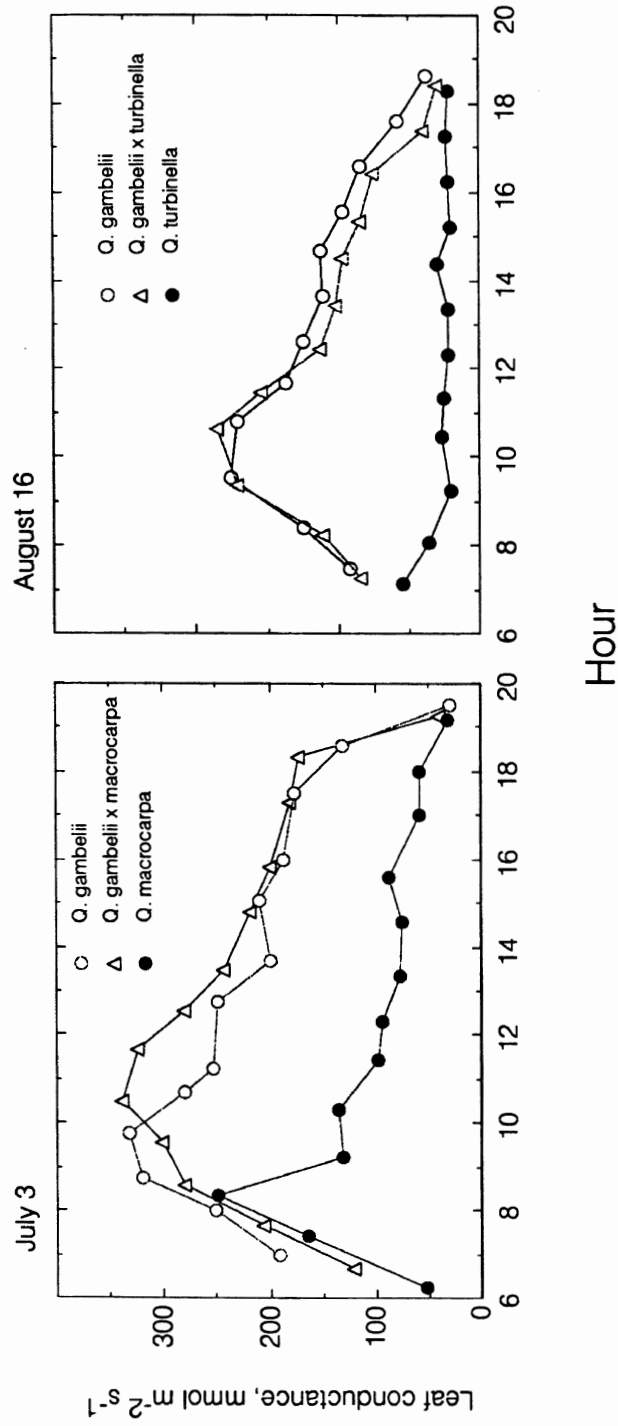


Fig 4. The diurnal course of leaf conductance to water vapor for mature plants of oak parents and their hybrids growing in the Cottam Oak Grove at the University of Utah. Left: *Q. gambelii* (○), *Q. macrocarpa* (●), and F<sub>1</sub> hybrids (△). Right: *Q. gambelii* (○), *Q. turbinella* (●), and F<sub>1</sub> hybrids (△). Individual data are means of four observations.

**Table II.** Leaf carbon isotope ratios ( $\delta^{13}\text{C}$ ) of *Q gambelii*, *Q macrocarpa*, *Q turbinella*, and their hybrids from mature plants growing in the Cottam Oak Grove at the University of Utah and at the Shields Grove Arboretum of the University of California at Davis during August 1993.

	Utah	California
<i>Q gambelii</i>	-27.3	-27.2
<i>Q gambelii</i> x <i>turbinella</i>	-26.7	
<i>Q turbinella</i>	-27.5	-27.8
<i>Q gambelii</i>	-27.3	-27.2
<i>Q gambelii</i> x <i>macrocarpa</i>	-27.5	-27.4
<i>Q macrocarpa</i> x <i>gambelii</i>	-27.1	
<i>Q macrocarpa</i>	-27.3	-28.2

Plants at the Utah garden were not irrigated, but spring and summer rains were well above average. Plants at the California garden were occasionally irrigated. Data are means; none of the values within a column or between rows are statistically different ( $P < 0.05$ ).

trast with previous observations by Ehleringer and Smedley (1989), indicating that leaf carbon isotope ratios were more positive in *Q macrocarpa* and *Q turbinella* than in *Q gambelii*. Yet leaf carbon isotope ratios for *Q gambelii* in that study were similar to those reported here. However, those earlier data were collected from plant materials that had been growing under nonirrigated conditions through a dry winter and dry summer in the same experimental garden. Leaf carbon isotope ratios represent an integrated long-term estimate of the ratio of intercellular to ambient  $\text{CO}_2$  concentrations and are known to be more positive for plants experiencing water stress (Farquhar et al, 1989). Thus, water stress effects on leaf carbon isotope ratios manifested in a previous study which had the typical summer drought period (1985) were absent when taxa experienced limited water stress (1993).

## DISCUSSION

Previous studies have concluded that the *Q gambelii* x *turbinella* and *Q gambelii* x *macrocarpa* hybrids represent relicts from previous wetter periods (Maze, 1968; Nielsen and Wullstein, 1983). Both winter-spring temperatures (Cottam et al, 1959; Nielsen and Wullstein, 1983) and summer drought (Nielsen and Wullstein, 1983) have been suggested as the factors pushing the northern boundary of *Q turbinella* southward. However, *Q turbinella* has been established in the Cottam Oak Grove at the University of Utah for approximately 30 years, and during that interval some of the lowest winter and spring air temperatures of the previous 150 years have been recorded (US Weather Bureau records). While cold temperatures may be an important factor limiting *Q turbinella*'s northern distribution, it is likely that this factor is less critical than previously suspected.

The persistence of *Q gambelii* x *turbinella* hybrids may be due to an increased capacity of these hybrids to utilize winter-derived moisture available in the deeper soil layers when soil moisture is absent from the surface layers. A clear differential utilization of surface versus deep soil moisture sources has been shown for Gambel's oak. Phillips and Ehleringer (1995) found that *Q gambelii* in northern Utah utilized only moisture from deeper soil depths arising from winter recharge events. Mature plants did not use moisture from the upper soil layers following summer rain events. Our results are consistent with that pattern. In a parallel study using Mediterranean oaks, Valentini et al (1992) showed that the drought-deciduous *Q cerris* and *Q pubescens* used moisture from deeper depths. Again, these species did not respond to and use summer moisture input, whereas the evergreen-leaved *Q ilex* utilized summer moisture. Our gas-exchange results indicate that *Q turbinella* lacks the deep rooting capacity which would

permit this species to remain active through a summer drought. The *Q gambelii* x *turbinella* hybrids are either intermediate in this rooting character or possess deeper root systems similar to *Q gambelii*. Since *Q gambelii* and *Q turbinella* exhibit nearly identical intrinsic water relations and drought-tolerance characteristics (Nielsen and Wullstein, 1985), the absence of summer rain on a predictable basis would then lead to the loss of *Q turbinella* from the northern habitats if they are not able to maintain summer gas-exchange activity on a regular basis.

When did adequate amounts of summer precipitation on a predictable basis disappear from the northern habitats now occupied only by *Q gambelii* and *Q gambelii* x *turbinella*? Pack rat midden data indicate that central and northern Utah had an extensive summer-precipitation climate following glacial retreat several thousand years ago, but the onset of regional summer drought is less clear from these records. There is evidence indicating pronounced shifts in climate over the past several hundred years – shifts in both the amount and timing of precipitation events. Stine (1994) observed that several extended droughts of more than 100 years occurred in the western United States earlier in this millennia. Feng and Epstein (1994) reported a shift in the hydrogen isotope ratios of bristlecone pine tree rings several hundred years ago, which is consistent with a reduction in summer precipitation in the Sierra Nevada Range. Coltrain (1994) reported that corn, once common, disappeared from the diet of native Americans living along the Wasatch Mountains of northern Utah approximately 700 years ago. Since corn is thought to have been cultivated only in regions with summer rains, these data could indicate a loss of monsoonal precipitation along the northern Wasatch Mountains. Lastly, Lanner (1974) reported hybrids of *Pinus monosperma* x *edulis* in the northern portions of the

Wasatch Range. Similar to *Q turbinella*, *P edulis* now only occurs in habitats with reliable summer precipitation. Since the nearest *P edulis* is approximately 200 km from the *P monosperma* x *edulis* hybrid populations and since trees in this hybrid population are less than 400 years old, these patterns suggest a relatively recent loss of reliable summer moisture in the northern habitats that now have only the relictual hybrid oak and piñon pine populations.

The hybrid persistence of *Q gambelii* x *turbinella*, *Q gambelii* x *macrocarpa*, and *P monosperma* x *edulis* may be the result of deeper rooting capacities that allow them to maintain gas-exchange activity through a prolonged summer drought. In a strict sense, the hybrids are likely all that remain from a recent historical period when the local region had a reliable monsoonal moisture input. While as a general pattern, most hybrid plants occur in an intermediate habitat or microclimate with both parents sympatric and persisting in the region, the oak and piñon pine hybrids describe relicts of a previous climate where now only one of the parents has persisted. The use of parental and hybrid oaks under common garden conditions allows us a means of teasing out the factors that have contributed to the loss of one parental species and therefore gain a stronger insight into historical climatic patterns influencing plant distribution.

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#### REFERENCES

- Betancourt JL, van Devander TR, Martin PS (1990) *Pack-rat Middens: The Last 40 000 Years of Biotic Change*. University of Arizona Press, Tucson, AZ, USA
- Coke K (1990) Late Quaternary zonation of vegetation in the eastern Grand Canyon. *Science* 217, 1142-1145

- Coleman ML, Shepherd TJ, Durham JJ, Rouse JE, Moore GR (1982) Reduction of water with zinc for hydrogen isotope analysis. *Anal Chem* 54, 993-995
- Coltrain JB (1994) The Great Salt Lake wetlands: a study in prehistoric diet. Society for American Archeology, 59th Annual Meeting, Anaheim, CA, USA
- Cottam WP, Tucker JM, Drobnik R (1959) Some clues to Great Basin post-pluvial climates provided by oak distributions. *Ecology* 40, 361-377
- Cottam WP, Ticker JM, Santamour Jr FS (1982) Oak hybridization at the University of Utah. State Arboretum of Utah, Publication No 1, Salt Lake City, UT, USA, 82 p
- Dawson TE, Ehleringer JR (1993) Isotopic enrichment of water in the 'woody' tissues of plants: implications for water source, water uptake, and other studies which use the stable isotopic composition of cellulose. *Geochim Cosmochim Acta* 57, 3487-3492
- Drobnik R (1958) The ecology of a relict oak hybrid in the Great Basin area of Utah. Msc Thesis, University of Utah, Salt Lake City, UT, USA
- Ehleringer JR (1991)  $^{13}\text{C}/^{12}\text{C}$  fractionation and its utility in terrestrial plant studies. In: *Carbon Isotope Techniques* (DC Coleman, B Fry, eds), Academic Press, New York, 187-200
- Ehleringer JR, Dawson TE (1992) Water uptake by plants: perspectives from stable isotope composition. *Plant Cell Environ* 15, 1073-1082
- Ehleringer JR, Smedley MP (1989) Stomatal sensitivity and water-use efficiency in oaks and their hybrids. In: *Symposium on Shrub Ecophysiology and Biotechnology* (A Wallace, ED McArthur, MR Haferkamp, eds), USDA Forest Service, Technical Report INT-256, 98-102
- Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. *Annu Rev Plant Physiol Mol Biol* 40, 503-537
- Feng X, Epstein S (1994) Climatic implications of an 8 000-year hydrogen isotope time series from bristlecone pine trees. *Science* 265, 1079-1081
- Lanner RM (1974) Natural hybridization between *Pinus edulis* and *Pinus monophylla* in the American Southwest. *Silvae Genet* 4, 108-116
- Miller HA, Lamb SH (1985) *Oaks of North America*. Naturegraph Publishers Inc, Happy Camp, CA, 317 p
- Maze JR (1968) Past hybridization between *Quercus macrocarpa* and *Quercus gambelii*. *Brittonia* 20, 321-333
- Neilson RP, Wullstein LH (1983) Biogeography of two southwest American oaks in relation to atmosphere dynamics. *J Biogeogr* 10, 275-297
- Neilson RP, Wullstein LH (1985) Comparative drought physiology and biogeography of *Quercus gambelii* and *Quercus turbinella*. *Am Midl Nat* 114, 259-271
- Neilson RP, Wullstein LH (1986) Microhabitat affinities of gambel oak seedlings. *Great Basin Nat* 46, 294-298
- Phillips SL, Ehleringer JR (1995) Limited uptake of summer precipitation by bigtooth maple (*Acer grandidentatum* Nutt) and Gambel's oak (*Quercus gambelii* Nutt). *Trees* 9, 214-219
- Stine S (1994) Extreme and persistent drought in California and Patagonia during medieval time. *Nature* 369, 546-549
- Tucker JM, Bogert BB (1973) Analysis of a progeny test of a hybrid oak, *Quercus gambelii* x *Q turbinella*. *Madroño* 22, 1-9
- Tucker JM, Maze JR (1966) Bur oak (*Quercus macrocarpa*) in New Mexico? *Southwest Nat* 11, 402-405
- Valentini R, Scarascia Mugnozza GE, Ehleringer JR (1992) Hydrogen and carbon isotope ratios of selected species of a Mediterranean macchia ecosystem. *Funct Ecol* 6, 627-631