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Response of two perennial grasses to root barriers and fissures

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Abstract

Above- and belowground biomass of contrasting grass growth forms (*Hilaria belangeri*—shortgrass vs. *Bouteloua curtipendula*—mid-height grass) was quantified with respect to partial root barriers (at 35 cm soil depth) with artificial fissures. We hypothesized (a) growth would be greatest in the absence of a barrier; and (b) the shallow-rooted *H. belangeri* would be relatively less affected by barriers with fissures than *B. curtipendula*. Alternatively (c) *B. curtipendula* with its deeper root system would exploit fissures and access the resources below barriers better than *H. belangeri*. The parameters used to evaluate these hypotheses for plants grown in subirrigated 150 cm pots included above- and belowground biomass after 4 months and monthly gravimetric soil moisture at 20 cm intervals to 150 cm. Root barrier treatments had no effect on either species' above-ground growth. As expected, the mid-height grass produced more root biomass and was more deeply rooted. However, partial root barriers had no effect on total root biomass for either species. Although, some 'perching' of root biomass above the barrier occurred in both species, it had no discernable influence on the pattern of soil moisture depletion with depth. Thus, under the conditions of this experiment, the lack of a significant

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species \times barrier interaction suggests the two growth forms were not differentially affected by partial root barriers.

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1. Introduction

“*It is the nature of roots to nose into cracks*”—Leopold (1949).

Soil depth, as measured by the depth to bedrock or a restrictive soil horizon, influences water and nutrient availability and imposes mechanical resistance to root penetration, thus affecting plant growth (Glinski and Lipiec, 1990). As such, it is a primary determinant of plant production and composition across landscapes (McAullife, 1994, 1999). Fissures or other interruptions in the continuity of subsurface barriers to plant growth may provide localized access to larger and more reliable soil resource pools at deeper depths. Although the occurrence of subsurface fissures is widely recognized as a factor controlling vegetation patterns (e.g. San José and Fariñas, 1983; Zwieniecki and Newton, 1994, 1995; Werner and Lüpnitz, 1999), there have been few experimental assessments of their importance.

Fissures and crevices represent belowground gaps that might be differentially exploited by plants with contrasting root architectures. Grasses generally have relatively shallow, fibrous root systems well-suited for intensively exploiting upper volumes of the soil (Richards, 1986), but there are species- and environment-specific variations (Fox et al., 1953; Bookman and Mack, 1982). In shallow soils, vertical stratification of root systems may not be possible, unless plants find and exploit cracks or fissures in the subsurface barriers (e.g. Zwieniecki and Newton, 1995; Witkowski and Liston, 1997).

In the western USA, *Hilaria belangeri*, a short-statured grass, and *Bouteloua curtipendula*, a mid-height grass, often co-occur in landscapes characterized by shallow soils underlain by fractured limestone. Because these species differ in their tolerance to defoliation (Hendrickson and Briske, 1997), it is generally assumed that their local patterns of distribution are a reflection of grazing (Smeins and Merrill, 1988). However, the two growth forms also differ in their rooting habits (Yoder et al., 1995), leading us to speculate that local patterns of distribution may also reflect a differential ability to exploit fissures in underlying bedrock. To test for this possibility, we quantified the above- and belowground growth of these short- and mid-height grass growth forms with respect to the presence/absence of root barriers with artificial fissures. We hypothesized (a) the growth of each species would be greatest in the absence of a root barrier; and (b) the shallow-rooted short-height growth form would be relatively less affected by barriers with fissures. Alternatively (c) the mid-height growth form with its deeper root system would exploit fissures and access resources below barriers better than the short grass growth form.

2. Methods

The response of contrasting grass growth forms to the presence or absence of an artificial rooting barrier at 35 cm depth was assessed with *Hilaria belangeri*, a perennial, mid-seral, short-statured stoloniferous grass, and *Bouteloua curtipendula*, a perennial, late-seral midgrass species (Smeins and Merrill, 1988). There were ten replicates of each treatment and species for a grand total of 40 experimental units.

The experiment was conducted on plants grown in cylinders (31 cm diameter; 150 cm length) constructed from clear, flexible 6 mil plastic tubing (Chiswick, Inc., Sudbury, MA) and filled with standard potting soil (Brazos Landscaping, Inc., College Station, TX). A wooden frame supported the flexible plastic growth cylinders and kept them at an angle of 20° from perpendicular to the ground. We sought to mimic common field conditions whereby upper soils are relatively dry and deeper soils are relatively moist. To achieve this gradient in soil moisture we perforated cylinder bottoms and placed them in 8 cm of standing water, thus sub-irrigating deep soils for the duration of the experiment. A root barrier consisting of a rigid plastic disk (ca. 3 mm thick) with a portal or 'fissure' (diameter (5.5 cm) and length (15 cm) arbitrarily set using a rigid plastic tube) was placed at 35 cm depth in half of the cylinders ($n = 20$); the other half had no barriers and served as controls. The portal was glued to the bottom of the root barrier and the barrier was glued to the sides of the cylinder with silicon adhesive to prevent roots from growing between the barrier and the cylinder wall. The experiment was conducted outdoors in College Station, TX (30°34'N; 96°22'W) from August 10, 1996 through December 15, 1996. Cylinders were encased in Reflectix[®] insulation (R-16.8 rated insulation factor, Relectix Inc., Markleville, IN) to block light and minimize soil heating. This insulation consists of a bubble pack polyethylene layer sandwiched between reflective aluminum layers. Our intent was not to test the effects of soil depth *per se* on plant performance, but rather to test whether biomass production and soil moisture depletion by plants with reduced access to deep soil resources would differ from that of their counterparts with full access to deep soil resources.

B. curtipendula seeds obtained from the Sonora Research Station 56 km south of Sonora, TX (31°18'N; 100°28'W) were sown in cylinders; tillers of *H. belangeri* (mean biomass \pm SE, $n = 5$ was 1.2 ± 0.2 g) were collected at the same site and transplanted. Plants were uniformly watered for 14 days to facilitate establishment. On 10 August 1996, *H. belangeri* and *B. curtipendula* plants were thinned to a uniform size with one plant per cylinder and surface water applications ceased. Soil gravimetric moisture content was checked in August, September and December by horizontal coring to extract 10–50 g of soil from 20, 60, 100, and 140 cm depths.

Plants were harvested after ca. four months by clipping at the soil surface. At the time of final harvest in early December, plants of both species were still green and had initiated flowering. Belowground biomass was quantified by partitioning the soils in cylinders into 10 cm segments for the first 30 cm of soil depth and into 15 cm segments afterwards. Large roots were removed by hand and the remaining roots were extracted by hydropneumatic elutriation (Smucker et al., 1982). Roots and

shoots were dried at 40 °C, weighed, and combusted in a muffle furnace at 650 °C to determine ash-free biomass (Böhm, 1979).

Soil moisture data were arcsin transformed (Sokal and Rohlf, 1981) and analysed using a double multivariate repeated measures analysis of variance to account for depth, time, barrier and species effects (Littell et al., 1991). Barrier effects on above-ground biomass were assessed using analysis of variance (SAS, 1982). Belowground biomass was analysed using multivariate repeated measures analysis, where depth was the repeated measure (Littell et al., 1991). Bonferoni corrections were performed on all contrast statements with α (set at 0.05) divided by the number of contrasts performed (seven in this case) making $\alpha = 0.0071$ (Sokal and Rohlf, 1981).

3. Results

Soil moisture content at 20 cm declined during the course of the experiment, whereas moisture content at deeper depths increased slightly (Fig. 1). At the beginning of the experiment (August), the water content of soils at 20 cm exceeded that of deeper soils, reflecting the water added to promote grass establishment. During this period there was some ‘perching’ of soil moisture above the partial root barrier. By the second month of the experiment, soil moisture throughout the columns was slightly and consistently lower in tubes with partial root barriers compared to that of tubes without root barriers. By the end of the experiment (December), sub-irrigated portions of the soil column had moisture content more than twice that of near surface soils and soil moisture profiles were nearly identical in columns with and without partial root barriers. Species main effects and interaction terms involving species effects on soil moisture were not significant. Linear order contrasts indicated significant depth \times date interactions ($P < 0.01$) but no barrier treatment effect ($P > 0.05$).

By the conclusion of the experiment, *B. curtipendula* (mid-height grass) had produced ca. 2X more above- and belowground biomass than *H. belangeri* (shortgrass) (Fig. 2). The mean maximum rooting depth for *B. curtipendula* (83.3 cm) exceeded that of *H. belangeri* (73.5 cm) by ca. 10 cm. The presence of a restrictive barrier did not affect shoot or belowground biomass production or root/shoot ratios in either grass (Fig. 2). Additionally, the relative response of belowground biomass for each species to the barrier was comparable (no significant species \times barrier interaction; $P < 0.05$). Both species exhibited an exponential decline in belowground biomass with depth and both exhibited a slight ‘perching’ of belowground biomass at 20–30 cm depth, leading to a significant barrier \times depth interaction (Fig. 3).

4. Discussion

It is reasonable to expect that on sites where soils are shallow and underlain by bedrock or indurated limestone, that patterns of above-ground plant distribution

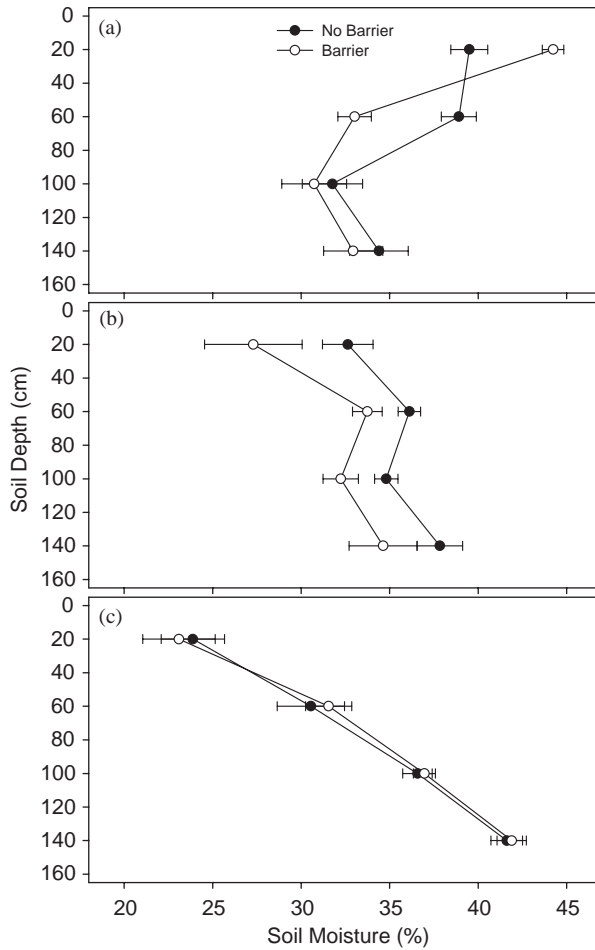


Fig. 1. Mean (\pm SE) gravimetric soil moisture content (%) by soil depth for cylinders with (open circles) and without (filled circles) a partial barrier during (a) August (start of experiment), (b) September, and (c) December, 1996 (harvest date). The type of grass grown in the cylinders (mid-height, *Bouteloua curtipendula* vs. shortgrass, *Hilaria belangeri*) had no significant effect on soil moisture, so data are pooled across species.

and production could be strongly influenced by belowground patterns of fissures and crevices (Quarterman et al., 1993; Ware, 2002); and that some species may be better adapted than others at exploiting fissures providing access to deeper soil resources (Werner and Lüpnitz, 1999). We tested these expectations in microcosm experiments with two contrasting grass growth forms, but found few differences. In our experiment, the presence of a small fissure in barriers to root growth gave plants sufficient access to deeper soil resources, such that for both species, patterns of soil water extraction, shoot production, and root production were comparable to that of plants with unrestricted access to soil resources. Our results pertain to partial barriers

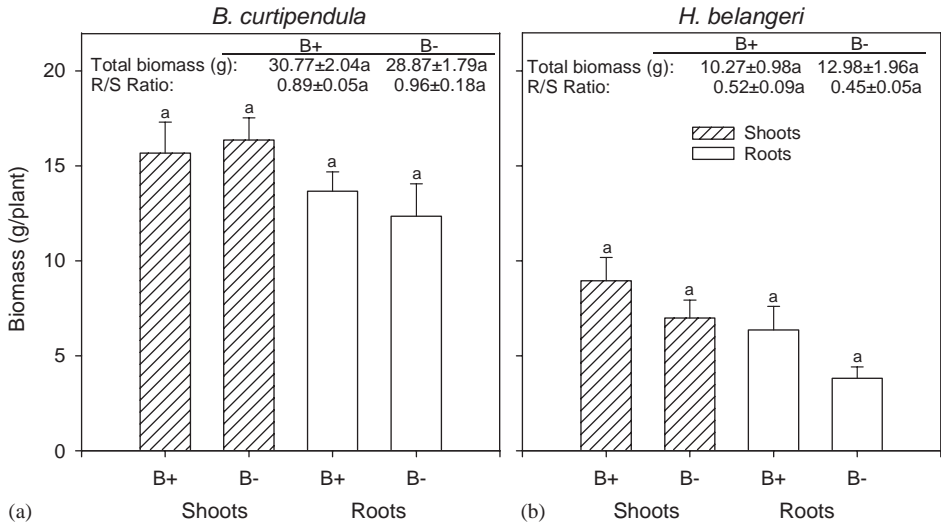


Fig. 2. Mean (\pm SE) (a) above-ground and (b) belowground biomass of *Bouteloua curtispendula* (open bars) and *Hilaria belangeri* (cross-hatched bars) grown with (B+) and without (B-) partial barriers to root penetration. For a given species and biomass component, bars with the same letters were not significantly different ($P > 0.05$). Insets depict total (root + shoot) biomass and root/shoot (R/S) ratios in which values for a given component with the same letter were not significantly different ($P > 0.05$).

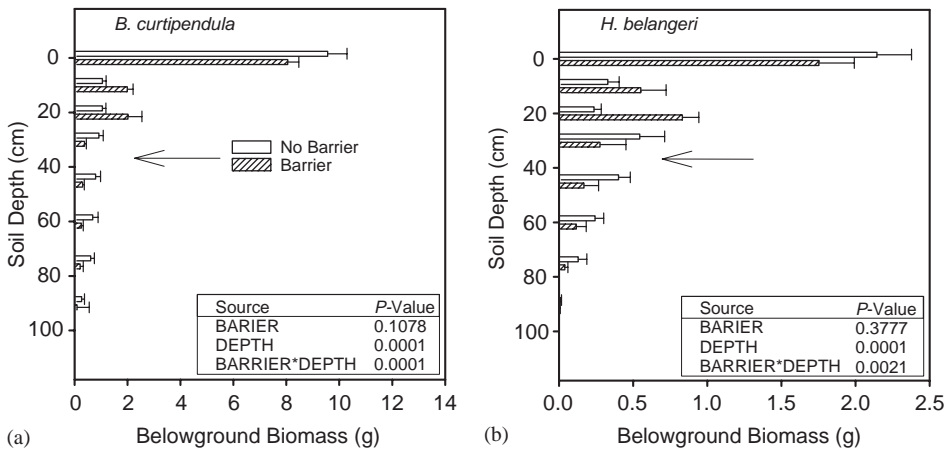


Fig. 3. Mean (\pm SE) root biomass depth distribution for (a) *Bouteloua curtispendula* and (b) *Hilaria belangeri* grown with (cross-hatched box) and without (open box) partial barriers to root penetration. Tables within each panel indicate ANOVA results. Arrows indicate depth of partial root barrier. Note differences in x-axis scales.

placed at 35 cm soil depth; it would be instructive to ascertain if species' exploitation of fissures might differ for barriers at shallower depths, for fissures of different dimensions, or for soils with lower water content and stronger depth gradients.

Although the mid-statured growth form (*B. curtipendula*) produced greater total and somewhat deeper belowground biomass than the short-statured grass growth form (*H. belangeri*), its relative response to the partial root barrier was comparable. Thus, we saw no evidence under the conditions of this experiment that the mid-height grass species might be more adversely affected by shallow soils or able to exploit fissures more effectively than the shorter-statured species. This would support the notion that differences in their field distributions may reflect factors other than differences in subterranean fissures and crevices. It should be noted that our experiments were designed to test for intrinsic and relative differences in fissure exploitation in the two species. It would be interesting to repeat the experiment to ascertain if competitive interactions would be affected. Would fissures affect interactions between an established and an establishing species? If both species were planted together at the same time, would one fare better than the other with regard to fissure exploitation? Would disturbances such as defoliation change how the two species might exploit fissures?

Both growth forms exhibited similar patterns of altered biomass allocation in response to the partial root barrier: ‘perching’ of belowground biomass above the barrier and slightly lower biomass at depths below the barrier. The former may reflect root proliferation during the first month of the experiment when soil moisture levels above the barrier were relatively high (Fig. 1). This is consistent with evidence that dryland grasses are highly responsive to small rainfall events that wet the upper soils (Sala and Lauenroth, 1982; Sala et al., 1989). It is noteworthy that neither species altered allocation patterns and root growth to take advantage of the abundant soil moisture which occurred at depths > 60 cm, regardless of the presence/absence of a root barrier. This supports the notion that on shallow soil sites underlain by fractured bedrock when grasses do not use these deeper resources, there may be an abundant reservoir for species with deep, tap root architectures (e.g. forbs, shrubs; Walter, 1979; Stark and Redente, 1985; Gibbens and Lenz, 2001). Experiments quantifying patterns of fissure exploitation by grasses, forbs and shrubs with highly contrasting root architectures would be interesting and instructive (e.g. Sydes and Grime, 1984).

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