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Journal
Tree Physiol, 16(4)

Author
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Publication Date
1996-04-01

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Carbon assimilation and water-use efficiency by neighboring Mediterranean-climate oaks that differ in water access

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Received November 17, 1995

Summary  Quercus agrifolia Nee and Quercus durata Jeps. are sclerophyllous evergreens that co-occur in regions of northern California that have a serpentine-derived soil. The species are of similar stature and density where they grow together, even though late-drought xylem pressure potentials indicate that Q. durata has access to more soil water than Q. agrifolia. To assess how carbon uptake and water-use efficiency (WUE) are affected by water access, I monitored leaf and canopy gas exchange of neighboring Q. durata and Q. agrifolia trees over a 15-month period. Transpiration and photosynthesis by Q. agrifolia peaked in spring and declined through the summer, whereas transpiration and photosynthesis by Q. durata continued at a moderate rate year round. When summed over the study, Q. agrifolia transpired 25% less water on a ground-area basis than Q. durata, but assimilated 25% more carbon. Quercus agrifolia achieved a greater integrated WUE by: (1) maintaining a 20% advantage in instantaneous WUE as a result of lower leaf intercellular CO2 concentrations; (2) responding rapidly to increased soil water following rain; and (3) assimilating carbon at high rates during periods of low evaporative demand.

Keywords: canopy gas exchange, gross production, Quercus agrifolia, Quercus durata, sap flow, serpentine.

Introduction

Quercus agrifolia Nee and Quercus durata Jeps. are sclerophyllous evergreens that co-occur in regions of northern California that have a serpentine-derived soil. Late-drought xylem pressure potentials indicate that Q. durata trees have access to more soil water than neighboring Q. agrifolia trees. Because primary production in Mediterranean climates is largely water limited (Mooney et al. 1975), and there is no evidence that Quercus agrifolia and Quercus durata differ in degree of nitrogen limitation (Goulden 1991), Q. durata should have a competitive advantage over Q. agrifolia. However, Q. durata is not dominant where the species co-occur, suggesting that some physiological, phenological, or structural feature allows Q. agrifolia to compensate for limited water access.

I examined the annual carbon uptake of the two oak species, and tested the hypothesis that Q. agrifolia offsets a deficit in water access by increasing its rate of carbon assimilation per unit of water transpired (water-use efficiency, WUE). The experimental goals were to: (1) characterize the seasonal courses of leaf and canopy gas exchange by the two oak species; (2) measure their seasonally integrated carbon uptake and WUE; and (3) partition any observed differences in WUE into physiological, structural, and phenological components (Cowan and Farquhar 1977, Mooney and Gulman 1979, Williams 1983, Caldwell et al. 1986, Rambal 1993)

Methods

Site and plant description

The study was conducted at Jasper Ridge Biological Preserve, San Mateo county, CA, 37°24’ N 122°13’ W. The site is on serpentine-derived soil with a bed of fractured rock about 50-cm deep. The vegetation is a mix of serpentine endemic and nonendemic shrubs, evergreen trees, and interspersed bare and grass-covered patches. The area has not burned for at least 100 years and is similar to a nearby plot characterized by Davis and Mooney (1985, 1986).

Quercus durata is an endemic shrub that grows on serpentine-derived soil in northern California. At the study site, the Q. durata shrubs were generally less than 3-m tall, with low leaf area indices (LAI), and small sclerophyllous leaves (1–2 by 2–4 cm). Quercus agrifolia is a common tree throughout coastal California that grows to a height of 20 m. At the study site, Q. agrifolia trees were 2 to 5-m tall, with a range of LAIs, and moderate-sized leaves (2–4 by 3–6 cm). The apparently reduced vigor of Q. agrifolia when growing on serpentine is typical of nonendemic plants (Kruckeberg 1992). The Q. agrifolia investigated here did not produce viable fruit during the study, and the plants may have originated from acorns imported from non-serpentine areas (50 to 200 m away).

Field observations were made at four subsites along a 200-m transect. Two plants of similar stature were selected from each species at each subsite (the complete set). Two easily accessible plants from each species were then selected from the complete set for canopy-level observations (the intensively
Climate was monitored from October 1989 through January 1991 at 1.5-m height in a clearing 100 m north of the site. Horizontal wind speed measured with a spinning cup, air temperature measured with a thermistor, incident short-wave radiation measured with a silicon pyranometer, photosynthetically active photon flux measured with a quantum sensor, and ambient relative humidity measured with an electrical-capacitance probe, were recorded hourly. Hourly rainfall was measured 1.2-km west of the site with a tipping bucket gauge (Campbell Scientific, Logan, UT).

**Soil and xylem water potentials**

Screen psychrometers were installed at depths of 10, 25, 50, 100, and 200 cm in the center of each subsite during the summer and fall of 1989 (Brown and Chambers 1987). The psychrometers at the three lowest depths were placed in 2.5-cm diameter holes that were bored with an extended masonry bit. The holes were backfilled with original soil following installation. Water was prevented from channeling down the psychrometer leads with bentonite seals at depths of 25, 75, and 150 cm, and by looping the leads through an adjacent hole at the soil surface. The psychrometers located at depths of 10 and 25 cm were placed in horizontal holes dug into the face of a trench.

The psychrometers were calibrated over the range -0.46 to -4.64 MPa with NaCl, and read with a dew-point microvoltmeter (Wescor, Logan, UT) every 2 to 4 weeks from August 1989 to December 1990. Measurements with zero offsets greater than 5 μV were excluded to reduce errors associated with thermal instability. Data were averaged by depth among the subsites (n = 1 to 4).

A Scholander pressure chamber was used to measure predawn xylem pressure potential (Ψp) every one to two months from September 1989 to October 1990 (Ritchie and Hinckley 1975). Two twigs from each plant were sealed in a polyethylene bag and analyzed within 45 min.

**Leaf area index (LAI)**

In May 1991, small-scale harvests were combined with spectral reflectance measurements to estimate the leaf areas of the intensively investigated plants. The simple ratio (SR; Gamo et al. 1995) was measured across each canopy with a narrow-band spectroradiometer (Spectron Engineering Inc., CO). The relationship between SR and LAI was determined by harvesting a 0.073-m² section through each of the four plants (LAI = 0.101×10^{0.235SR}, r² = 0.99, 2 < LAI < 15). Mean LAI of the intensively investigated *Q. agrifolia* plants (7.6) was greater than that of the intensively investigated *Q. durata* plants (2.0), a pattern that was confirmed by summing the leaf fall from November 1989 to February 1991 beneath these plants (*Q. agrifolia* 2.1, *Q. durata* 1.2; Goulden 1991). However, the LAIs of the intensively investigated *Q. agrifolia* were atypical and the litterfall beneath the complete set of plants did not differ between species. Because selection of *Q. agrifolia* for canopy work was constrained by accessibility, intensively investigated plants were larger and bushier than most nearby members of the species.

**Leaf gas exchange and δ^{13}C**

A portable gas-exchange system (LI-6200, Li-Cor, Inc., Lincoln, NE) was used every one to two months from September 1989 to December 1990 to measure leaf photosynthesis (A_l) and stomatal conductance (g_s) of the complete set of plants. Five sunlit leaves per plant were measured within 1.5 h of solar noon on sunny days. Midday ambient CO₂ concentration (c_a) at the site was 350 to 370 μl⁻¹, and the intercellular CO₂ concentration (c_i) was calculated based on the CO₂ concentration in the chamber at the start of each measurement. Leaf water-use efficiency (WUE) was calculated from g_s, A_l and ambient vapor saturation deficit (D, 1100 to 1400 h PST average). The area of each leaf was determined following the gas-exchange measurements (Delta-T area meter, Cambridge, UK). Because the gas-exchange system was serviced in July 1990, the c_i and g_s observations before and after are not directly comparable.

Integrated leaf-level water-use efficiency was computed by summing A_l and daily leaf transpiration (E_l) from September 7, 1989 to December 5, 1990. Daily E_l was calculated by multiplying D.g_s, and the period with photon flux density (Q_o) > 400 μmol m⁻² s⁻¹. Daily A_l was calculated by multiplying instantaneous A_l and the period with Q_o > 400 μmol m⁻² s⁻¹. Seasonal courses of instantaneous g_s and A_l were calculated by linear extrapolation.

The δ^{13}C/δ^{12}C ratios (δ^{13}C) of 4- to 6-month-old leaves collected in October 1989 and September 1990 were determined by mass spectrometry. Ground tissue from five sun-exposed leaves per plant was pooled, oxidized with cupric oxide, purified on a vacuum line, and analyzed for isotopic composition at the University of Utah, Salt Lake City, UT (Ehleringer and Osmond 1989).

**Canopy gas exchange**

A ventilated chamber was used to measure canopy gas exchange of each intensively investigated tree over one day in spring 1991 (Goulden and Field 1994). A blower forced air into the chamber, and a second fan in the chamber assured mixing. Air entering and leaving the chamber was sampled for water vapor with electrical-capacitance humidity probes, and for CO₂ with an infrared gas analyzer. Flow into the chamber was measured with a thermal-mass anemometer. Leaf temperatures in the chamber were measured with fine-wire thermocouples. Rates of ground-area-based carbon assimilation (A_c), transpiration (E_c), and stomatal conductance (g_c) were calculated as described by Field et al. (1989). Canopy carbon assimilation, E_c, and g_c are the net for the whole canopy, including stem and leaf but not soil exchange. The CO₂ concentration in the chamber was calculated assuming that the concentration of CO₂ entering the chamber was 365 μl⁻¹.

**Sap-flow measurement and calculation**

Sap flow through five *Q. agrifolia* and four *Q. durata* plants, including the intensively investigated plants, was monitored from October 1989 to January 1991 with stem-implanted heat-
balance sensors (Granier 1985, Granier 1987, Goulden and Field 1994). Comparisons with the ventilated chamber established that sap-flow sensor output \( (k) \) was linearly related to \( E_c \) with a lag of up to 1 h due to water storage within the trees \( (r^2 = 0.8 \text{ to } 0.95, \text{ Goulden and Field 1994}) \). The quantitative relationship between \( E_c \) and \( k \) varied between trees, necessitating a separate calibration for each plant.

Daily Penman-Monteith evaporation (PME) was calculated as described previously (Goulden and Field 1994). Surface conductance was set at 0.22 mol m\(^{-2}\) s\(^{-1}\), typical of the whole-plant stomatal conductance \( (g_c) \) of both species in spring 1991.

Measurements of sap flow were combined with climatic observations to calculate hourly whole-plant ground-area-based transpiration \( (E_s) \), surface conductance \( (g_s) \), carbon assimilation \( (A_s) \), and water-use efficiency \( (\text{WUE}_s) \) of the intensively investigated plants from October 1989 to January 1991. Sap-flow-based \( E \) was calculated as the product of \( k \) and the ratio of \( k \) to \( E_c \) observed for each plant in the ventilated chamber (Goulden and Field 1994). Canopy conductance was calculated from \( E_s \), ambient temperature \( (T_a) \), ambient humidity \( (h_a) \), net radiation \( (R_n) \), and aerodynamic conductance \( (g_a) \) by inverting the Penman-Monteith equation (Campbell 1977). Canopy aerodynamic conductance was calculated from wind speed based on an analysis of the energy budget of an individual \( Q. \) durata (Goulden and Field 1994).

Both carbon assimilation \( (A_s) \) and water-use efficiency \( (\text{WUE}_s) \) were calculated using a form of the relationship between stomatal conductance, carbon assimilation, surface relative humidity \( (h_s) \), and ambient CO\(_2\) concentration \( (c_a) \) reported by Ball et al. (1987):

\[
g_c = m(h_s A_c c_a^{-1}) + b. \tag{1}
\]

Equation 1 is based on tight coupling between assimilation and stomatal conductance, and the consequent tendency for \( c_i \) to remain constant for a given humidity and \( c_a \). The constants \( (m \text{ and } b) \) were determined independently for each plant during spring days using the ventilated chamber \( (m = 7.5 \text{ to } 10.5, \text{ } b = 0.02 \text{ to } 0.07, \text{ } r^2 = 0.85 \text{ to } 0.95; \text{ Goulden 1991}) \). Ground-area-based assimilation of individual canopies \( (A_s) \) was then calculated from sap flow and microclimate observations using the reciprocal of Equation 1:

\[
A_s = (g_s - b)c_a \text{ m}^{-1} \text{ h}_s^{-1}. \tag{2}
\]

Leaf surface humidity \( (h_s) \) was calculated from ambient vapor pressure and leaf temperature. Ambient CO\(_2\) \( (c_a) \) was set at 365 \( \mu \text{l} \text{l}^{-1}\), and leaf temperature was calculated from \( R_n, g_s, T_i \) and \( E_s \) (Campbell 1977). Sap-flow-based WUE was calculated from \( E_s \) and \( A_s \). Sap-flow-based \( E \) and \( A_s \) were subsequently summed for periods with \( Q_o > 10 \) \text{ mol m}^{-2} \text{ s}^{-1}\) from October 12, 1989 to December 31, 1990. Sap-flow-based \( A \) is not strictly gross assimilation, but is the net assimilation after aboveground daytime respiration.

Results and discussion

Water access

Only 44.9 cm of rain, or 60% of average, fell at Jasper Ridge from October 1, 1989 through December 31, 1990 (Figure 1). The soil column was not recharged to 1 m until midwinter, and even then soil water potential \( (\Psi_s) \) at 2-m depth did not return completely to zero at all subsites (Figure 2). Water in the surface 2 m of soil was severely depleted during the summer drought, with a particularly extreme drawdown during 1990.
when summer \( \Psi_s \) values were 1 to 2 MPa lower than those recorded the previous summer.

Predawn xylem pressure potential (\( \Psi_{pd} \)) of both species paralleled the seasonal availability of soil water (Figure 2, Table 1). Quercus agrifolia \( \Psi_{pd} \) was low at the start of the study, recovered partially after a light rain (1.2 cm on September 16, 1989), and recovered completely following the first major storm of the season (4.6 cm from October 21 to October 25, 1989). With the exception of the winter months, \( \Psi_{pd} \) of \( Q. \) agrifolia was significantly lower than that of \( Q. \) durata. The impact of the dry winter in 1990 (Figures 1 and 2) was especially severe for \( Q. \) durata. Quercus durata \( \Psi_{pd} \) was high at the end of summer 1989, but declined steadily through summer 1990.

Predawn xylem pressure potential is generally interpreted as the \( \Psi_t \) at the root-soil interface (Ritchie and Hinckley 1975). Simultaneous measurements of \( \Psi_{pd} \) and \( \Psi_t \) have been used to estimate root distribution (Poole and Miller 1975, Burk 1978, Davis and Mooney 1986, Virginia and Jarrell 1987). Following this logic, the majority of active \( Q. \) agrifolia roots during the 1989 drought were confined to the top 25–50 cm of soil, whereas those of \( Q. \) durata penetrated to a depth of more than 1 m (Figure 2, Table 1).

**Seasonal activity**

Leaf stomatal conductance and photosynthesis by \( Q. \) agrifolia (Figure 3) paralleled the availability of shallow soil water (Figure 2), peaking in spring and declining through the summer drought. Leaf gas exchange by \( Q. \) durata followed a markedly different course, reaching a minimum in winter and a maximum in late-summer that coincided with acorn production.

Seasonal patterns at the canopy level were similar to those at the leaf level. Sap flow by \( Q. \) agrifolia (Figure 4c) was related to both soil water availability (Figure 2) and evaporative demand (Figure 4a), with reduced transpiration during low evaporative demand in winter and during drought in summer. \( Q. \) agrifolia sap flow increased sharply in March 1990, was temporarily reduced by cool, wet weather in late May 1990, and declined as soil water was depleted in summer. Similarly, \( Q. \) agrifolia \( g_s \) and \( A_s \) were high during the wet spring and decreased during the summer, implying that carbon uptake was limited by water access (data not shown). The seasonal course of transpiration by \( Q. \) durata (Figure 4b) was closely related to evaporative demand (Figure 4a), with only a moderate decline during the summer drought. Likewise, \( g_s \) and \( A_s \) of \( Q. \) durata were largely independent of shallow soil water, and showed a modest increase in spring, and a larger decrease in summer 1990 than in summer 1989 (data not shown).

**Peak activity**

Concentrations of foliar nitrogen (\( N_l \)) and maximum rates of leaf photosynthesis \( (A_{c,max}) \) were similar for both species \( (A_{c,max} = 10 \text{ to } 12 \mu \text{mol m}^{-2} \text{s}^{-1}; \text{Figure 3}; N_l = 0.16 \text{ to } 0.18 \text{ mol m}^{-2}; \text{Goulden 1991}) \). In contrast, maximum rates of canopy photosynthesis \( (A_{c,max}) \) differed markedly between species \( (Q. \) agrifolia \( A_{c,max} = 27 \mu \text{mol m}^{-2} \text{s}^{-1}; Q. \) durata \( A_{c,max} = 8 \mu \text{mol m}^{-2} \text{s}^{-1}) \). The interspecific difference in peak canopy photosynthesis relative to peak leaf photosynthesis was related to the difference in LAI (Table 2). Average LAI of the intensively investigated \( Q. \) agrifolia was three to four times that of the intensively investigated \( Q. \) durata, a trend that allowed greater peak canopy assimilation despite comparable leaf activity.

![Fig3.png](https://example.com/Fig3.png)

**Table 1.** Seasonal courses of \( Q. \) agrifolia and \( Q. \) durata predawn water potentials (\( \Psi_{pd} \), MPa). Data are means for eight plants per species (two twigs per plant), statistical analysis by unpaired Student’s \( t \)-test.

<table>
<thead>
<tr>
<th>Date</th>
<th>( \Psi_{pd} ) ± SE</th>
<th>( Q. ) agrifolia</th>
<th>( Q. ) durata</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sept 7, 89</td>
<td>-2.78 ± 0.28</td>
<td>-1.04 ± 0.26</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td>Oct 7, 89</td>
<td>-2.22 ± 0.15</td>
<td>-0.98 ± 0.15</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td>Nov 7, 89</td>
<td>-0.74 ± 0.09</td>
<td>-0.69 ± 0.07</td>
<td>ns</td>
<td></td>
</tr>
<tr>
<td>May 7, 90</td>
<td>-0.77 ± 0.08</td>
<td>-0.61 ± 0.05</td>
<td>ns</td>
<td></td>
</tr>
<tr>
<td>June 7, 90</td>
<td>-1.21 ± 0.13</td>
<td>-0.73 ± 0.09</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td>Aug 7, 90</td>
<td>-2.86 ± 0.29</td>
<td>-1.68 ± 0.49</td>
<td>0.050</td>
<td></td>
</tr>
<tr>
<td>Oct 7, 90</td>
<td>-3.68 ± 0.12</td>
<td>-2.48 ± 0.36</td>
<td>0.001</td>
<td></td>
</tr>
</tbody>
</table>
Integrated transpiration and carbon uptake

Integrated transpiration by both species (Table 2) was equal to or greater than cumulative rainfall (44.9 cm). Because additional water must have evaporated from the soil surface, both species either depleted the soil water beneath their canopies or withdrew water from nearby sparsely vegetated areas. Rates of integrated transpiration (40 to 60 cm) were comparable to the annual evapotranspiration measured for a Quercus coccifera L. scrub (60.3 cm per year, Rambal 1984), and also to the annual transpiration estimated for chaparral in southern California (Miller and Poole 1979). The integrated rates of carbon assimilation were 1500 to 1900 g C m\(^{-2}\) (Table 2), which is similar to that estimated for isolated mature Q. agrifolia growing on grassland at Jasper Ridge (Hollinger 1983), and somewhat higher than that measured for a deciduous forest in northeastern United States (Wofsy et al. 1993).

Total canopy transpiration of Q. agrifolia was 25% less than that of Q. durata (Table 2). Despite this disadvantage in water use, integrated carbon assimilation of Q. agrifolia was 25% greater than that of Q. durata. The canopy measurements were limited to two plants per species. The leaf areas of the intensively investigated plants may have been unrepresentative, and it is unlikely that the carbon uptake of all Q. agrifolia exceeded that of all Q. durata. Nonetheless, seasonal and short-term patterns of leaf water use and carbon gain (Figure 3, Table 2),

![Figure 4. Seasonal courses of (a) Penman-Monteith daily evaporation (PME, mol H2O m\(^{-2}\) day\(^{-1}\)), (b) Q. durata mean normalized sap flow, and (c) Q. agrifolia mean normalized sap flow. The PME was calculated for a surface conductance of 0.22 mol m\(^{-2}\) s\(^{-1}\) from hourly measurements of the physical environment. The normalized sap flow for four Q. durata and five Q. agrifolia trees was calculated by dividing the daily sap flow by the maximum observed over the study. Plots show daily totals (histograms) and daily totals smoothed through 20 passes of a Gaussian filter to illustrate the seasonal trend (solid line).](image)

Table 2. Summary of LAI, integrated whole-canopy transpiration (\(\Sigma E_s\)), integrated whole-canopy carbon assimilation (\(\Sigma A_s\)), and integrated whole-canopy water use efficiency (\(\Sigma WUE_s\)) for the two intensively studied plants per species. Summary of integrated leaf water-use efficiency (\(\Sigma WUE_l\)) and leaf \(\delta^{13}C\) for 5–8 plants per species. Leaf area index was determined by harvest and spectral reflectance measurement in May 1991. Whole-canopy gas exchange (\(E_s, A_s\) and \(WUE_s\)) was determined hourly from October 12, 1989 to December 31, 1990 by combining sap flow, ventilated chamber, and meteorological measurements. The significance of interspecific variations in leaf WUE and \(\delta^{13}C\) was determined by unpaired Student’s t-test.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Q. agrifolia</th>
<th>Q. durata</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean ± SE</td>
<td>n</td>
<td>Mean ± SE</td>
</tr>
<tr>
<td>Leaf area index</td>
<td>7.6 ± 2</td>
<td>2</td>
<td>2.0 ± 2</td>
</tr>
<tr>
<td>(\Sigma E_s) (cm H2O)</td>
<td>44.3 ± 2</td>
<td>2</td>
<td>57.0 ± 2</td>
</tr>
<tr>
<td>(\Sigma A_s) (g C m(^{-2}))</td>
<td>1900 ± 2</td>
<td>2</td>
<td>1500 ± 2</td>
</tr>
<tr>
<td>(\Sigma WUE_s) ((\mu)mol mmol(^{-1}))</td>
<td>6.4 ± 0.3</td>
<td>2</td>
<td>3.9 ± 0.3</td>
</tr>
<tr>
<td>(\Sigma WUE_l) ((\mu)mol mmol(^{-1}))</td>
<td>4.9 ± 0.3</td>
<td>7</td>
<td>3.4 ± 0.3</td>
</tr>
<tr>
<td>1989 (\delta^{13}C) (%)</td>
<td>−25.01 ± 0.66</td>
<td>8</td>
<td>−27.15 ± 0.81</td>
</tr>
<tr>
<td>1990 (\delta^{13}C) (%)</td>
<td>−25.07 ± 0.81</td>
<td>8</td>
<td>−26.67 ± 0.56</td>
</tr>
</tbody>
</table>
and canopy transpiration (Figure 4) were consistent within species. A similar interspecific difference in integrated WUE was observed at both the leaf and canopy levels (Table 2), and it is likely that 40% greater long-term WUE by *Q. agrifolia* was typical. Three characteristics allowed *Q. agrifolia* to improve its long-term WUE: (1) a high instantaneous water-use efficiency; (2) a rapid response to increased soil water; and (3) a high peak rate of activity during periods of low evaporative demand.

**Low intercellular CO$_2$ concentration**

The small leaves and rough canopy at the site resulted in high aerodynamic conductances and a tight coupling between leaf and air temperature (Goulden and Field 1994). The leaf-to-air vapor pressure deficit was horizontally homogenous, and an interspecific difference in $c_l$ should have led to a difference in water-use efficiency. The $\delta^{13}$C of foliage, as well as the leaf and ventilated-chamber gas-exchange measurements, indicated that *Q. agrifolia* operated at a lower $c_l$ than *Q. durata* (Table 2, Figure 3, Goulden 1991). Even during events when soil water was high, the $c_l$ of *Q. agrifolia* was 20 μl l$^{-1}$ below that of *Q. durata* (Figure 3d). A 20 μl l$^{-1}$ difference in $c_l$ should have allowed *Q. agrifolia* 10 to 30% more CO$_2$ uptake per water loss than *Q. durata* (Figure 3e). Likewise, assuming similar leaf temperatures and temporal activities, the $\delta^{13}$C of 1990 leaves indicates that *Q. agrifolia* was 19% more efficient in its use of water than *Q. durata* (Table 2, Farquhar et al. 1989).

Interspecific difference in $c_l$ was not the result of intrinsic genetic pattern, but rather of acclimation. When grown in irrigated pots, *Q. agrifolia* seedlings had a $\delta^{13}$C of $-26.1\%$ and *Q. durata* seedlings had a $\delta^{13}$C of $-26.5\%$ (Goulden, unpublished data). Likewise, the $\delta^{13}$C of *Q. durata* differed between years as a function of rainfall (Table 2). *Quercus agrifolia* $\delta^{13}$C was stable from 1989 to 1990, whereas $\delta^{13}$C of *Q. durata* increased by 0.5‰ ($P < 0.1$, paired Student’s $t$-test). The 1990 increase in *Q. durata* $\delta^{13}$C and WUE coincided with an unusually harsh drought, and a marked reduction in late-summer predawn xylem pressure potential (Ψ$_{pd}$) relative to 1989 (Figures 1 and 2, Table 1). In contrast, *Quercus agrifolia* was severely stressed during both summers, and its $\delta^{13}$C and late-drought Ψ$_{pd}$ did not differ dramatically between years.

**Rapid response to increased soil water**

*Quercus agrifolia* also enhanced its carbon gain by responding rapidly to increased soil water availability (Figure 5). Four days after the first rain of the 1989 wet season (October 27, 1989), Ψ$_{s}$ was $-0.7$, $-0.5$, $-0.3$ and $-2.6$ MPa at 10, 25, 50 and 100 cm, respectively, indicating a rapid withdrawal of water from the surface layers (Figure 2). The predawn xylem pressure potential of *Q. agrifolia* recovered from $-2.2$ to $-0.7$ MPa during this period (Table 1), a rate consistent with past reports (Poole and Miller 1975, Burk 1978, Davis and Mooney 1986). Sap flow of *Q. agrifolia*, which had been negligible at the end of the 1989 drought, began to increase within three days of the rain (Figures 4 and 5). Sap flow of *Q. durata*, which was high throughout the previous drought, was unaffected by the rain.

Before the October 1989 rain, Ψ$_{s}$ in the surface 25 cm was less than Ψ$_{pd}$ of *Q. agrifolia* (Figure 2, Table 1). The water moves to a region of lower potential, even if it is out of a plant (Richards and Caldwell 1987), and the hydraulic conductance of shallow roots of *Q. agrifolia* was probably reduced during the drought (Nobel and Sanderson 1984). The 3-day lag before transpiration commenced after the rain events (Figures 4 and 5) may represent the time required for root-surface hydraulic conductance of *Q. agrifolia* to recover from drought (Kummerow et al. 1978, Nobel and Sanderson 1984, Passioura 1988). The ability of *Q. agrifolia* to capitalize on sudden increases in soil water is likely a common characteristic of plants growing in arid ecosystems. The carbon assimilation of Mediterranean-climate ecosystems is limited by light and temperature during the winter (Mooney et al. 1975), and the rapid response to an increase in Ψ$_{s}$ allowed *Q. agrifolia* to photosynthesize under favorable autumn conditions for several weeks.

**High activity during cool periods**

Evaporative demand at the site was low from December through April, and high from May through October (Figure 4a). The seasonal course of WUE was strongly controlled by this cycle. Despite an elevated $c_l$ during spring (Figure 3d), water use by both species was most efficient from December through June (Figure 3c). *Quercus agrifolia* effectively increased its long-term water use efficiency by carrying out a greater proportion of its activity during periods with low evaporative demand. Integrated WUE by *Q. agrifolia* exceeded that of nearby *Q. durata* by over 40% (Table 2). The interspecific difference in $c_l$ accounted for half this difference. The remaining 20% advantage for *Q. agrifolia* was caused by the difference in activity-weighted vapor pressure deficit.
The high leaf areas of the intensively investigated *Q. agrifolia* played a key role in allowing the species to maximize its winter and spring carbon uptake. Peak canopy assimilation of the four intensively investigated plants was linearly related to LAI (plot not shown; $A_{c,max} = \text{LAI} \times 3.8, r^2 = 0.96, n = 4$). Plants at Jasper Ridge were sparsely distributed, allowing appreciable light absorption on the sides of crowns and resulting in a high marginal gain for each leaf layer added. This permitted individual *Q. agrifolia* to achieve a peak canopy assimilation in excess of that reported for continuous canopies (Valentini et al. 1991, Wofsy et al. 1993). Light typically limits photosynthesis at the bottom of closed canopies, reducing the benefit of adding more layers. However, the sparse uneven canopy at Jasper Ridge, which is typical of Mediterranean-climate ecosystems, allowed individual plants to increase their winter carbon uptake by increasing canopy thickness.

Both $E_c$ and $A_t$ appeared to be under the direct control of soil water availability. In *Q. agrifolia*, the long-term improvement in WUE associated with lower activity-weighted $D$ reflected the climatic correlation between $\Psi_c$ and evaporative demand. The long-term pattern of carbon uptake suggests that this seasonal correlation, which is characteristic of Mediterranean climates, permits two similarly productive strategies that are differentiated by phenology. Some species may allocate a greater proportion of resources to leaf production, allowing high carbon accumulation during the winter at the expense of summer activity. Other species may concentrate on acquiring below-ground resources, permitting a longer period of relatively slow photosynthesis. When summed over the year, the two strategies, which are consistent with the activities of *Q. agrifolia* and *Q. durata*, may achieve comparable rates of carbon uptake despite a difference in summer water access.

Conclusions

Measurements of sap flow, whole-canopy gas exchange, leaf gas exchange, and tissue isotopic composition were combined to characterize the water use and carbon uptake by whole trees growing in the field. Leaf and canopy gas exchange of *Q. agrifolia* paralleled the availability of shallow soil water, peaking in spring and declining through the summer drought, whereas gas exchange by *Q. durata* was comparatively unrelated to soil water. Cumulative transpiration of *Q. durata* canopies exceeded that of *Q. agrifolia* by 25%. Despite this difference in water use, canopies of *Q. agrifolia* assimilated 25% more carbon than neighboring canopies of *Q. durata*. *Quercus agrifolia* achieved greater carbon gain by: (1) maintaining a 20% advantage in instantaneous water-use efficiency compared with *Q. durata* as a result of a lower leaf intercellular CO$_2$ concentration; (2) responding rapidly to increased soil water following rain; and (3) assimilating more carbon than *Q. durata* during periods of low evaporative demand.

Acknowledgments

I thank the members of the physiological and ecosystem ecology groups at Stanford and Carnegie for their ideas, advice, technical support and encouragement. Dr. Nona Chiariello provided the meteorological data sets. Craig Cook provided instruction and assistance on the mass spectrometer. Jeff Amthor, John Gamon, Jim Collatz, and Chris Field commented on earlier versions of this manuscript. This work was supported by Stanford University, the Carnegie Institution of Washington, a grant from the A. W. Mellon Foundation to Stanford University for work at Jasper Ridge, and NSF dissertation improvement grant BSR-8901070. This is CIWDPB Publication No. 1169.

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