

## STOMATAL SENSITIVITY AND WATER-USE EFFICIENCY IN OAKS AND THEIR HYBRIDS

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**ABSTRACT:** The sensitivities of stomata to changes in the leaf to air water vapor gradient ( $\Delta w$ ) were measured on oaks (*Quercus gambelii*, *Q. macrocarpa*, and *Q. turbinella*) and their hybrids growing under common field conditions in the Cottam Oak Hybrid Grove at the University of Utah. The ranking order for decreasing sensitivity of leaf gas exchange to changes in  $\Delta w$  was *Q. turbinella*, *Q. gambelii*, and *Q. macrocarpa*. In addition, leaf carbon isotope ratios, an indicator of long-term water-use efficiency, were measured on these same plants. These data suggest that leaf water-use efficiencies are lowest in *Q. gambelii* and higher in both *Q. macrocarpa* and *Q. turbinella*.

### STOMATA AND HUMIDITY

Stomata serve to regulate the diffusion of water vapor out of a leaf and carbon dioxide into the leaf and thus play a primary role in controlling both photosynthesis and transpiration. It is now well known for a large number of species that the stomata of leaves are sensitive to changes in the leaf to air water vapor gradient ( $\Delta w$ ), independent of changes in bulk leaf water status (Lange and others 1971; Schulze and Hall 1982). This response, often referred to as the stomatal sensitivity to humidity, is usually measured as the decrease in the leaf conductance to water vapor diffusion as the air becomes progressively drier. While numerous studies have documented differences in the stomatal sensitivity to humidity among species, few have attempted to correlate this parameter with plant performance or with plant distribution.

In their review, Schulze and Hall (1982) suggested that there was no systematic trend in stomatal sensitivity to  $\Delta w$  other than that those species which had the highest leaf conductances seemed to show the greatest absolute decrease in leaf conductance with increasing  $\Delta w$ . On the other hand, Losch (1979) and Losch and Tenhunen (1981) suggested in their reviews that although complete data sets were lacking there appeared to be a greater stomatal sensitivity to humidity in plants adapted to dry sites than in plants adapted to wetter sites. Furthermore, they

suggested that these differential sensitivities resulted in different rates of carbon gain in respective habitats and ultimately affected plant distributions. As evidence of this, Johnson and Caldwell (1976) compared stomatal sensitivity to increased  $\Delta w$  in four alpine tundra species, two adapted (=restricted?) to wet, moist sites and two adapted to drier, drained slopes. The stomates of the species adapted to wet sites were only slightly sensitive to decreased humidity, whereas leaf conductances of species from dry habitats decreased quickly in response to an increase in  $\Delta w$ . Supporting evidence for this pattern can also be seen in the comparative study of two *Diplacis aurantiacus* populations from coastal and inland habitats by Mooney and Chu (1983). In that study, leaves of plants of the population from the drier locations again had stomata that were more sensitive to changes in humidity than leaves of plants from the wetter habitat population.

### GAS EXCHANGE AND WATER-USE EFFICIENCY

Since limited water availability is of major concern for the cultivation of crop plants and as well appears to limit the productivity of most if not all native plants, it is not too surprising that for many years there has been an intense interest in trying to understand how leaves simultaneously regulate carbon dioxide uptake and transpirational water loss (Tanner and Sinclair 1983; Sinclair and others 1984). Photosynthetic rates (A) tend to decline in response to a decreased leaf conductance (g), because carbon dioxide diffusion rates into the leaf and hence intercellular carbon dioxide concentrations ( $c_i$ ) are progressively reduced with a reduction in leaf conductance. However, if leaf temperatures do not change substantially as the stomata close, there may be an increase in the water-use efficiency (molar ratio of photosynthesis to transpiration).

The rate of net photosynthesis as influenced by stomatal activity can be described as:

$$A = (c_a - c_i) g / 1.6 \quad (1)$$

and the transpiration rate (E) as

$$E = \Delta w g \quad (2)$$

where  $c_a$  is the atmospheric carbon dioxide concentration and 1.6 is the ratio of the diffusivities of water to carbon dioxide in air and is used to convert the conductance to water vapor through the stomata to the conductance to carbon dioxide through the stomata.

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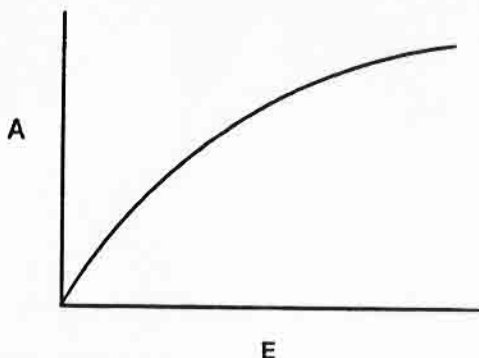


Figure 1--The relationship between net photosynthesis (A) and transpiration (E).

Combining these two equations we see that the water-use efficiency (A/E) becomes

$$A/E = (c_a - c_i)/(1.6 \Delta w) \quad (3)$$

Thus, under natural field conditions the leaf water-use efficiency depends on both the intercellular carbon dioxide concentration and the leaf to air water vapor gradient.

For a given decrease in stomatal or leaf conductance, the water-use efficiency of a leaf is typically increased (assuming leaf temperature remains constant). This is because a unit decrease in leaf conductance has a smaller impact on photosynthetic rate than it does on transpiration rate. In Figure 1, the relationship between A and E is plotted. Note that the relationship is curvilinear and that the slope of this relationship, which is water-use efficiency, decreases as the flux rates increase. The decrease in photosynthesis with decreased leaf conductance is best visualized by examining the dependence of net photosynthesis on intercellular CO<sub>2</sub> and the role that leaf conductance plays in regulating c<sub>i</sub> values (Figure 2). While a unit decrease in leaf conductance results in a unit decrease in transpiration rate, its impact is smaller on photosynthesis because the A vs. c<sub>i</sub> response curve is usually nonlinear and has a nonzero intercept on the x-axis (that is C<sub>3</sub> plants have a positive compensation point). In our analyses, we have assumed that the A vs c<sub>i</sub> response curves were similar among the different oak species; preliminary data on leaf amino nitrogen contents of these species are supportive of this assumption (Ehleringer, Hogle and Blackmore, unpublished observations).

#### CARBON ISOTOPE RATIO

Measuring leaf water-use efficiency over long time periods has been difficult because of the necessity to simultaneously measure biomass production and water consumption in a nondestructive manner. However, Farquhar, O'Leary and Berry (1982b) first proposed an alternative means of estimating leaf water-use

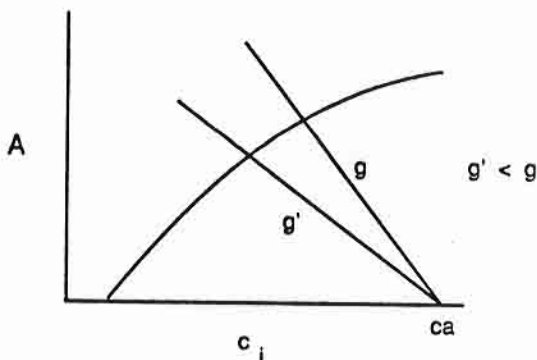


Figure 2--The dependence of net photosynthesis (A) on intercellular CO<sub>2</sub> concentration (c<sub>i</sub>), often referred to as the "demand function" for photosynthesis. The linear lines represent the leaf conductance to CO<sub>2</sub> diffusion through the stomata, often referred to as the "supply function". The intersection of the demand and supply functions is the operational point, given those leaf characteristics. In this figure g > g', so that the reduced leaf conductance of g' results in a lower intercellular CO<sub>2</sub> concentration and thus also a lower photosynthetic rate.

efficiencies using carbon isotope ratios at natural abundance levels.

The carbon isotope ratio ( $\delta^{13}C$ ) is the ratio of the <sup>13</sup>C/<sup>12</sup>C composition of a sample (R<sub>sample</sub>) relative to the <sup>13</sup>C/<sup>12</sup>C composition of a standard (R<sub>std</sub>),

$$\delta^{13}C = (R_{\text{sample}}/R_{\text{std}} - 1) 1000 \quad (4)$$

where  $\delta^{13}C$  has units of parts per mil (o/oo) and represents the deviation in composition of the sample from the standard, a fossil belemnite from the Pee Dee Formation (PDB).

Farquhar and others (1982b) proposed that there should be a relationship between the average c<sub>i</sub> during the photosynthetically active period and  $\delta^{13}C$ . Their idea is based upon two observations: first <sup>13</sup>CO<sub>2</sub> in air diffuses more slowly than <sup>12</sup>CO<sub>2</sub>, and second, that RuBP carboxylase, the initial carboxylating enzymatic reaction of photosynthesis in C<sub>3</sub> plants will discriminate against <sup>13</sup>CO<sub>2</sub>. While RuBP carboxylase can discriminate against <sup>13</sup>CO<sub>2</sub>, it does so only as a function of CO<sub>2</sub> levels actually at the sites where carboxylation is occurring (i.e., c<sub>i</sub> level). Thus, it is predicted that

$$\delta^{13}C_{\text{leaf}} = \delta^{13}C_{\text{air}} - a - (b-a) c_i/c_a \quad (5)$$

where a is the discrimination due to diffusion differences (4.4 o/oo) and b is the discrimination due to RuBP carboxylase (27 o/oo). A number of data sets exist which verify the expected relationships between  $\delta^{13}C$  and intercellular CO<sub>2</sub> (Farquhar and others 1982a; Bradford and others 1983; Ehleringer and others 1985).

Cottam Oak Grove

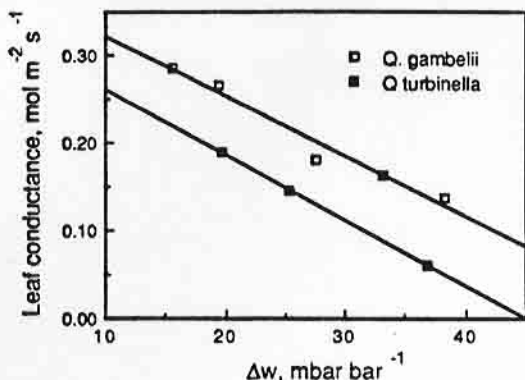


Figure 3--The dependence of leaf conductance to water vapor on the leaf to air water vapor gradient ( $\Delta w$ ) for leaves of *Quercus gambelii* and *Quercus turbinella* under common field conditions in the Cottam Oak Hybrid Grove at the University of Utah.

The advantage of using stable isotopes is that since carbon is continually being fixed by a leaf, measuring the carbon isotope ratio of a leaf provides a long-term indication of  $c_1$ . Therefore, carbon isotope ratio is useful as a long-term indicator of leaf-water use efficiency (assuming leaf temperatures are held constant). Since various environmental factors (such as drought, temperature, salinity) influence gas exchange and thus  $c_1$ , carbon isotope ratios can be used to estimate how water-use efficiency changes in response to a diversity of environmental conditions.

#### OAKS IN THE COTTAM OAK HYBRID GROVE

In the 1960's Dr. Walter Cottam of the University of Utah began assembling a diversity of oak species from North America, Europe and Asia for experimental studies (Cottam, Tucker and Santamour 1982). His interest was in producing and examining various hybrid combinations, some of which might naturally arise in zones where the species naturally overlapped in distribution. Parents and hybrids from his studies have now been established for many years at an experimental garden (Cottam Oak Hybrid Grove) adjacent to the University of Utah campus.

In this paper, we examine the stomatal characteristics and carbon isotope ratios of three of the oaks, *Quercus gambelii*, *Q. macrocarpa*, and *Q. turbinella* and their hybrids. We have chosen these species as they represent the three most important oak species in the intermountain west, they occur in habitats of contrasting aridity and water availability, and in areas of overlap do indeed form hybrid zones.

The three oak species occur in contrasting ecological zones. *Q. gambelii* has deciduous leaves and occurs in relatively mesic zones

Cottam Oak Grove

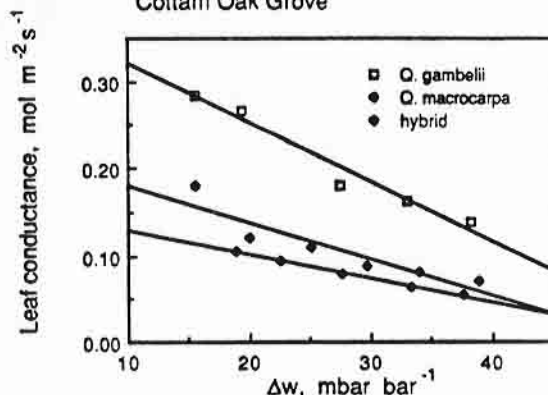


Figure 4--The dependence of leaf conductance to water vapor on the leaf to air water vapor gradient ( $\Delta w$ ) for leaves of *Quercus gambelii*, *Quercus macrocarpa* and hybrids under common field conditions in the Cottam Oak Hybrid Grove at the University of Utah.

between grassland and coniferous forests, primarily in northern Arizona, Colorado and Utah. In the drier, more southern portions of Arizona, California, New Mexico and Utah, *Q. gambelii* is replaced by the evergreen-leaved species *Q. turbinella*. *Q. macrocarpa* occurs on the eastern margins of the intermountain west and its distribution extends across much of the Great Plains region. It is a deciduous-leaved species, effectively restricted to riparian habitats.

#### STOMATAL SENSITIVITY TO HUMIDITY IN OAKS

Stomatal responses to changes in humidity between a  $\Delta w$  of 20 and 40 mbar bar<sup>-1</sup> were essentially linear in all oak species examined. The major differences between species were due to changes in the slopes and intercepts of these relationships. The stomata of *Q. turbinella* were more sensitive to changes in  $\Delta w$  than were the stomata of either *Q. gambelii* or *Q. macrocarpa* (Figures 3-4). On average the change in leaf conductance per unit change in  $\Delta w$  ( $\delta g / \delta \Delta w$ ) was -0.077, -0.066, and -0.024 for the three species respectively (Tables 1-2).

In the crosses between *Q. gambelii* and *Q. turbinella*, the performance of the hybrids was reduced below that of either parent (Table 1). Both the slope and intercept of the leaf conductance versus  $\Delta w$  response curve were very much lower in magnitude.

For the crosses between *Q. gambelii* and *Q. macrocarpa*, the stomatal behavior of the hybrids was intermediate between that of the parents (Table 2). Both the slope and the intercept of the leaf conductance versus  $\Delta w$  response curve were intermediate between the two parents.

There was no significant correlation among species and hybrids between the slope and

Table 1--Mean slope (mol bar mbar<sup>-1</sup> m<sup>-2</sup> s<sup>-1</sup>) and intercept (mol m<sup>-2</sup> s<sup>-1</sup>) values for the dependence of leaf conductance to water vapor on the leaf to air water vapor gradient ( $\Delta w$ ) for Q. gambelii, Q. turbinella and hybrids between them growing in the Cottam Oak Hybrid Grove at the University of Utah

	<u>Q. gambelii</u>	<u>Q. gambelii x turbinella</u>	<u>Q. turbinella</u>
slope	-0.066	-0.0030	-0.077
intercept	0.380	0.275	0.350

Table 2--Mean slope (mol bar mbar<sup>-1</sup> m<sup>-2</sup> s<sup>-1</sup>) and intercept (mol m<sup>-2</sup> s<sup>-1</sup>) values for the dependence of leaf conductance to water vapor on the leaf to air water vapor gradient ( $\Delta w$ ) for Q. gambelii, Q. macrocarpa and hybrids between them growing in the Cottam Oak Hybrid Grove at the University of Utah

	<u>Q. gambelii</u>	<u>Q. gambelii x macrocarpa</u>	<u>Q. macrocarpa</u>
slope	-0.066	-0.0042	-0.024
intercept	0.380	0.224	0.157

intercept of the leaf conductance versus  $\Delta w$  response curve. The independence of these two characters suggests that leaves of species with intrinsically higher gas exchange rates are not necessarily more sensitive to changes in  $\Delta w$  than leaves of species with lower gas exchange rates.

#### WATER-USE EFFICIENCY IN OAKS

There was a large intraspecific variation in long-term water-use efficiencies as indicated by leaf carbon isotope ratios for both Q. gambelii and Q. turbinella (Figure 5). For both species, there was slightly more than a 2 o/oo range in carbon isotope ratios values. This suggests that mean  $\delta^{13}C$  values among genotypes of each species differed by more than 30  $\mu$ l l<sup>-1</sup>. Unfortunately as there was only a single Q. macrocarpa tree within the experimental garden, it is not possible to say much about the variation within this species.

The impact of the changes in  $\delta^{13}C$  on actual water-use efficiency will depend on the atmospheric humidity conditions. If we assume typical daytime summer values for Salt Lake City of 32 C for both air and leaf temperatures and a 20% relative humidity, then the calculated change in water-use efficiency in going from a carbon isotope ratio of -27 o/oo to -25 o/oo is an increase of 25%, increasing from an absolute value of 1.47 to 1.84. Thus, there would appear to be substantial genetic variation in water-use efficiency within oak genotypes. The implications of these differences in water-use efficiency to long-term plant performance are not understood at this time.

The hybrids growing in the Cottam Oak Grove also exhibited a wide variation in leaf carbon isotope ratios (Figures 5-6). For the crosses between Q. gambelii and Q. turbinella, there was as much isotopic variation as in each of the parents and the values overlapped completely with the range of Q. turbinella. However, for the Q. gambelii and Q. macrocarpa crosses, even though the range of leaf isotope ratios of the hybrids was similar to the parents (at least of the Q. gambelii parent), the mean isotope ratios were intermediate between those of the two parents (given the limited data available for Q. macrocarpa).

#### CORRELATIONS BETWEEN WATER RELATIONS AND OAK DISTRIBUTION

In the intermountain west, Q. gambelii occupies wetter, higher elevation sites than does Q. turbinella. It is then not too surprising to note that leaf carbon isotope ratio data suggest that water-use efficiency is higher in Q. turbinella than in Q. gambelii. What is perhaps surprising is the observation that water-use efficiency in Q. macrocarpa, a species which occupies riparian habitats is so much higher than that of Q. gambelii. Whether these differences are due to water conditions in the experimental garden or whether Q. macrocarpa has an intrinsically higher water-use efficiency is unclear at this time. The leaf carbon isotope ratio data for the Q. gambelii x macrocarpa and Q. macrocarpa x gambelii hybrids do suggest that Q. macrocarpa may indeed have a higher water-use efficiency under natural field conditions.

## Cottam Oak Grove

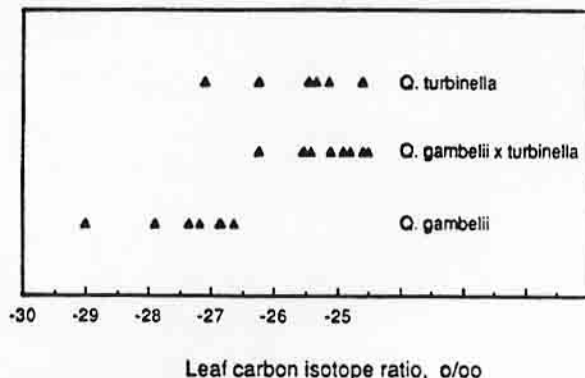


Figure 5--Leaf carbon isotope ratios for leaves of different individual trees of *Quercus gambelii*, *Quercus turbinella*, and hybrids between them at the Cottam Oak Hybrid Grove.

## Cottam Oak Grove

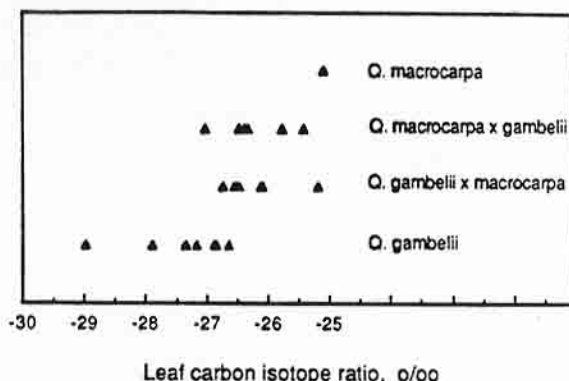


Figure 6--Leaf carbon isotope ratios for leaves of different individual trees of *Quercus gambelii*, *Quercus macrocarpa*, and hybrids between them at the Cottam Oak Hybrid Grove.

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