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Ragan M. Callaway

University of Montana - Missoula, Ray.Callaway@mso.umt.edu

Bruce E. Mahall

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## VARIATION IN LEAF STRUCTURE AND FUNCTION IN QUERCUS DOUGLASII TREES DIFFERING IN ROOT ARCHITECTURE AND DROUGHT HISTORY

RAGAN M. CALLAWAY<sup>1</sup> AND BRUCE E. MAHALL

Division of Biological Sciences, University of Montana, Missoula, Montana 59812; and Department of  
Biological Sciences, University of California, Santa Barbara, California 93106

Seasonal changes in leaf specific mass, nitrogen, chlorophyll, and photosynthetic properties were measured for two groups of spatially intermixed *Quercus douglasii* trees with different drought histories and apparently different root architectures. One group, referred to as “high- $\psi_{pd}$ ” trees, included trees with low amounts of fine root biomass in the upper 50 cm of soil and high predawn xylem pressure potentials ( $\psi_{pd}$ ) during summer drought. These two characteristics indicate that trees in this group have deep roots, which may reach the water table. The second group, referred to as “low- $\psi_{pd}$ ” trees, had three to five times higher fine root biomass in the upper 50 cm of soil and low  $\psi_{pd}$  during summer drought. These two characteristics indicate that these trees may not have access to the water table and are dependent on shallow soil moisture, which decreases rapidly during the rainless summers of central California. In the spring, after the full expansion of new leaves, but prior to significant divergence in  $\psi_{pd}$  between the groups, leaf area per leaf, leaf specific mass, chlorophyll per leaf area, incident quantum yield, leaf respiration rate, and irradiance at light compensation were lower for low- $\psi_{pd}$  trees than for trees with high  $\psi_{pd}$ . Nitrogen per leaf area did not differ between the groups. Net photosynthetic capacity at 2000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  ( $A_{max}$ ) per leaf area was similar among all trees in the spring, but  $A_{max}$ /leaf mass during the spring was higher for trees that eventually would develop low seasonal  $\psi_{pd}$ . Since differences existed between new cohorts of leaves produced in the spring before summer drought, when  $\psi_{pd}$  was similar, we suggest that some leaf characteristics of *Q. douglasii* trees are determined by the degree of drought exposure experienced in previous years, or by genetic variation within the species. During the rainless summer and fall seasons,  $A_{max}$ /leaf area,  $A_{max}$ /leaf mass, and total leaf chlorophyll/leaf mass decreased more rapidly in trees with low  $\psi_{pd}$  than in trees with high  $\psi_{pd}$ , so that from August to the beginning of leaf senescence in October, leaves of high- $\psi_{pd}$  trees had higher  $A_{max}$ /leaf area,  $A_{max}$ /leaf mass, and total leaf chlorophyll/leaf mass than those of low- $\psi_{pd}$  trees. Overall, variations in root architecture and summer  $\psi_{pd}$  for *Q. douglasii* were correlated with substantial differences in morphological and physiological leaf characteristics. This apparent coordination of aboveground and belowground organs may explain, in part, how *Q. douglasii* tolerates the exceptionally broad range of topography and soil moisture conditions in which it occurs.

### Introduction

Movement of water through plants requires integration of roots, stems, and leaves, and the structure and function of these systems may vary with water stress in a coordinated process (Grant et al. 1989; Monson and Grant 1989; Nguyen and Lamant 1989; Ranney et al. 1990; Callaway et al. 1994). Variable root architecture has been postulated to affect intra- and interspecific differences in whole-plant morphology and physiology (Landsberg 1984; Becker and Castillo 1990) and ecological functions (Wieland and Bazzaz 1975; Park 1990; Callaway et al. 1991), but the relationship between variation in root architecture and the morphology and physiology of aboveground plant parts in naturally developing large woody plants in the field is poorly understood.

A unique opportunity to study the relationship between root architecture and aboveground function is available in stands of *Quercus douglasii* H. & A. (blue oak). This winter-deciduous tree is abundant from northern to central California and occurs on topography that varies extensively in soil moisture, including xeric slopes and ridges, mesic valleys, and alluvial plains in the foothills of the western Sierra Nevada and the coastal ranges of California (Griffin 1977). Predawn xylem pressure potentials ( $\psi_{pd}$ ) of individual *Q.*

*douglasii* vary widely among and within geographical regions and even among trees a few meters away from each other (Griffin 1973; Rundel 1980; Callaway et al. 1991), indicating that this species can exist at a wide range of soil moisture conditions. Callaway et al. (1991) reported that individual *Q. douglasii* within stands varied in root architecture. They compared fine root biomass in the upper 50 cm of soil and the  $\psi_{pd}$  of individual trees and found that some trees had low root biomass in shallow soils and late summer  $\psi_{pd}$  rarely less than  $-1.5$  MPa, whereas other trees had high shallow root biomass (three to five times that of the former trees) and late summer  $\psi_{pd}$  of less than  $-3.5$  MPa. They concluded that the former trees tapped the water table but that the latter trees were dependent on relatively shallow lateral root systems that did not reach the water table. Summer  $\psi_{pd}$  of trees with high shallow root biomass was much lower over 3 yr of measurements than those of trees with low shallow root biomass (Callaway et al. 1991, and unpublished data), indicating that the former individuals may consistently experience greater drought stress as a consequence of their root morphology. Wide variation in root architecture among *Q. douglasii* trees may occur elsewhere. Griffin (1973), Rundel (1980), and Baker et al. (1981) reported  $\psi_{pd}$  of  $-4.0$  to  $-5.0$  MPa for *Q. douglasii* at several different sites. Lewis and Burghy (1964), however, reported that *Q. douglasii* in the Sierra Nevada foothills were able to take up tritiated water placed in the water table over 20 m below the soil surface.

<sup>1</sup>Author for correspondence and reprints.

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In the current work we have compared leaf specific mass, nitrogen, incident quantum yield, respiration, chlorophyll, and photosynthesis of two subsets of the *Q. douglasii* trees described by Callaway et al. (1991), each with different drought histories and apparently different root architectures.

## Material and methods

### STUDY SITE

The field site was located at the University of California Hastings Natural History Reservation in the Santa Lucia Mountains of central California (34°41'N, 120°2'W). The climate is Mediterranean, with 90% of the 540 mm of annual precipitation occurring between November and April. Monthly mean minimum temperatures range from 1.4°C in January to 9.7°C in August, and monthly mean maximum temperatures range from 8.5°C in January to 20.1°C in July. *Quercus douglasii* trees are usually leafless between November and March. Trees were sampled in a savanna on a south-facing slope, with Vaqueros sandstone as parent material, and a total tree density of  $\approx 100$  individuals per hectare. The open grassland and understory vegetation consisted primarily of the European winter annual grasses *Avena fatua* L. and *Bromus diandrus* Roth.

### SAMPLING AND MEASUREMENTS

We measured  $\psi_{pd}$  monthly with a Scholander pressure chamber (Waring and Cleary 1967) for four low- $\psi_{pd}$  and four high- $\psi_{pd}$  trees each month from February to November 1988. Sampling dates were always in the last week of the month. These trees were chosen to represent the extremes of  $\psi_{pd}$  measurements taken the previous year (Callaway et al. 1991). Pressure-volume relations were measured following Tyree and Hammel (1972) for three twigs on each of two trees, each representing extremes of seasonal  $\psi_{pd}$ , in May and August. Transpiring portions were sealed in plastic bags and fully hydrated by placing the cut stems in water before placing them in the pressure chamber.

In April and October, 15 fully expanded, south-facing sun leaves from the lower portion of the canopy of each of the eight trees were measured for leaf area and leaf specific mass (LSM). Leaves were photocopied, and areas of images were measured with a planimeter. Leaves were then dried at 60°C and weighed. LSM was calculated as leaf dry mass (g) divided by leaf area (cm<sup>2</sup>).

Total Kjeldahl nitrogen (TKN) was measured in April and October in eight of the leaves per tree that were collected for LSM analysis. Leaf disks were ionized in a Technicon BD/20/40 block digester, and TKN was measured using a modified indophenol method (Setaro and Jones 1989) and a Perkins-Elmer atomic absorption spectrophotometer.

Total chlorophyll and leaf photosynthetic characteristics were measured on fully expanded leaves monthly from April through November of 1988 on the eight trees. Four leaves that were fully exposed to the sun and on the south-facing sides of the canopies were collected monthly from each tree within an hour after sunrise. Leaves were kept cool and in the dark immediately after collection, and total chlorophyll and photosynthetic capacities were measured within 25 h. Time-series measurements of leaves collected in April and September indicated that chlorophyll concentration and photosynthetic capacity decreased less than 5% over 30 h for leaves stored at 3°C and in the dark. By August, some leaves on trees with low  $\psi_{pd}$  had begun to turn brown. In August,

September, and October we only sampled leaves that were still green. In December all leaves had either abscised or turned brown. Results for each of the eight trees were averaged for the April–May, June–July, August–September sampling periods.

Chlorophyll was extracted from leaf disks of known area by grinding them in 90% acetone, 10% water, and a small amount of magnesium carbonate for chlorophyll stabilization. The homogenates were centrifuged at 15,000 rpm for 20 min in 2RB Sorvall centrifuge and absorbances of the supernatants were measured at 647 and 664 nm in a Varian 634 spectrophotometer. Total chlorophyll per leaf area ( $\text{Chl}_{\text{area}}$ ) and total chlorophyll per leaf mass ( $\text{Chl}_{\text{mass}}$ ) were calculated from these absorbances using the formulas of Jeffrey and Humphrey (1975).

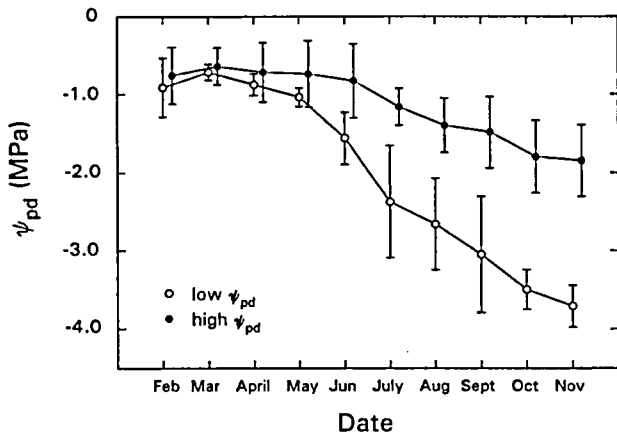
Photosynthetic capacities at  $\text{CO}_2$  saturation (ambient  $\text{CO}_2 = 5 \times 10^4 \mu\text{mol/mol}$ ) at 25°C were estimated by measuring  $\text{O}_2$  exchange rates using a Hansatech leaf disk electrode system (Decagon Devices, Pullman, Wash.; Delieu and Walker 1981, 1983) fitted with a quartz iodide light source (Walker and Osmond 1986). In April, May, and October,  $\text{O}_2$  exchange rates were measured for one leaf from each tree at approximately 50, 90, 160, 300, 800, 1500, and 2500–3000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD following the experimental procedure of Björkman and Demmig (1987). These light levels varied slightly because aging lamps were replaced between July and August. Curves were fitted to the photosynthetic data using a nonlinear, least squares fitting technique that employed the Marquardt algorithm discussed by Leverenz (1987). Statistical comparisons of photosynthetic capacities were conducted for responses at single irradiance levels. In June, July, August, and September  $\text{O}_2$  exchange rates were measured for four to six leaves from each tree only at 1450–1500 and 2500–3000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD.

Incident quantum yields were calculated as the slopes of the light-response curves for measurements taken at irradiances of 50 and 90  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . No corrections for leaf absorbances were made. Light compensation points and dark respiration rates were estimated by interpolation and extrapolation of incident quantum yield regressions. Maximum photosynthetic capacities ( $A_{\text{max}}$ ) at 2000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD were estimated by interpolation between the measurements of  $\text{O}_2$  evolution at 1450–1500 and 2500–3000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD.

## Results

Leaves began to emerge in late March and were fully expanded by April 26, 1988, our first leaf sampling date; however,  $\psi_{pd}$  did not differ significantly between the low- and high- $\psi_{pd}$  groups until June (fig. 1). After May, the extent to which  $\psi_{pd}$  declined during summer drought varied significantly between the two groups of *Quercus douglasii*. Average  $\psi_{pd}$  from April (when leaves were fully expanded) to November (leaves on low- $\psi_{pd}$  trees were no longer functional) ranged from  $-0.95$  to  $-1.53$  MPa (mean  $\pm 1$  SE =  $-1.24 \pm 0.24$  MPa) for the high- $\psi_{pd}$  group, and from  $-2.12$  to  $-2.41$  MPa (mean  $\pm 1$  SE =  $-2.23 \pm 0.14$  MPa) for the low- $\psi_{pd}$  group ( $n = 4$ ,  $T_{\text{group}} = 7.23$ ,  $P < 0.001$ ).

In one high- $\psi_{pd}$  tree,  $\psi_{pd}$  decreased from  $-0.4$  MPa in May to  $-1.2$  MPa in August, while full turgor osmotic potential of its shoots changed from  $-1.3$  MPa in May to  $-1.4$  MPa in August (fig. 2A), suggesting

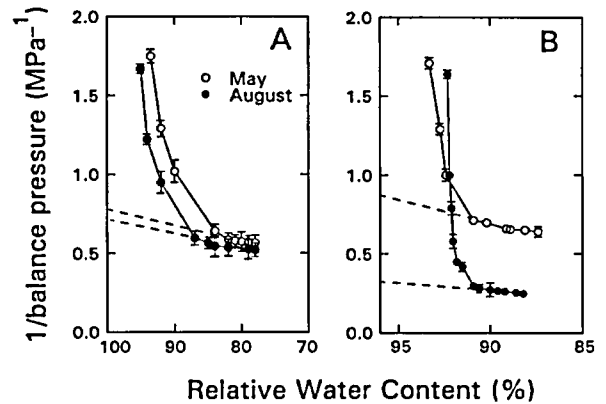


**Fig. 1** Predawn xylem pressure potentials for two groups of *Quercus douglasii* trees over the growing season of 1988. Error bars show 2 SEs on either side of the means. There were no leaves on the trees in February; leaves were 8% of their final size in March and fully expanded in April.

that minimal osmotic adjustment occurred. In comparison, substantial osmotic adjustment appeared to occur in a low- $\psi_{pd}$  tree in which  $\psi_{pd}$  decreased from  $-0.8$  MPa in May to  $-3.1$  MPa in August, while full turgor osmotic potential decreased from  $-1.2$  MPa in May to  $-2.7$  MPa in August (fig. 2B).

The average LSM of low- $\psi_{pd}$  trees was 23% less than that of high- $\psi_{pd}$  trees, and average LSM did not change for either group during the spring and summer (table 1). In May, leaf area averaged  $76 \pm 2$  (1 SE,  $n = 4$ )  $\text{cm}^2/\text{leaf}$  for high- $\psi_{pd}$  trees and  $33 \pm 1$   $\text{cm}^2/\text{leaf}$  for low- $\psi_{pd}$  trees (group  $\times$  tree ANOVA,  $F_{\text{group}} = 136.5$ ,  $df = 1,3$ ,  $P < 0.001$ ). Leaf nitrogen per leaf area was not different between the high- and low- $\psi_{pd}$  trees in May or October (table 1). Because of differences in LSM, leaf nitrogen per leaf mass was higher for low- $\psi_{pd}$  trees in both the spring and October than for high- $\psi_{pd}$  trees.

During each sampling period,  $\text{Chl}_{\text{area}}$  was higher for high- $\psi_{pd}$  *Q. douglasii* than for low- $\psi_{pd}$  trees (fig. 3A).  $\text{Chl}_{\text{area}}$  of low- $\psi_{pd}$  trees decreased by 50% from  $0.59$   $\text{g}/\text{m}^2$  in April–May to  $0.30$   $\text{g}/\text{m}^2$  in October, and by November all leaves on these trees had either abscised or turned brown.  $\text{Chl}_{\text{area}}$  of high- $\psi_{pd}$  trees declined only by 29%, from  $0.66$  to  $0.47$   $\text{g}/\text{m}^2$ , during the same time, and most leaves were still green in November.  $\text{Chl}_{\text{mass}}$ , however, was similar between the two groups throughout the growing season until October, when  $\text{Chl}_{\text{mass}}$  of



**Fig. 2** Pressure-volume relations for two individual *Quercus douglasii* trees in May and August. A, Mean seasonal  $\psi_{pd} = -0.95$  MPa, May  $\psi_{pd} = -0.40$  MPa, August MPa =  $-1.1$ . B, Mean seasonal  $\psi_{pd} = -2.41$ , May  $\psi_{pd} = -0.8$  MPa, August  $\psi_{pd} = -3.1$  MPa. Error bars show 2 SEs ( $n = 3$ ) on either side of the means. Extrapolation of straight line forming the lower part of the pressure-volume relationship to the Y-axis estimates the negative inverse of full-turgor osmotic potential at the Y-intercept.

high- $\psi_{pd}$  trees significantly exceeded those of low- $\psi_{pd}$  trees (fig. 3B).

Incident quantum yields, dark respiration rates, and light compensation points were significantly higher for leaves from high- $\psi_{pd}$  trees than for those from low- $\psi_{pd}$  trees throughout the sampling period (table 2). Between April–May and October incident quantum yield decreased 34% for high- $\psi_{pd}$  trees (date  $\times$  group  $\times$  tree ANOVA,  $F_{\text{date}} = 82.2$ ,  $df = 1,3$ ,  $P < 0.001$ ) and 49% for low- $\psi_{pd}$  trees (date  $\times$  group  $\times$  tree ANOVA,  $F_{\text{date}} = 117.1$ ,  $df = 1,3$ ,  $P < 0.001$ ). Estimated dark respiration rates of high- $\psi_{pd}$  trees were consistently higher than those of low- $\psi_{pd}$  trees throughout the spring and fall. Between April–May and October respiration rates decreased by only 28% for high- $\psi_{pd}$  *Q. douglasii* (date  $\times$  group  $\times$  tree ANOVA,  $F_{\text{date}} = 10.9$ ,  $df = 1,3$ ,  $P = 0.003$ ), while in leaves from low- $\psi_{pd}$  trees they decreased by 75% (date  $\times$  group  $\times$  tree ANOVA,  $F_{\text{date}} = 22.9$ ,  $df = 1,3$ ,  $P < 0.001$ ). Irradiance at light compensation for leaves from high- $\psi_{pd}$  trees increased slightly between April–May and October (date  $\times$  group  $\times$  tree ANOVA,  $F_{\text{date}} = 25.0$ ,  $df = 1,3$ ,  $P < 0.001$ ), but they decreased 43% during the same time for low- $\psi_{pd}$  trees (date  $\times$  group  $\times$  tree ANOVA,  $F_{\text{date}} = 7.7$ ,  $df = 1,3$ ,  $P = 0.010$ ).

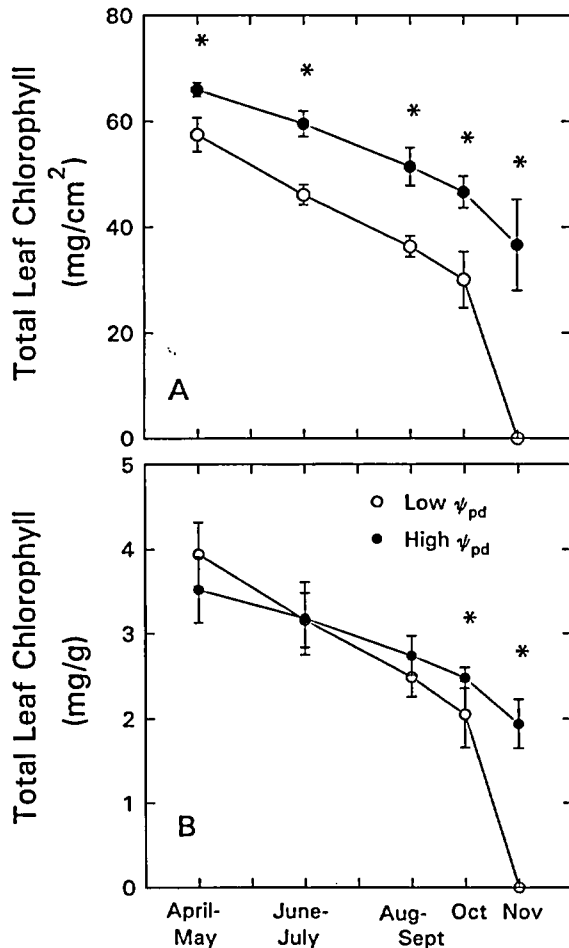
Net photosynthetic capacities calculated for 2000

**Table 1**

MEANS AND STANDARD ERRORS ( $n = 4$ ) FOR LEAF SPECIFIC MASS (LSM) AND LEAF NITROGEN FOR TWO GROUPS OF QUERCUS DOUGLASII THAT DIFFER IN SEASONAL  $\Psi_{pd}$

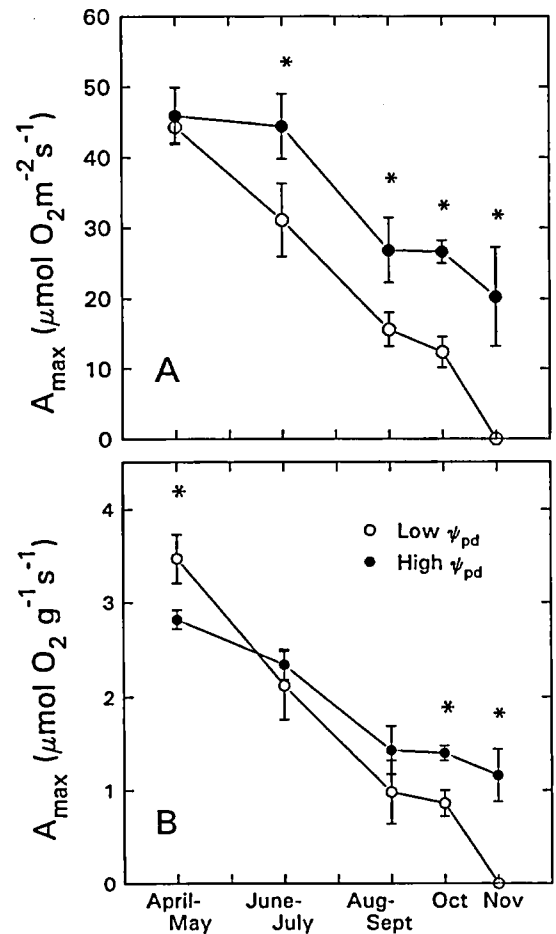
|                        | LSM ( $\text{g}/\text{m}^2$ ) |                | Leaf nitrogen ( $\text{g}/\text{m}^2$ ) |                    | Leaf nitrogen ( $\text{mg}/\text{g}$ ) |                  |
|------------------------|-------------------------------|----------------|---|--------------------|--|------------------|
|                        | April                         | October        | May                                     | October            | May                                    | October          |
| Low $\Psi_{pd}$ .....  | $164 \pm 8^a$                 | $148 \pm 8^a$  | $2.4 \pm 0.2^{ab}$                      | $2.1 \pm 0.1^a$    | $14.5 \pm 0.8^a$                       | $14.0 \pm 0.7^a$ |
| High $\Psi_{pd}$ ..... | $191 \pm 12^b$                | $192 \pm 15^b$ | $2.4 \pm 0.1^b$                         | $2.1 \pm 0.2^{ab}$ | $12.4 \pm 1.1^b$                       | $10.8 \pm 1.5^b$ |

Note. Shared letters denote no significant difference (ANOVA, post-ANOVA Tukey,  $P < 0.05$ ).



**Fig. 3** Total leaf chlorophyll per leaf area (A) and leaf mass (B) for *Quercus douglasii* with low or high seasonal  $\psi_{pd}$  (see fig. 1) during the growing season of 1988. Error bars represent 2 SEs ( $n = 4$ ) on either side of the means. Asterisks indicate means that were significantly different as determined by two-way ANOVA (group  $\times$  tree);  $P_{\text{group}} < 0.05$ .

$\mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD ( $A_{\text{max}}$ /leaf area) and photosynthetic capacities at all irradiances above  $90 \mu\text{mol m}^{-2} \text{s}^{-1}$  were similar between the two groups of trees in the spring when monthly  $\psi_{pd}$ 's were similar (fig. 4A, B). Between the April–May and June–July sampling periods, however,  $A_{\text{max}}$ /leaf area ( $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD) decreased significantly for low- $\psi_{pd}$  trees, but not for high- $\psi_{pd}$  trees (fig. 4A). Both high- and low- $\psi_{pd}$



**Fig. 4** Net photosynthetic capacities ( $A_{\text{max}}$ ) per unit leaf area (A) or per unit leaf mass (B) for *Quercus douglasii* trees with low or high seasonal  $\psi_{pd}$  (see fig. 1) during the growing season of 1988. Error bars represent 2 SEs ( $n = 4$ ) on either side of the means. Asterisks indicate means that were significantly different as determined by two-way ANOVA (group  $\times$  tree);  $P_{\text{group}} < 0.05$ .

trees decreased significantly in  $A_{\text{max}}$ /leaf area between June–July and October, and in November leaves capable of photosynthesis occurred only on high- $\psi_{pd}$  trees. In October, light-response curves differed substantially between the groups, with the photosynthetic capacities of high- $\psi_{pd}$  trees being lower at 50 and 90  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD, and higher at 900, 1450–1500, and 2500–3000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  than those of the low- $\psi_{pd}$  trees (fig. 5).  $A_{\text{max}}$ /leaf mass was significantly higher

**Table 2**

MEANS AND STANDARD ERRORS ( $n = 4$ ) FOR INCIDENT QUANTUM YIELD, ESTIMATED DARK RESPIRATION RATES, AND LIGHT COMPENSATION POINTS FOR TWO GROUPS OF QUERCUS DOUGLASII THAT DIFFER IN SEASONAL  $\psi_{pd}$

|                      | Incident quantum yield<br>(moles $\text{O}_2$ /moles photons) |                                | Respiration<br>( $\mu\text{mol O}_2 \text{m}^{-2} \text{s}^{-1}$ ) |                               | Irradiance at light compensation<br>( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) |                             |
|----------------------|---|--------------------------------|--|-------------------------------|--|-----------------------------|
|                      | April–May   | October                        | April–May  | October                       | April–May  | October                     |
| Low $\psi_{pd}$ .... | 0.043 $\pm$ 0.002 <sup>c</sup>                                | 0.022 $\pm$ 0.001 <sup>d</sup> | -2.07 $\pm$ 0.14 <sup>c</sup>                                      | -0.51 $\pm$ 0.06 <sup>d</sup> | 47.4 $\pm$ 4.2 <sup>c</sup>  | 27.0 $\pm$ 1.8 <sup>d</sup> |
| High $\psi_{pd}$ ... | 0.053 $\pm$ 0.002 <sup>a</sup>                                | 0.035 $\pm$ 0.001 <sup>b</sup> | -4.20 $\pm$ 0.16 <sup>a</sup>                                      | -3.03 $\pm$ 0.14 <sup>b</sup> | 80.5 $\pm$ 5.5 <sup>a</sup>  | 95.6 $\pm$ 3.4 <sup>b</sup> |

Note. Shared letters denote no significant difference (ANOVA, post-ANOVA Tukey,  $P < 0.05$ ).

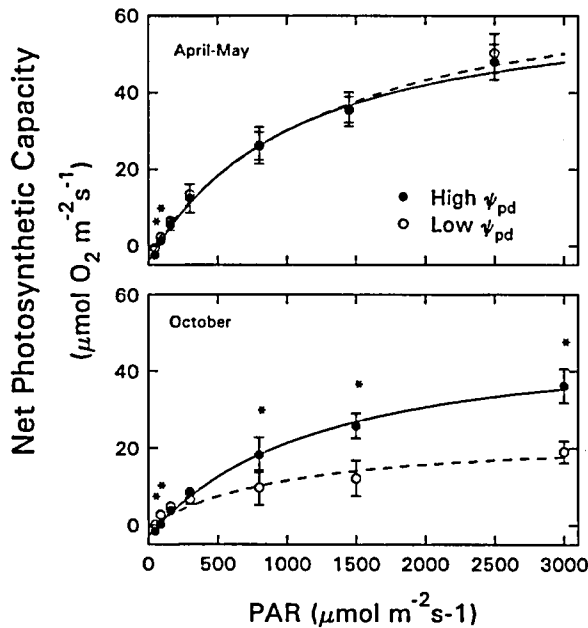


Fig. 5 Light curves for *Quercus douglasii* trees with low or high seasonal  $\psi_{pd}$  (see fig. 1) during the growing season of 1988. Error bars represent 2 SEs ( $n = 4$ ) on either side of the means. Asterisks indicate means that were significantly different as determined by one-way ANOVA at each date;  $P < 0.05$ .

in April–May for low- $\psi_{pd}$  *Q. douglasii*, but by October it had declined to 61% of  $A_{max}$ /leaf mass of high- $\psi_{pd}$  trees (fig. 4B).

### Discussion

Leaves on *Quercus douglasii* trees with apparently shallow root systems (rapidly decreasing summer  $\psi_{pd}$  and high root biomass near the surface) were smaller; had lower LSMs, respiration rates, and compensation points; appeared to undergo larger seasonal osmotic adjustments; and decreased more rapidly in photosynthetic capacity and chlorophyll content than leaves on *Q. douglasii* trees with deep root systems (slowly decreasing summer  $\psi_{pd}$ , and much lower root biomass near the surface). For *Q. douglasii* with shallow root systems, smaller leaves, rapid osmotic adjustment, and higher spring  $A_{max}$  per leaf mass may function to conserve water and to maximize seasonal water-use efficiency as surface soils dry during the rainless California summer. In comparison, large leaves that sustain relatively high  $A_{max}$  throughout the summer may function to maximize total seasonal carbon gain rather than water-use efficiency on trees with deep root systems.

Although some leaf characteristics appeared to change as a function of water potential similarly for both groups of trees, perhaps the strongest evidence in this study for coordination between root and shoot systems of mature *Q. douglasii* was the production of morphologically and physiologically different leaves on low- $\psi_{pd}$  versus high- $\psi_{pd}$  trees in April and May, before the onset of significant differences in water potential in June. Seasonal trends in  $\psi_{pd}$  of individual

trees measured in 1988, the year of this study, were very similar to  $\psi_{pd}$ 's measured in 1987 and in 1986 for the same trees (Callaway 1990, and unpublished data). Thus the differences we measured in leaf area, LSM, quantum yield, respiration rate, and compensation point in 1988 may have been the result of acclimatization to long-term exposure to different soil water potentials. Others have found that intraspecific changes in LSM (Nobel 1980), quantum yield (Björkman and Powles 1984; Ben et al. 1987), respiration rate (Gaff 1980; Dougherty and Hinckley 1981), and compensation point (Tenhunen et al. 1984, 1985) occur concurrently with water stress, as we also found for *Q. douglasii*, but to our knowledge our results provide the first evidence for physiological and morphological acclimation of leaves to drought prior to the onset of drought. This apparent "anticipation" of drought might be influenced by some form of hysteresis via such factors as water relations during the previous year or carbohydrate reserves. Leaf development of other winter-deciduous oaks has been shown to be dependent on stored carbohydrate reserves (Dougherty et al. 1979).

Alternatively, it is possible that the morphological and photosynthetic differences in leaves measured in the spring represented genetic, ecotypic differences or were related to differences in soil nutrients. Comparisons of selected isozymes for our two sample groups were performed by the Pacific Southwest Experiment Station (U.S. Forest Service), and no significant differences were found (Callaway 1990). Although these data do not compare the enzymes that regulate the specific morphological and physiological characteristics studied here, they indicate that the sampled trees were not hybrids. Total nitrogen, phosphorus, magnesium, and calcium were higher in the surface soils under high- $\psi_{pd}$  trees than under low- $\psi_{pd}$  trees (Callaway et al. 1991), but leaf nitrogen per leaf mass was higher for low- $\psi_{pd}$  trees than for high- $\psi_{pd}$  trees in both the spring and October. The differences in fine root concentration in shallow soil under high- and low- $\psi_{pd}$  trees, however, may have been affected by differences in soil nutrients.

There are several mechanisms that may be involved in the loss of photosynthetic capacity (independent of stomatal regulation) in the leaves of *Q. douglasii* during ensuing summer drought. First, osmotic adjustment in leaves may require nitrogen that otherwise might be incorporated in chlorophyll and photosynthetic enzymes. In support of this, we found that osmotic adjustment occurred in a low- $\psi_{pd}$  tree, and leaf chlorophyll,  $A_{max}$ , and dark respiration rates declined during the summer drought, but total leaf nitrogen did not change. Other species of oaks have been reported to adjust osmotically in response to water stress (Hinckley et al. 1978; Bahari et al. 1985). Our data on osmotic adjustment must be interpreted with caution because of our low sample size ( $n = 1$ ), and because estimates of full turgor osmotic potential using fully hydrated rather than nonhydrated leaves are problematic (Meinzer et al. 1986, 1988). Second, water stress

may have directly suppressed enzyme activity related to photosynthesis (Hsiao 1973; Becker and Fock 1986). Third, water stress combined with exposure to high light may have damaged photosynthetic components or induced protective mechanisms (Long et al. 1994). Björkman and Powles (1984) reported that slowly applied water stress reduced quantum yield in *Nerium oleander* in laboratory experiments and was associated with a light-dependent reduction in photochemical activity and electron transport. Kaiser (1987) reported that photosynthetic capacity in several plant species was insensitive to cell dehydration down to 50%–70% relative water content and suggested that photoinhibition, together with general senescence phenomena, may interact with long-term water stress to inhibit photosynthetic capacity under natural drought conditions. Finally, water stress may have caused a decrease in cell volume, concentrating cell metabolites, and directly inhibiting photosynthetic capacity (Kaiser 1982).

The association of leaf size and LSM with  $\psi_{pd}$  may be related to temperature. Using the general equations of Nobel (1983), we estimated average boundary layers at a wind speed of 5 m s<sup>-1</sup> to be 30% thicker for leaves on high- $\psi_{pd}$  trees (10.1 cm long) than for low- $\psi_{pd}$  trees (6.0 cm long). Leaves with thin boundary layers require less transpirational cooling to maintain temperatures near ambient than leaves with thick boundary layers (Taylor 1975).

Water stress typically reduces photosynthetic rates by lowering stomatal conductances (Gollan et al. 1985; Doley et al. 1987; Harley et al. 1987). However, the reductions in photosynthetic capacity of mature *Q. douglasii*, which we measured during ensuing summer drought, were not the result of lower stomatal conductances since the O<sub>2</sub> electrode measurements were conducted under very high, and probably saturating, CO<sub>2</sub> partial pressures (5 kPa). We do not know the relative proportions by which total carbon assimilation of *Q. douglasii* is limited by the effects of water stress on photosynthetic capacity versus stomatal conductances in the field. Harley et al. (1987) reported that *Cistus salvifolius* shrubs utilized about one-half of their photosynthetic capacities (capacities were measured at lower ambient CO<sub>2</sub> levels than in this study) when experiencing water stress in the late summer. The difference between photosynthetic capacities and actual rates in the field were attributed to stomatal closure. Partial utilization of photosynthetic capacity at high

light irradiances while under water stress has also been reported for *Q. suber* and *Q. coccifera* (Tenhunen et al. 1984, 1985; Harley et al. 1986) and was also attributed to stomatal limitation.

Species-specific differences in root architecture, and thus access to soil water, have been cited as being important to the distributions of several California oak species (Cooper 1926; Hellmers et al. 1955; Griffin 1973; Kummerow and Mangan 1981; Matsuda and McBride 1986; Callaway 1991). Our results indicate that the plasticity of root systems may also be important. Coordination of root architecture and above-ground structures and functions may contribute to the ability of *Q. douglasii* to adapt to the exceptionally broad range of geographical, topographical, and soil moisture conditions in which it is found (Griffin 1977). Other ecological consequences of root-shoot coordination in mature *Q. douglasii* also appear to be substantial. Trees with low  $\psi_{pd}$  grow slower, produce fewer and smaller acorns, cycle smaller quantities of nutrients to surface soils through canopy litterfall and throughfall, and interact differently with understory plants than do trees with high  $\psi_{pd}$  (Callaway et al. 1991, unpublished data).

Overall, our results indicate that leaf morphology and physiology are correlated with variable root architecture under natural field conditions, and such coordination may contribute substantially to the unusually wide range of habitats in which this species occurs. Understanding the coordinated responses of leaves and roots may provide greater insight into the factors that control the distributions of other plants than studies of leaf and root characteristics in isolation from each other. Our data provide strong circumstantial evidence for root and shoot coordination of mature trees under natural field conditions, but confirmation of such coordination will require experimental manipulations, quantitative measurements of leaf and root characteristics at the whole-tree level, and diurnal and seasonal measurements of in situ leaf performance.

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