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Author(s): Ragan M. Callaway

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EFFECTS OF SOIL WATER DISTRIBUTION ON THE LATERAL ROOT DEVELOPMENT OF THREE SPECIES OF CALIFORNIA OAKS¹

RAGAN M. CALLAWAY

Department of Biological Sciences, University of California, Santa Barbara, California 93106

The responses of seedling root systems of three species of oaks in California to two experimental soil moisture regimes were studied by comparing lateral root development, root and shoot weights, and root : shoot ratios. In the first soil moisture treatment the taproot was allowed to extend into moist soil throughout the duration of the experiment (control), while in the second treatment (shallow) the taproot grew into a dry substrate below 30 cm of moist soil. The treatments were intended to approximate soil moisture conditions experienced by oak seedlings in the field when deep soil water sources vary in their accessibility (control : accessible, shallow : inaccessible). Lateral root growth of *Quercus agrifolia* did not increase significantly when the primary root tip died in the shallow treatment, resulting in an overall decrease in the percent of the root system composed of lateral roots. *Q. douglasii* and *Q. lobata* increased lateral root weights by 80% and 70%, respectively, on the upper 30 cm of the primary root when the primary root tip died. *Q. lobata* was the only species that decreased in shoot and root weight (25% and 21%, respectively) with the loss of the root tip, indicating that, unlike the other species, it was dependent on the primary root for maximum growth. The morphological responses of these species correspond with their distributions and also may be a factor that influences their interactions with other species.

Excavations of plant roots have shown that root structure varies widely within the same species and that the variation is often correlated with environmental differences (Biswell, 1935; Muller, 1949; Kummerow, 1980; Riedacker and Belgrande, 1983). Richards (1986), in a review of root form and depth distribution, stated that the development of deep taproots vs. wide-spreading roots in phreatophytes appears to be facultative and is dependent on environmental conditions such as depth to the water table. The morphological flexibility of the root systems of these plants may contribute to their ability to adapt to a range of habitat conditions. It is likely that intraspecific root plasticity also affects the distributions of other species, but the interrelationships of root plasticity and plant distributions have rarely been investigated.

The distribution of oaks in the foothill woodlands of California is thought to be largely determined by gradients of moisture availability and the adaptations of different oak species to utilize soil water at different depths (Jepson, 1910; Cannon, 1914; Cooper, 1926; Griffin, 1973, 1977; Matsuda and McBride, 1986). *Quercus agrifolia* Nee (coastal live oak) tends to occupy relatively mesic habitats and has been thought to utilize the water table in

some habitats (Cannon, 1914; Cooper, 1926; Griffin, 1973). *Quercus lobata* Nee (valley oak) occurs primarily on alluvial terraces and large valleys, but also extends onto lower rolling hills (Griffin, 1977). *Q. lobata* has been thought to be dependent on water table access (Jepson, 1910; Cannon, 1914; Cooper, 1926; Griffin, 1973) and to have deeper roots than *Q. agrifolia* (Cannon, 1914; Cooper, 1926). *Quercus douglasii* H. & A. (blue oak) occupies more xeric habitats than the other two oaks, including fringes of the grassland in the Central Valley, habitat transitional to Great Basin vegetation, and upper slopes and ridgetops in the Santa Lucia Mountains (Griffin, 1977). *Q. douglasii* is not restricted to these habitats, however, and is often abundant on valley floors. Access to the water table appears to vary with this species. Griffin (1973) and Rundel (1980) reported low predawn xylem pressure potentials (XPP) for some trees, suggesting that they were dependent on shallow soil moisture and not the water table. Lewis and Burghy (1964), however, reported that *Q. douglasii* was able to take up tritiated water placed in water tables over 20 m deep. Callaway and Nadkarni (1988) reported that *Q. douglasii* was variable in root morphology, with some trees exhibiting low predawn XPPs and dense surface roots, and other trees exhibiting high predawn XPPs and low quantities of surface roots.

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Although these three species of oaks tend to be distributed in different habitats, they each occupy a diverse range of soil and topographical environments and overlap with each other locally and geographically (Griffin, 1977). This fact, and the variable predawn XPPs and shallow root biomasses recorded for *Q. douglasii*, suggests that the distributions of these species may be affected by the adaptability of their root systems to different environmental conditions. The objective of this study was to quantify the adaptability of the root morphology of seedlings of *Q. agrifolia*, *Q. lobata*, and *Q. douglasii* when soil water was available to the growing taproot tip and when soil water was not available to the taproot tip. In this paper I examined the development of lateral roots and changes in root weights, shoot weights, and root : shoot ratios under two different soil water regimes, one with shallow and deep soil water available and the other with only shallow soil water available. The results have implications for the distributional patterns of the oaks themselves and their interactions with other species.

MATERIALS AND METHODS

Species and habitat—All three of the oak species studied here are widely distributed throughout California and occupy ranges with a distinct Mediterranean climate. Precipitation occurs primarily between September and May, and the summers are often rainless. *Q. lobata* and *Q. douglasii* are winter-deciduous and usually are in leaf between late March and November (however, seedlings germinate in the fall and retain leaves for at least the first year), whereas *Q. agrifolia* is evergreen. The former two species are more common in the interior of the state in the eastern foothills of the Coast Ranges and the western foothills of the Sierra Nevada (Griffin and Critchfield, 1972). *Q. agrifolia* is the dominant oak on the western side of the Coast Ranges but it overlaps extensively with the other oaks throughout the central and eastern parts of its range. *Q. lobata* and *Q. douglasii* are endemic to California, whereas *Q. agrifolia* extends into Baja California, Mexico. All of these species typically grow in a tree form and can be well over 100 cm in diam at breast height and over 25 m tall. *Q. agrifolia* and *Q. douglasii* in dry habitats are often much smaller.

Data collection—Acorns were collected in the Santa Ynez Valley in Santa Barbara Co. (34°30'N, 119°45'W) from ten parent trees for each species between 1 November and 7 No-

vember 1988. Acorn weights used in the experiment were: *Q. agrifolia*, 3.0–3.5 g; *Q. douglasii*, 3.5–4.0 g; and *Q. lobata*, 5.0–5.5 g. These weights were chosen because they represented the approximate intraspecific means of the acorns that were collected, and to reduce variation due to acorn size. Acorns were air-dried and planted within 2 weeks of collection. The experiment was conducted outdoors in Santa Barbara, California between 15 November 1988 and 19 June 1989.

Acorns of each species were germinated, and seedlings were grown in two different treatments that varied the soil water environments experienced by the growing roots. Containers used for the experiment consisted of two 20-liter plastic buckets, one fastened on top of the other (Fig. 1). The top bucket in both treatments was filled with an 80:20 mixture of 30-grit sand and potting soil. Thirty holes, 1 cm diam, were drilled into the bottom of each top bucket to allow oak taproots access to the bottom bucket. In one treatment, designed to expose the seedling taproots to a dry substrate, the bottom bucket was filled with pea gravel (gravel consisting of stones approximately 0.6 cm diam) and was drained by 20 large holes, 1 cm diam. Throughout this paper this treatment will be referred to as the “shallow water” treatment. In the other treatment, designed to provide soil water to the growing taproots throughout the duration of the experiment in addition to the water in the upper bucket, the bottom bucket was filled with a 50:50 mixture of 30-grit silica sand and pea gravel and was drained by 20 small holes 1 mm diam. This mixture contained approximately the same amount of gravel by weight, but interstitial spaces were filled with sand. This treatment is referred to as the “control treatment.” Ten acorns, chosen randomly from the weight classes mentioned above, were planted in each container, and each species-treatment combination was replicated in three different containers. In addition to natural rainfall, the upper buckets were watered once per week until water flowed from the drainage holes in the bottom buckets. Gravimetric measurements of soil moisture after the experiment was terminated indicated that 3 days after watering, the pea gravel was dry, and that the pea gravel and sand combination contained between 10% and 15% water.

Seedlings were harvested after 6 mo of growth on 18 June 1989, which minimized curling of the taproot at the bottom of the control buckets. The containers were cut open, soil was washed from the roots, and root systems of each individual were separated. Each seedling

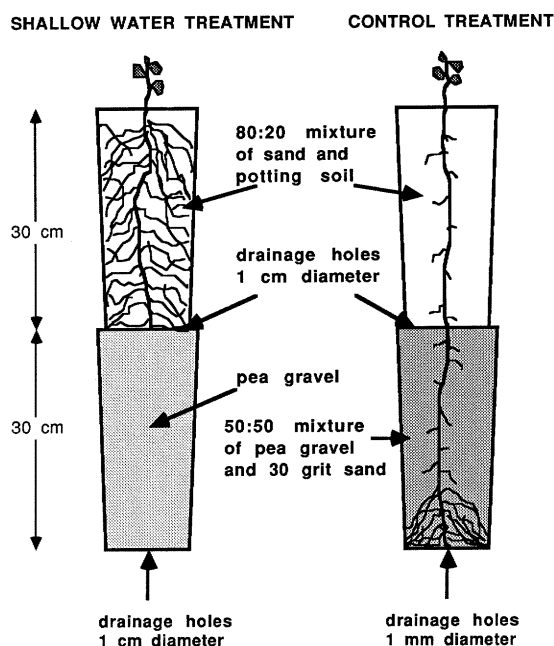


Fig. 1. Container design for manipulation of the distribution of soil water. In the experiment ten seedlings were in each container.

was dried separately at 60 C and afterwards was divided into roots and shoots. Lateral roots were removed from the primary roots in 10-cm sections. Because some curving of the main roots occurred as they elongated, 10-cm increments in soil depth were used, rather than increments of primary root length.

Separate ANOVAs showed that variation within buckets and between buckets of a given treatment was insignificant, so treatment effects for each species were tested using ANOVAs with six to ten replicates nested within each of the three buckets, and followed with Tukey tests for differences between means. I have assumed that the results presented here were not significantly biased by the statistical analysis of variables that were not independent from each other (e.g., different 10-cm sections on the same root).

RESULTS

The root tips of the seedlings of all three species died when they penetrated into the gravel of the shallow water treatment, whereas the taproots of all of the seedlings in the control treatment grew the entire 60 cm to the bases of the lower bucket, and in some cases curled up to 6 cm at the bottom. The small drainage holes used for the control treatment prevented the taproots from growing out of the buckets and into the ground.

The soil water treatments had significant effects on several other aspects of root development, but these effects were not consistent among species. Lateral root development on the upper 30 cm of primary root increased significantly for *Q. lobata* and *Q. douglasii* in the shallow water treatment (Figs. 2, 3). In this treatment, *Q. douglasii* lateral root number increased by twofold and lateral root weight by over sixfold on the upper 30 cm of primary root (Figs. 2, 3). *Q. douglasii* root weights, shoot weights, root : shoot ratios, and percent lateral roots, however, did not differ between treatments (Table 1). This suggests that under plentiful soil water conditions, lateral root systems of *Q. douglasii* can compensate for the loss of the root tip of the primary taproot and maintain a normal rate of growth. *Q. lobata*, on the other hand, produced more and heavier lateral roots on the upper 30 cm of primary root (Figs. 2, 3), but had significantly lower shoot and root weights (Table 1), which suggests that lateral roots did not completely compensate for the loss of the taproot tip with respect to overall seedling growth.

For *Q. agrifolia*, the loss of the taproot tip coupled with the loss of lateral roots normally present at the ends of healthy taproots resulted in a 50% decrease in the percentage of the root system of *Q. agrifolia* composed of laterals and a 33% decrease in total root weight (Table 1). Shoot weight of *Q. agrifolia*, however, did not decrease significantly in the shallow water treatment, which indicates that this species was able to maintain normal shoot growth even with reduced lateral root development. Lateral root number for *Q. agrifolia* in the control treatment was significantly higher ($P < 0.05$) than for the *Q. lobata* controls between 0 and 30 cm and for *Q. douglasii* controls in the 20–30-cm section. Also, the mean lateral root weight was higher in the three upper 10-cm sections for *Q. agrifolia* in the control than the other two species. This suggests that *Q. agrifolia* may develop more extensive shallow lateral root systems than the other two species when the primary root tips remain intact.

DISCUSSION

Seedlings that were provided with deep water did not develop extensive lateral root systems on the upper 30 cm of primary roots even though the soil in the upper buckets was kept wet. Seedlings of *Q. douglasii* and *Q. lobata*, however, developed higher weights and numbers of lateral roots on the upper 30 cm of primary roots when taproot tips died after penetrating into a drier substrate. This suggests a

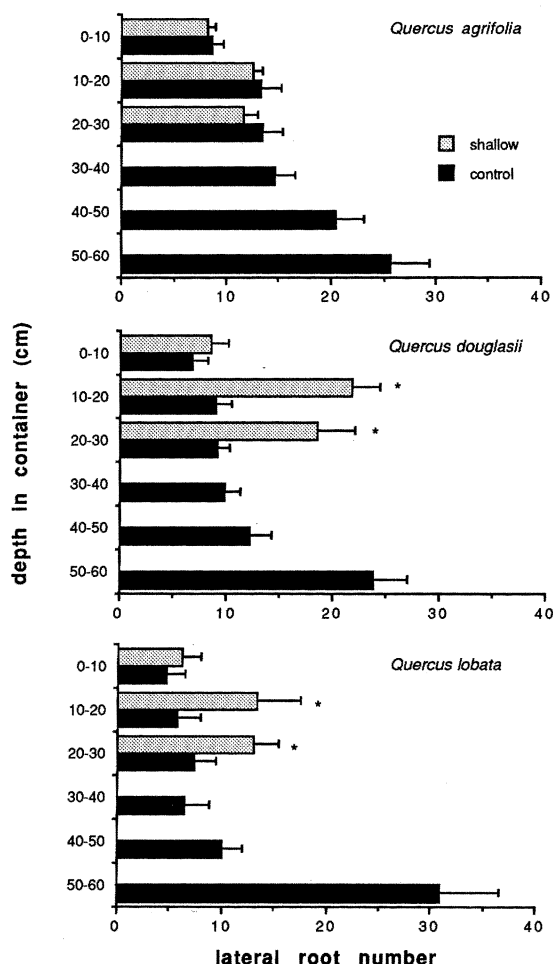


Fig. 2. Comparisons of lateral root weight on 6-month-old seedlings of three species of California oaks in two soil water treatments. Means \pm two standard errors are presented for each 10-cm section of the primary root. * denotes significant differences determined by ANOVAs and post-ANOVA Tukey analysis of means ($P < 0.01$).

mechanism by which these species may minimize energy allocation to lateral roots in drier, shallow soil when deep water is attained, and by which these species may exploit surface water when deep soil water is not attained. These results also indicate that the root morphology of a given individual may be partially dependent on the fate of the taproot. Thus, individuals with taproots damaged by predation, substrate characteristics (rocks, hardpans, etc.) or drought may develop root systems with more laterals than those with undamaged taproots.

Control of root morphology by the apical meristem of the taproot has been reported elsewhere for oaks as well as for other plants. Riedacker and Belgrande (1983) reported that the growth and geotropism of lateral roots of *Q. robur*, a European deciduous oak, were con-

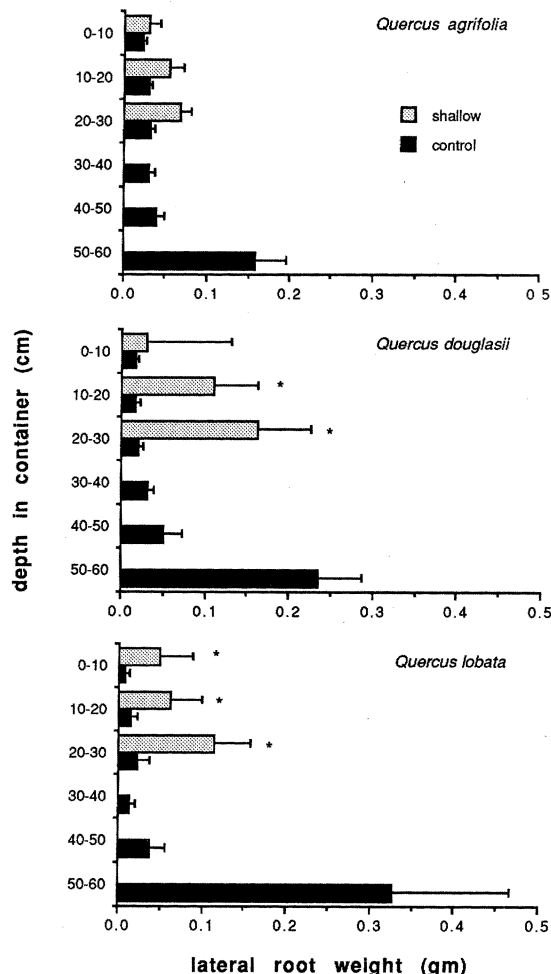


Fig. 3. Comparisons of lateral root numbers on 6-month-old seedlings of three species of California oaks in two soil water treatments. Means \pm two standard errors are presented for each 10-cm section of the primary root. * denotes significant differences determined by ANOVAs and post-ANOVA Tukey analysis of means ($P < 0.01$).

trolled by the tip of the primary root. They found that when vertical downward growth of taproots was physically stopped, lateral roots became longer, thicker, and acquired the geotropism of the original taproots. When the growth of the taproots was only slowed, lateral roots increased in length but remained horizontal. As was observed in this experiment, short laterals developed throughout primary roots with intact root tips, but growth was low unless the apical root tips of the taproots were damaged or stopped. In *Betula papyrifera*, paper birch, injury to primary root tips stimulated lateral root growth along the entire length of the axis of the primary root (Horsley, 1971). Vartanian (1981) found that decreasing soil moisture slowed taproot growth of *Sinapsia alba*, an annual in the Brassicaceae family, and

TABLE 1. Shoot weights, root weights, root : shoot ratios, and the percentages of root systems comprised of lateral roots for 6-month-old seedlings of three species of California oaks in two soil water treatments*

	<i>Quercus agrifolia</i>		<i>Quercus lobata</i>		<i>Quercus douglasii</i>	
	Control (n = 22)	Shallow (n = 29)	Control (n = 17)	Shallow (n = 18)	Control (n = 26)	Shallow (n = 23)
Shoot weight (g)	1.42 (0.35) ^a	1.31 (0.31) ^a	1.14 (0.50) ^a	0.85 (0.24) ^b	0.96 (0.23) ^a	0.92 (0.27) ^a
Root weight (g)	0.99 (0.15) ^a	0.64 (0.17) ^b	3.17 (0.88) ^a	2.50 (0.67) ^b	1.96 (0.23) ^a	1.99 (0.56) ^a
Root : shoot ratio	0.70 (0.16) ^a	0.49 (0.09) ^b	2.78 (0.70) ^a	2.94 (0.61) ^a	2.04 (0.33) ^a	2.16 (0.49) ^a
Lateral roots (% of root system)	32 (9) ^a	15 (6) ^b	18 (17) ^a	24 (9) ^a	26 (17) ^a	30 (8) ^a

* Numbers in parentheses are standard deviations; shared letters within a species denote no significant differences as determined by nested ANOVAs and post-ANOVA Tukey comparisons of means ($P < 0.01$).

at a soil water potential of -1 MPa rapid lateral root production was stimulated.

Little is known about the morphology of oak roots in natural soils because their excavation is problematic. The data presented here, however, are consistent with the results of field observations of oaks in general (Holch, 1931; Biswell, 1935; Jenik, 1957) and of the species studied here. Cannon (1914) described the root system of *Q. agrifolia* as being primarily composed of “superficial” or lateral, roots rather than having a deep taproot-dominated system. Roberts and Smith (1980) reported that lateral root disturbance in the upper 2 m of soil (trenching for suburban development) decreased diurnal XPPs for both *Q. agrifolia* and *Q. lobata*. Their data showed that *Q. agrifolia* tended to be more water-stressed when lateral roots were disturbed, which suggests that it was more dependent on the water in the upper 2 m of soil. The greater development of lateral roots on *Q. agrifolia* controls compared to the other controls in this study is consistent with these observations. The scarcity of *Q. agrifolia* in consistently drier habitats (Griffin, 1973), and the abundance of *Q. agrifolia* on alluvial terraces with relatively high water tables (Cooper, 1926) and in many riparian associations (Holland and Keil, 1989), may be due in part to dependence on lateral roots and the lack of plasticity of the root system.

The development of extensive lateral roots by *Q. douglasii* in the shallow water treatment is consistent with the findings of Callaway and Nadkarni (1988), who reported that mature *Q. douglasii* in the field may either tap deep water and produce few surface roots or utilize mainly shallow soil water via a dense lateral root system. Other research also indicates that some *Q. douglasii* access the water table and other individuals do not (see Introduction). The wide range of habitats occupied by *Q. douglasii* may be due, in part, to the morphological plasticity of its root system. Callaway and Nadkarni (1988) also reported that this variable rooting morphology was associated with different in-

teractive effects on understory species. Oaks with low root biomass in shallow soils facilitated the growth of understory species via litterfall and throughfall nutrient addition, whereas oaks with high shallow root biomass suppressed understory species.

A critical component of the ability of a species to survive using only shallow soil water in a xeric habitat is the physiological tolerance of water stress. *Q. douglasii* has been shown to be able to tolerate XPP of below -5.0 MPa (Rundel, 1980). Thus, the ability of this species to survive without access to the water table may be due in part to the morphological adaptability of its root system and to its tolerance to lower soil water potentials that exist above the water table.

Q. lobata “is characterized by a well-developed taproot” (Cannon, 1914) and has been thought to consistently utilize the water table (Cooper, 1926; Griffin, 1973). In this study, *Q. lobata* seedlings had high root : shoot ratios and root weights (over four and three times that of *Q. agrifolia*, respectively). In the experiment reported here, *Q. lobata* did increase lateral root production on the upper 30 cm of primary root when taproot tips grew into dry substrate, which suggests that the root systems of this species can also adapt morphologically to dry substrates. *Q. lobata*, however, is rarely found in habitats as xeric as is *Q. douglasii*, which suggests that the ability of an oak to develop a lateral root sytem is not the only prerequisite to occupying xeric environments. *Q. lobata* may be restricted to habitats with accessible water tables by physiological intolerance to high water stress and the inability to survive on the limited water available in shallow soils during the rainless summer. This is substantiated by Hollinger (1984), who has reported high rates of transpiration and low water-use efficiencies for *Q. lobata* under some conditions. Data are not available, however, that compare both *Q. lobata* and *Q. douglasii*. Data presented here also indicate that even in wet shallow soils *Q. lobata* seedlings do not grow as well when they

become more dependent on lateral roots (Table 1).

In conclusion, the three oak species studied had quantitatively different responses when taproot tips grew into a dry substrate. *Q. lobata* and *Q. douglasii* seedlings produced very little lateral root growth on the upper primary root when root tips were intact but large amounts when the root tips died. *Q. agrifolia* produced moderate amounts of lateral roots in both treatments and did not increase lateral root production significantly when the taproot tips died.

The death of the taproot and subsequent development of lateral roots were attributed to different soil moisture regimes, but other factors (such as low nutrient availability in the lower containers and lack of mycorrhizal infections) may have contributed to the species-specific responses as well. Clearly, the morphological plasticity of the roots of these species may be a mechanism by which they can reduce the allocation of resources to lateral roots when deep soil water is not available. Root plasticity, or lack of it, may contribute to the distribution of these oaks, and to their interactive effects on neighboring species. Quantitative field analyses of the root systems of both seedlings and adults will be required to better understand the significance of the morphological plasticity of roots to the distributions of these species.

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