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The influence of simulated browsing on tissue water relations, growth and survival of *Quercus douglasii* (Hook and Arn.) seedlings under slow and rapid rates of soil drought

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Abstract. This study examines the interactive effects of (a) the rate at which water stress is applied and (b) simulated browsing on seedling morphology, physiology and survival of blue oak (*Quercus douglasii* (Hook and Arn.)). The experiment employs two rates of soil water depletion and three intensities of defoliation. Tissue water relations, growth, stomatal conductance to water vapour, and second year survivorship were assessed. Severe defoliation, which included removal of apical meristem, resulted in a 50% increase in total and osmotic water potential, and a similar increase in the water potential at zero turgor, only where water stress was applied rapidly. However, the total growth period and subsequently total biomass was reduced by 60 days and 100%, respectively. Only those seedlings which experienced slow rates of induced water stress and received severe defoliation survived to produce green leaf tissue in the second year. Water stress and herbivory may thus significantly interact to affect both physiological acclimation to drought and tolerance to browsing in juvenile blue oaks. Under the current conditions of oak seedling association with annual species in blue oak savannas and woodlands, tolerance to periodic browsing is severely reduced because of the rapid rates of soil water depletion caused by annual grass and forb transpiration.

Key-words: Browsing, *Quercus douglasii*, water relations

Introduction

The understorey of the California blue oak (*Quercus douglasii* (Hook and Arn.)) savanna provides

an example of a community which has undergone both floristic and faunal changes (Bartolome, Klukkert & Barry, 1986; Welker & Menke, 1987). Before European settlement, perennial bunchgrass species such as *Stipa pulchra* Hitch. and *Elymus glaucus* Buckl. were predominant in the presence of few large-hooved herbivores (Bartolome *et al.*, 1986; Jackson, 1985). These former dominant plant species have been replaced by introduced annual species such as *Bromus*, *Avena*, *Vulpia*, *Hordeum* and *Lolium* while herbivore densities have increased dramatically with the introduction of livestock (Wagner, 1989). The annual plant species produce a much greater leaf area in the spring which deplete soil water faster than perennial species do (Jackson & Roy, 1986; Gordon *et al.*, 1989). Simultaneously, the large numbers of livestock expose woody species to browsing levels uncommon in earlier times (Wagner, 1989).

Changes in the understorey flora and fauna have direct and indirect impacts on the native vegetation. Introduced herbivores can directly reduce plant biomass and repeated grazing or browsing can increase mortality of seedlings and mature plants. Indirectly, introduced annual plants can either deplete soil water levels too low for native species to maintain a favourable water status (Harris, 1967); or annuals can deplete water too rapidly for plants to ameliorate physiologically the effects of decreasing soil water potentials (Osonubi & Davies, 1981). With the rapid onset of drought, plants are unable to modify their allocation patterns and produce osmotically active compounds quickly enough to prevent tissue desiccation and turgor loss (Jones & Rawson, 1979; Turner & Jones, 1980; Hanson & Hitz, 1982; Flower & Ludlow, 1986).

The responses of woody plants to browsing or defoliation are not as well understood as those for graminoids (Caldwell *et al.*, 1981; Welker *et al.*, 1985; Welker, Briske & Weaver, 1987). Heichel & Turner (1983, 1984) have, however, investigated defoliation responses of *Q. rubra* trees under field

conditions. Shifts in bud activation patterns, carbon allocation to refoliated material and photosynthetic rates of residual leaf tissue are all influenced by defoliation. Habitat type can also significantly alter browsing responses in woody species (Danell, Huss-Danell & Bergstrom, 1985). Birch juveniles browsed by moose showed changes in shoot longevity, mineral content and bud demography as a function of the local environment; while the variability in stress resistance of woody seedlings has been attributed to the interaction of soil water conditions and defoliation intensity (Wright, Hall & Peacock, 1989). These studies have not however, addressed the question of how woody plants respond to prolonged drought typical of Mediterranean climate; nor were the causal mechanisms of tissue water relations examined.

The density and morphology of associated vegetation competing for soil water can influence the rate at which associated oak seedlings experience drought (Jackson & Roy 1986; Gordon *et al.*, 1989). We have observed that when blue oak seedlings are grown amongst native perennial *S. pulchra* tussocks in 1 m tall containers, soil and seedling water potentials remain above -1.0 MPa until June, at which time soil water potentials decrease to -5.0 MPa by mid July. Soil and seedling water potentials decrease more rapidly when oaks are growing amongst annual *Bromus mollis* plants, reaching -3.5 MPa by June (Gordon *et al.*, 1989; J. M. Welker, unpublished observations). If soil water depletion by native perennial grasses permits the maintenance of positive turgor late into the summer drought, then simulated conditions of slow vs rapid rates of oak seedling water stress should result in significant improvements in biomass accumulation, growing season length, survivorship and plant water relations in blue oak seedlings.

In this study we have used controlled rates of soil drying to simulate soil water conditions of annual and perennial dominated understoreys in the California oak savannas and woodlands. We combined two water depletion rates with three intensities and two timings of simulated browsing to quantify the interaction effects of: (a) the rate of induced water stress in oak seedlings, (b) defoliation intensity, and (c) the timing of defoliation on water relations, growth and survivorship of *Q. douglasii* seedlings. We hypothesize that the consequences of severe defoliation and rapid rates of soil drought are increased levels of seedling mortality and reductions in root and shoot biomass. Further, we hypothesize that oak seedling alter-

ations in tissue water relations and physiological responses are not of a magnitude great enough to offset dual stress.

Materials and methods

Blue oak acorns were collected in the fall of 1986 from five trees growing in the western foothills of the Sierra Nevada Mountains, Yuba Co., California. Acorns germinated in sealed plastic bags which were filled with vermiculite and kept at 5°C . Containers of two different volumes were used to induce two rates of soil water depletion (Flower & Ludlow, 1986). Polyvinyl-chloride (PVC) tubes 100 cm in length with diameters of 5 cm (small) and 10 cm (large) were constructed. The small containers were used to induce rapid rates of water stress simulating conditions of oak seedlings growing among annual species. Large containers were used to induce slow rates of water stress simulating conditions of oak seedlings growing among perennial bunchgrass species. The tubes were filled with soil collected from a blue oak understorey and saturated with deionized water.

On 13 February 1987, three and two germinated acorns were planted in the large and small containers, respectively. On 4 April 1987 seedlings were thinned to one per container and the soil was maintained at field capacity with weekly watering of deionized water until 18 April 1987. Afterwards, water supply was interrupted for 160 days until late September.

Soil water potential was measured using screen cage psychrometers calibrated under isothermal conditions (Brown & Bartos, 1982; Merrill Inc., Logan, Utah). Psychrometers were installed through access holes in the PVC at depths of 30 and 75 cm when soil profiles were wet. Soil water potential measurements were taken before sunrise using a CR-7 micro logger (Campbell Scientific, Utah) with cooling times of either 15 or 30 s and water potentials averaged for the two depths.

Four intensities of defoliation and two container sizes were combined into an incomplete factorial design. Each treatment combination was replicated five times and each set of replicates was randomly assigned to over 150 containers with morphologically uniform seedlings. The following treatments were applied to seedling groups in either large or small containers: (a) no defoliation (ND); (b) light defoliation (LD), i.e. removal of every other leaf on day 11 of the drought (23.5 cm^2 of leaf area removed); (c) severe defoliation (SD), i.e. stem severing on day 11 of the drought leaving six axillary buds (37.8 cm^2 leaf area removed); and

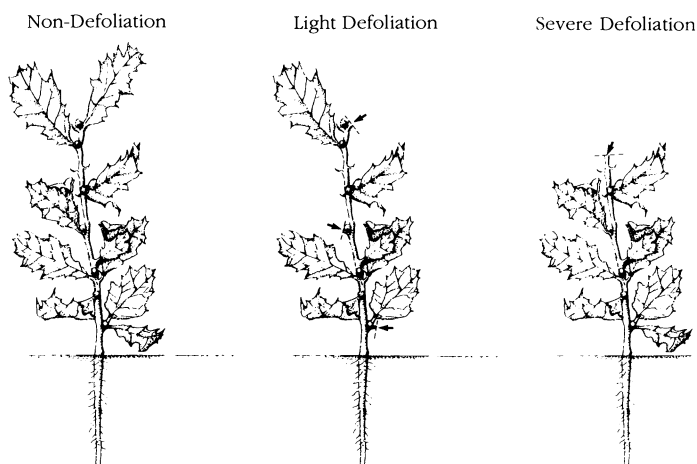


Fig. 1. Defoliation treatments on first year blue oak seedlings.

(d) severe defoliation (2SD), i.e. stem severing on day 71 of the drought (73.2 cm^2 leaf area removed) (Fig. 1). Four whole seedlings from each treatment combination were collected on six occasions between April and September for pressure-volume and morphometric analyses. A small subset of plants was maintained under well-watered conditions throughout the experimental period. Non-defoliated seedlings were watered to field capacity each week and harvested at the last two dates under slow rates of stress and on the last sample date under rapid rates of stress. Well-watered plants were used in an attempt to differentiate changes in tissue water relations associated with drought and those attributed to tissue ontogeny (Saruwatari & Davis, 1989).

At each sample date the morphometric and physiological characteristics assessed were: (a) seedling shoot and root biomasses; (b) osmotic, turgor and total water potentials plus the water potential at zero turgor (Roberts & Knoerr, 1977); (c) midday stomatal conductance to water vapour; and (d) soil water potential. Seedlings with attached leaves were collected before dawn, placed in a zip-lock bag containing moist paper towels and immediately brought to the lab for pressure-volume analysis. Fresh weights were recorded to the nearest 0.1 mg and seedlings were placed into pressure chambers lined with moist filter paper. Each seedling has 1 cm of basal stem protruding from the chamber gasket. Six pressure-volume curves were simultaneously obtained using six pressure chambers connected in sequence. Each pressure chamber had its own pressure gauge, regulating needle valve, and three-way pressure valve. End points were assessed with

the aid of a $10\times$ dissecting scope (Tyree & Hammel, 1972).

We used the over-pressure modification of the initial pressure-volume technique proposed by Tyree & Hammel (1972). This approach assumes that each new 'balancing pressure' is the shoot water potential (Clayton-Greene, 1983). Numerous studies have opted for samples resaturation because the initial osmotic potentials can always be assessed at 100% relative water content (Osonubi & Davies, 1981; Clayton-Greene, 1983). However, we did not rehydrate our samples before pressure-volume analysis to insure more accurate measurements of tissue water parameters (Meinzer *et al.*, 1986). The initial osmotic potentials at 100% relative water content were extrapolated from the pressure-volume curve to estimate turgid weight (Wilson *et al.*, 1980). Turgor pressure was calculated as the difference between the total and initial osmotic potentials.

Sap expressed from the end of blue oak seedlings was collected in 10 cm long polyethylene tubes filled with dry tissue paper and pre-weighed to the nearest 0.1 mg . The balance pressure was increased in increments of approximately 0.2 MPa . After 15 min at each pressure, the chamber pressure was reduced until sap flow ceased. The tube was then reweighed and the exudate weight was converted to volume, assuming a sap density of 1 g cm^{-3} . Each pressure-volume curve consisted of 10–13 balancing pressures. Chamber pressures were slowly reduced and seedling weight determined following the final balancing pressure.

Data analysis

Water relation components and morphometric

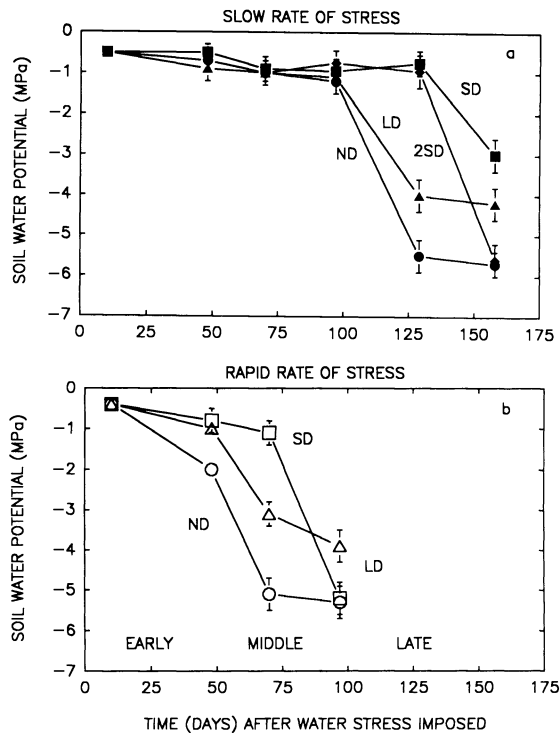


Fig. 2. Soil water potential in the large (slow rates of water stress) and small (rapid rates of water stress) seedling containers during the 158-day drought period. ND = non-defoliated seedlings; LD = lightly defoliated seedlings; SD = severely defoliated seedlings; 2SD = severely defoliated seedlings during the mid-drought period (mean \pm SE).

parameters were analysed using a general linear model (GLM) analysis of covariance ($\alpha = 0.10$) and GLM analysis of variance with a Bonferonni mean separation (SAS, 1985). Analysis of covariance was conducted with date as a covariant between the forty-eighth and ninety-seventh day of the drought period. Covariance analysis was limited to this period because not all treatments were present at other dates. At 10, 128 and 158 days after drought was initiated, Bonferonni mean separation was used to make treatment comparisons within a date ($\alpha = 0.020$).

Results

Soil water potential

For simplification, the drought period is discussed as three periods; early drought (days 0–48), mid-drought (days 48–97) and late drought (days 97–160). Defoliation effects on soil water potential were only realized after day 127 of the drought. At this point in the drought, soil profiles with defoliated seedlings maintained significantly higher

water potentials. By day 158, soil profiles with severely defoliated seedlings (SD) had 111% higher soil water potentials than profiles with non-defoliated seedlings (ND) (Fig. 2a). Defoliation also slowed soil water loss in the middle drought period for the rapidly drying condition. Soil profiles with severely defoliated seedlings maintained the highest water potential of -1.0 MPa on day 70 of the drought, but they decreased to the same potential as soil profiles with non-defoliated seedlings by day 97 (Fig. 2b).

Plant water potential

Total water potential of oak seedlings decreased significantly during the mid-drought period in large containers (Fig. 3a) (Table 1). Seedlings which had been severely defoliated on the eleventh day of the drought cycle maintained the highest water potential of -0.8 MPa on day 127 while at this same time, seedlings which were severely defoliated on day 71 had a significantly lower water potential of -1.25 MPa. By the end of the experimental drought, seedlings which were severely defoliated on day 11 had significantly higher total water potentials than either seedlings which were non-defoliated or seedlings which were severely defoliated in the mid-drought period (Fig. 3a).

Osmotic potentials decreased during the mid-drought period and were significantly affected by defoliation (Fig. 3b). The most dramatic decreases occurred during the late drought period, between days 97 and 129. At the end of the drought only seedlings which were severely defoliated on the eleventh day maintained significantly ($P = 0.020$, $t = 2.97$) higher osmotic potentials while maintaining positive turgor potentials.

Turgor pressure was much more variable during the analysis period and the overall GLM model was only marginally significant ($P = 0.05$, $F = 2.23$) compared to the other water potential components (Fig. 3c). During the mid-drought period both light and severe defoliation significantly reduced seedling turgor potential. Forty-eight days after the drought began, lightly defoliated seedlings had the lowest turgor potential of 0.81 MPa vs 0.91 and 1.1 for severe and non-defoliated seedlings, respectively.

Seedlings experiencing slow rates of water stress had water potentials at zero turgor (WPZT) which were significantly affected by the duration without water and defoliation treatment (Fig. 3d). Non-defoliated seedlings retained WPZT which were equal to lightly defoliated seedlings but

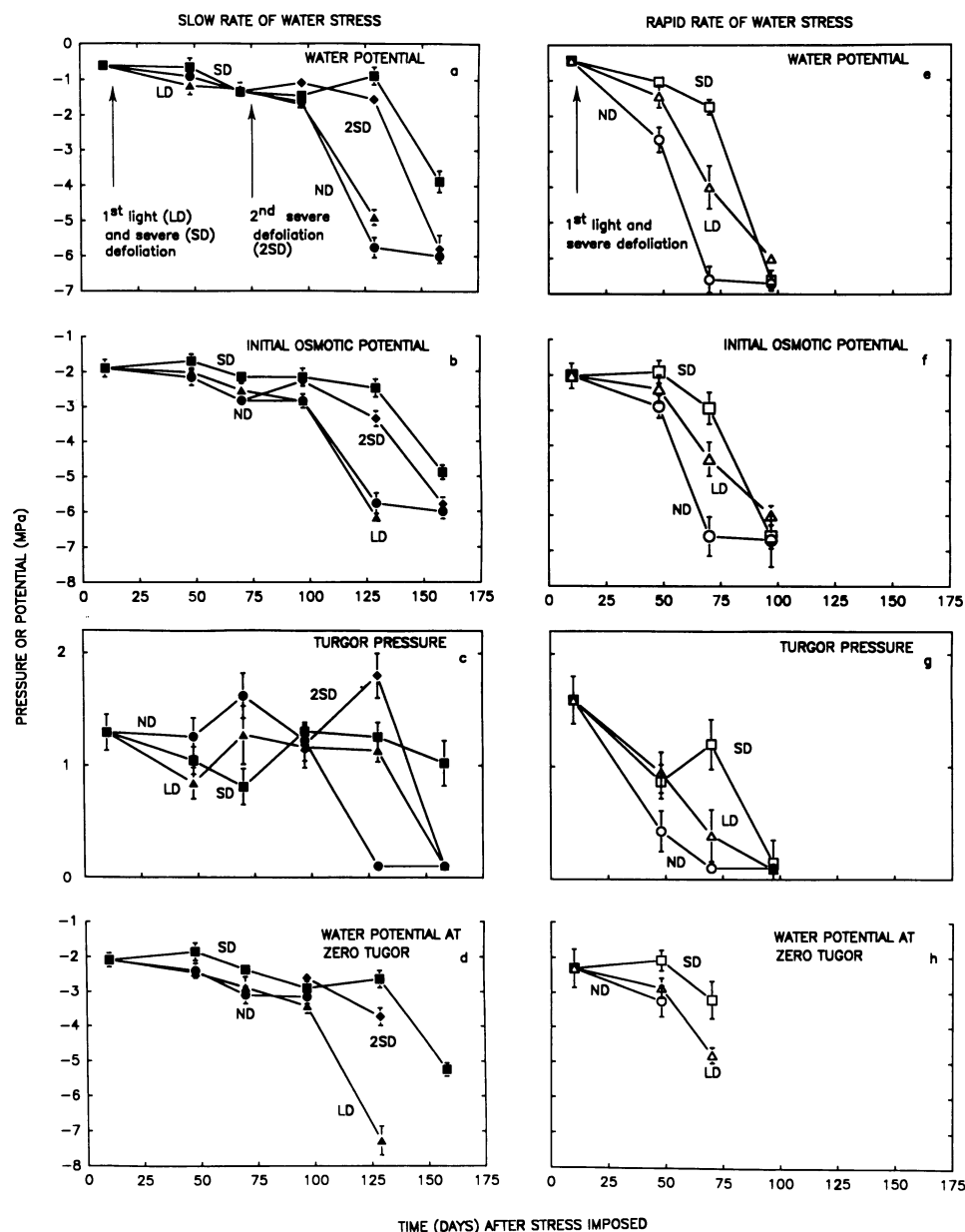


Fig. 3. Tissue water relations of blue oak seedlings experiencing slow and rapid rates of water stress (mean \pm SE). Nomenclature is the same as in Fig. 2.

significantly different from severely defoliated seedlings. By the late drought period, the WPZT of lightly defoliated seedlings had decreased to -7.0 MPa, while seedlings which were severely defoliated on days 11 and 71 had WPZT of -2.1 MPa and -3.5 MPa, respectively. Only seedlings which had positive turgor could be analysed for WPZT on day 158.

The symplastic fraction (SF) and the fresh weight/dry weight ratio (FW/DW) of seedlings experiencing slow rates of water stress were

unaffected by defoliation or days after drought induction until late in the drought period (data not shown) (Table 1). No change in the SF and the FW/DW occurred when the total water potential, initial osmotic potentials, and WPZT significantly decreased, suggesting solute accumulation (Saruwatari & Davis, 1989) (Fig. 3). However, by the late drought period, the turgor potential of non-defoliated seedlings reached zero, and thus decreases in the osmotic potential during the late drought are attributable to tissue dehydration (Saruwatari &

Table 1. Summary of analysis of variance for tissue water relation components during the mid-drought period (48–97 days).

	Water potential components					
	Y_t^a	$Y_{o(sat)}$	$Y_{o(tlp)}$	Y_p	SF	FW/DW
<i>Slow rate of stress</i>						
Defoliation (DF)	*	***	**	**	NS	NS
Days after drought induction (DI)	***	***	***	NS	NS	NS
DF × DI	NS	NS	NS	NS	NS	NS
<i>Rapid rate of stress</i>						
Defoliation (DF)	**	**	***	**	**	**
Days after drought induction (DI)	**	**	***	**	**	**
DF × DI	***	***	NS	***	**	**

^a Y_t = total water potential; $Y_{o(sat)}$ = osmotic potential at full turgor; $Y_{o(tlp)}$ = osmotic potential at zero turgor; Y_p = pressure potential; SF = symplastic fraction; FW/DW = fresh weight/dry weight.

* $P < 0.10$; ** $P < 0.05$; *** $P < 0.01$; NS = not significant.

Davis, 1989). Simultaneously, severely defoliated seedlings had a 28% decrease in FW/DW and a 14% decrease in SF when the osmotic potentials of these seedlings decreased from -2.2 MPa to -4.7 MPa between day 127 and day 158 (Fig. 3b).

Seedlings which were well watered in large containers experienced no significant changes in tissue water relations until the last harvest. Non-defoliated seedlings had total water potentials of -0.49 ± 0.11 MPa, initial osmotic potentials of -1.79 ± 0.21 MPa, symplastic fractions of 0.75 and FW/DW ratios of 2.20 on day 127 ($n = 2$) and total water potentials of -1.65 MPa, osmotic potentials of -2.25 MPa, symplastic fractions of 0.65 and FW/DW of 1.90 at the last date ($n = 2$).

Defoliation significantly affected the total water potential of seedlings subjected to rapid rates of water stress during the mid-drought period (Fig. 3e). Water potential was significantly higher for lightly and severely defoliated seedlings. During the mid-drought period total water potential of non-defoliated seedlings decreased at a rate of 0.19 MPa day⁻¹, vs a decrease of 0.10 MPa day⁻¹ for lightly defoliated seedlings.

Seedlings which had been lightly or severely defoliated maintained significantly higher osmotic potentials than non-defoliated seedlings under rapid rates of water stress ($P = 0.001$, $F = 7.71$) (Fig. 3f). Differences in osmotic potential were most pronounced on day 70 of the drought when severely defoliated seedlings had a potential of -2.60 MPa and lightly defoliated seedlings were 65% less than severely defoliated and 63% greater than non-defoliated seedlings. Blue oak seedlings which were lightly defoliated had turgor pressures which were significantly higher than non-defoliated seedlings (Fig. 3g). Turgor pressure de-

creased immediately from the tenth to the forty-eighth day at a rate of 0.03 MPa day⁻¹ for non-defoliated seedlings and at a rate of 0.02 MPa day⁻¹ for lightly defoliated seedlings. Between day 48 and 70, turgor pressure decreased from 0.5 MPa. This is in sharp contrast to seedlings experiencing slow rates of water stress, where turgor pressure in non-defoliated seedlings was >0.0 for the first 120 days.

Severely defoliated blue oak seedlings exhibited higher turgor pressure compared to non-defoliated seedlings. While these differences were consistent during the mid-drought period, the largest difference occurred on day 70. At this time, turgor pressure was 1.20 MPa for severely defoliated seedlings and 0.0 for non-defoliated seedlings. These higher turgor pressures were, however, short lived and by day 97, turgor pressure of severely defoliated seedlings was 0.0 .

The water potential at zero turgor was significantly affected by days after stress and defoliation. The overall decrease in all treatments strongly supports the interpretation of osmotic adjustment, which appears to have occurred in defoliated seedlings to a greater degree than non-defoliated seedlings (Fig. 3h). Non-defoliated seedlings had an initial decrease of -1.20 MPa between days 10 and 48, but since the total water potential was 0.0 on days 70 and 97, the water potential at zero turgor could not be estimated.

The SF and FW/DW ratio of non-defoliated seedlings experiencing rapid rates of water stress decreased significantly in the mid-drought period from 0.71 to 0.61 and from 1.9 to 1.5 , respectively. During this time, all tissue water characteristics decreased with the slower reductions in the osmotic potentials of lightly and severely defoliated

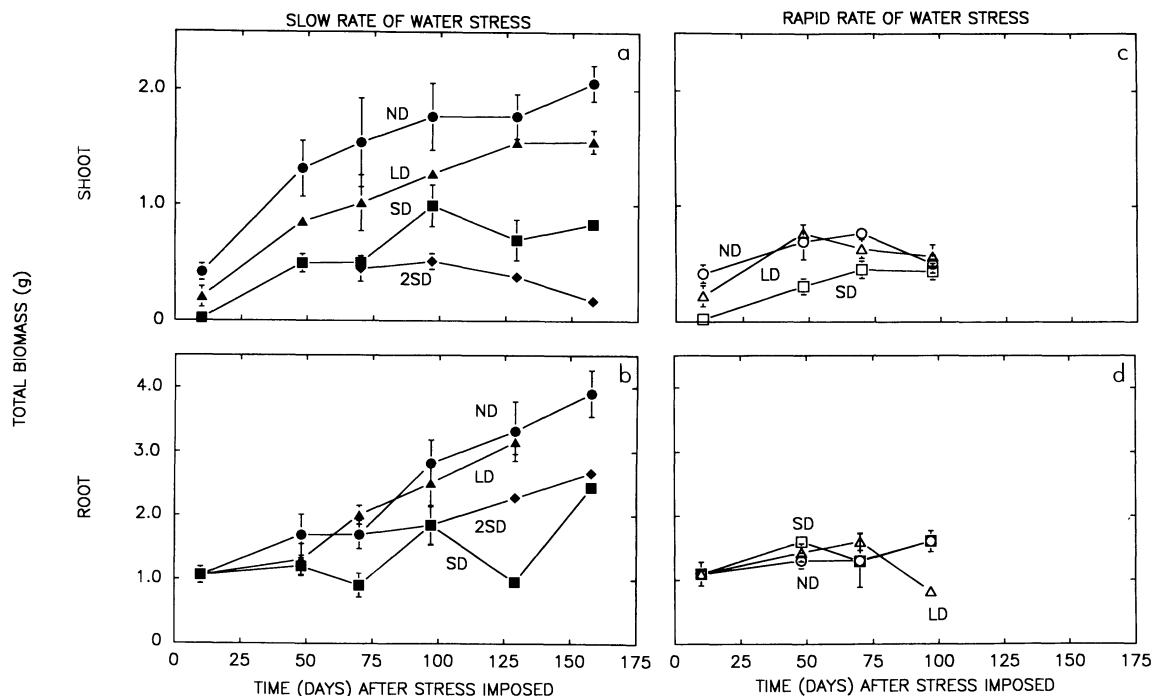


Fig. 4. Shoot and root biomass of blue oak seedlings experiencing slow and rapid rates of water stress over a 158-day drought period (mean \pm SE). Nomenclature is the same as in Fig. 2.

seedlings accompanied by a 13% and 56% decrease, respectively, in the FW/DW ratio between days 48 and 70 (Fig. 3f). Well-watered seedlings in small containers retained favourable tissue water potentials through day 97 of the drought. Total and initial osmotic potentials, turgor pressure, and WPZT were -1.75 MPa, -2.64 MPa, 0.89 MPa and -2.88 MPa, respectively, at the time of last harvest ($n = 2$).

Shoot biomass

Non-defoliated seedlings experiencing slow rates of water stress progressively accumulated leaf and stem tissue throughout the drought, however the growth rate was greatest between days 10 and 48, reaching 23.6 mg day^{-1} (Fig. 4a). Shoot growth slowed after this period and was only 0.10 mg day^{-1} between the mid- and late drought period. By the late drought period however, lightly defoliated seedlings had shoot biomass which was not significantly different from non-defoliated seedlings.

Severe defoliation (leaving six axillary buds) in the early part of the drought reduced seedling shoot biomass from 415 mg to 20.1 mg on day 11. Severely defoliated seedlings never accumulated biomass to levels which approached non-defo-

liated seedlings. However, on average, two axillary buds elongated within 15 days producing re-growth shoot material. This occurred before seedling water potentials reached -0.8 MPa. After day 97 shoot biomass decreased as leaves senesced, and by the end of the period shoot biomass was 60% less than that for non-defoliated seedlings.

Defoliation significantly reduced seedling shoot biomass throughout the experimental period when seedlings were exposed to rapid rates of stress (Fig. 4c). Non-defoliated seedlings accumulated leaf and stem material at a rate of 4.1 mg day^{-1} between days 10 and 70. During the same period, severely defoliated seedlings had less shoot biomass but accumulated biomass at a rate of 6.4 mg day^{-1} between days 11 and 70, reaching a maximum of 0.40 g . Lightly defoliated seedlings exhibited no significant difference in shoot biomass from those of non-defoliated seedlings. In all cases, irrespective of defoliation status, shoot growth did not proceed beyond 100 days of drought.

Root biomass

Defoliation significantly reduced seedling root biomass throughout the drought period when plants were exposed to slow rates of stress (Fig.

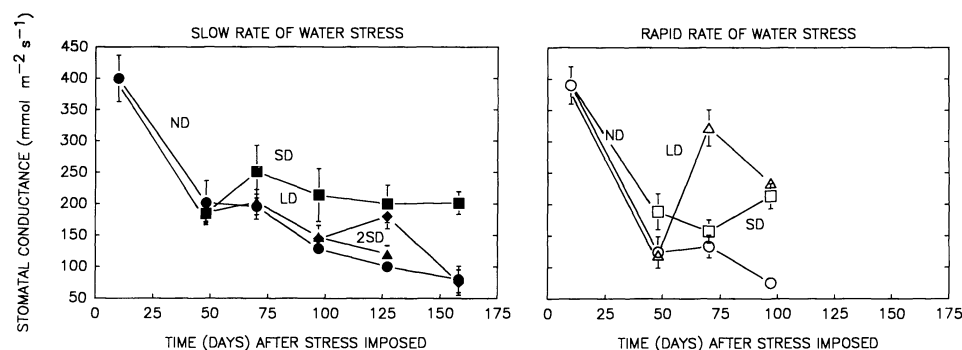


Fig. 5. Mid-day stomatal conductance of blue oak seedlings experiencing slow and rapid rates of water stress over a 158-day drought period (mean \pm SE). Nomenclature is the same as in Fig. 2.

4b). Light defoliation consistently resulted in only minimal differences in root biomass compared to non-defoliated seedlings while severe defoliation in early and late season substantially reduced root growth. While non-defoliated seedlings exhibited the greatest shoot growth rate between days 10 and 48, root growth was greatest between days 70 and 97 reaching 37.3 mg day^{-1} .

Root growth of seedlings severely defoliated under high soil and plant water potentials completely ceased between days 48 and 127 of the drought. The cessation resulted in a 71% reduction in root weight between non-defoliated and severely defoliated seedlings at 128 days of drought. However, between days 128 and 159, root growth of severely defoliated seedlings increased dramatically to a rate of 49.9 mg day^{-1} at a time when total water potentials were decreasing from -0.8 MPa to -3.6 MPa . Thus, even though plant and soil water potentials were below -3.5 MPa , seedlings were capable of root growth when favourable plant water status ($< -1.0 \text{ MPa}$) had been maintained up to 128 days of soil drought. This delayed growth response is in concert with the maintenance of seedling turgor potential above 1.0 MPa at the end of the drought cycle for seedlings severely defoliated early in the drought.

Overall root biomass of seedlings exposed to rapid rates of stress was not significantly affected by defoliation except for seedlings which were lightly defoliated where linear contrasts revealed a significant ($P = 0.0302$, $F = 5.23$) difference. On day 97 non-defoliated seedling root biomass was 1.70 g and lightly defoliated seedling root biomass was 0.95 g (Fig. 4d).

Stomatal conductance

Midday stomatal conductance for non-defoliated seedlings experiencing slow rates of water stress

rapidly declined between days 10 and 48 from 398 to $200 \text{ mmol m}^{-2} \text{ s}^{-1}$ (Fig. 5a). This 50% reduction occurred at a time when total water potential decreased from -0.5 to -1.0 MPa . Midday conductance of non-defoliated seedlings continued to decline during the mid-drought period and by day 97 was only $140 \text{ mmol m}^{-2} \text{ s}^{-1}$. By the end of the drought period midday conductance was $< 100 \text{ mmol m}^{-2} \text{ s}^{-1}$. Accelerated levels of conductance by regrowth foliage of severely defoliated seedlings resulted in a two-fold difference in conductance after day 48 and remained above non-defoliated levels throughout the drought period.

Midday stomatal conductance of seedlings experiencing rapid rates of water stress decreased dramatically from 390 to $125 \text{ mmol m}^{-2} \text{ s}^{-1}$ in the early drought period (Fig. 5b). This decline occurred when the total water potential decreased from -0.5 to -2.5 MPa . Conductances were significantly higher for seedlings defoliated in the early drought period (day 11) ($P = 0.04$, $F = 5.11$). Midday conductance of lightly defoliated seedlings was initially similar to non-defoliated seedlings but increased to 180% higher than non-defoliated seedlings on day 70. Conductances of lightly defoliated seedlings remained above non-defoliated seedlings levels and were 100% higher at the end of the drought period.

Survivorship

The only oak seedlings to survive into the second year after experiencing drought stress were those grown under slow rates of soil drought and were severely defoliated. On day 11 100% of the seedlings severely defoliated ($n = 9$) and refoliated in year 2, while 80% of those severely defoliated on day 71 survived into the second growing season ($n = 6$). None of the non-defoliated ($n = 14$) seedlings

experiencing slow rates of water stress and none of the seedlings experiencing rapid rates of water stress (non-defoliated [$n = 5$] and/or severely defoliated [$n = 5$] produced green leaf material in year 2.

Discussion

The different rates of decline in seedling water potential are comparable to those observed for blue oak seedlings under field conditions (Welker & Menke, 1987). We have observed total water potential declines of $0.05 \text{ MPa day}^{-1}$ by blue oak seedlings growing in areas dominated by high densities of annual grasses. We have observed total water potential declines of $0.04 \text{ MPa day}^{-1}$ in blue oak seedlings in adjacent ungrazed areas where the perennial bunchgrass *S. pulchra* is abundant and the density of annuals is low. These differences, while small on a daily basis, result in seedling water potential differences at the end of a growing season of 1.0 MPa (-5.5 MPa and -4.5 MPa for oak seedlings in the annual grass and perennial bunchgrass dominated areas, respectively) (Welker & Menke, 1987; Momen, 1988).

The different rates of soil water potential decline in this study were distinct enough to result in significant differences in seedling responses to simulated browsing. Short-term increases in oak seedling water potential due to defoliation were much greater in seedlings experiencing rapid rates as opposed to slow rates of water stress. The amelioration of increasing seedling water stress associated with leaf tissue removal was however shortlived. By 100 days of drought, defoliation treatment had no effect on oak seedling water potential when seedlings experienced rapid rates of stress.

Conversely, when seedlings were experiencing slow rates of water stress, severe defoliation had less immediate effect on seedling water potentials but a much greater effect on water conservation late in the drought. By extending the availability of soil water, stomatal conductance was higher late in the drought and the growing season was extended by 30 days. Higher rates of conductance following stem severing has also been observed for clones of *Populus* species, but this was on the remaining, not the new regrowth foliage (Blake & Tschaplinski, 1986). In addition, Wright *et al.* (1989) have shown that defoliation of red oak seedlings may ameliorate the consequences of decreasing soil water supplies, and enhance survivorship when 50 or 75% of the leaf area is removed.

In our Mediterranean ecosystem, we would thus expect that seedlings growing amongst annuals may have shorter growing seasons and a reduction in capture of resources and/or space, while seedlings growing amongst perennial grasses may have longer growth periods. In oak/annual grass communities grown outdoors, soil water is depleted almost continuously from the onset of drought. In oak/perennial grass communities, the decline in soil water potential is significantly slower. Soil water potentials remained above -1.0 MPa for up to 30 days after drought induction in perennial neighbourhoods, at which time soil and oak seedling water potentials decline. These differences result in a longer oak seedling growing season and higher seedling biomass (D.R. Gordon, personal communication; J.M. Welker, unpublished observation).

Blue oak seedlings exhibit significant physiological responses to both slow and rapid rates of stress. Under both conditions, significant decreases in the osmotic potential at full and zero turgor occurred (Fig. 3). In addition, stomatal conductance was sensitive to both rates of stress and curtailed water loss, with only a small decrease in the soil water potential (Figs. 2 and 5). The initial osmotic potentials observed here before tissue dehydration are similar to other values reported for *Quercus* species and North American trees in general (Abrams, 1988). In this review, the osmotic potential at full turgor for eight oak species ranged from a high of -1.66 MPa to a low of -3.25 MPa . This range of osmotic potential included both saplings and trees. Seedlings of *Q. robur* develop osmotic potentials of up to -2.5 MPa after 15 days of drought, which correspond to the maintenance of turgor and stomatal conductance (Osonubi & Davies, 1981). The initial osmotic potentials we observed (-4.5 MPa) for defoliated seedlings experiencing slow rates of water stress are thus, some of the lowest reported for this genus and provide support for blue oak occupation of summer dry, Mediterranean climates.

The seasonal changes in seedling water relations can be the result of cellular changes associated with tissue dehydration (i.e. osmotic adjustment), changes in tissue characteristics associated with maturation, or some combination of the two. Our irrigated seedlings suggest that tissue maturation is indeed an important contribution to changes in tissue water relations, but at the same time solute accumulation is especially critical when seedlings have been severely defoliated and have experienced slow rates of water stress. The importance of

tissue ontogeny has been reported elsewhere, but changes in tissue water stress and simulated grazing can also influence osmotic potentials (Osonubi & Davies, 1978; Hinckley *et al.*, 1983; Flower & Ludlow, 1986; Toft, McNaughton & Georgiadis, 1987; Saruwatari & Davis, 1989).

Central to the current plant–herbivore model is the consideration of external forces affecting compensatory growth following defoliation (McNaughton, 1983; Toft *et al.*, 1987). Data presented here as well as those of others support the theme of reductions in shoot/root ratios with the removal of transpirational tissue, thus improving plant water status (Wright *et al.*, 1989). However, the paradigm of conservation of soil water and improved soil water potential in grazed vs ungrazed areas cannot be extrapolated to all plant–herbivore systems. In ecosystems where woody plant seedlings are consumed by browsers, soil water conservation is unlikely. This occurs because annual and/or perennial grasses occupying the same soil volume will extract any residual water resources not transpired by browsed woody plants. In the case of grasslands like the Serengeti, where many species may receive the same reductions in transpirational surface, soil water conservation may indeed extend the growing season of grazed plants (Georgiadis *et al.*, 1989). The detrimental impact of the large herbivores on soil water infiltration, organic matter and water-holding capacity could however negate any beneficial effects derived from alterations in shoot/root ratios (Welker & Menke, 1987).

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