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The influence of *Larrea divaricata* on soil moisture and on water status and growth of *Stipa tenuis* in southern Argentina

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We studied the effect of a dominant shrub (*Larrea divaricata*) on soil moisture, and how this affected water potential and growth of a dominant grass (*Stipa tenuis*) in a shrubland located in southern Argentina. Soil moisture in the upper 10 cm of the soil was lower ($p < 0{\cdot}05$) or similar ($p < 0{\cdot}05$) under the shrub canopy than in the open intercanopy spaces. Concordantly, predawn leaf water potential and growth of *Stipa tenuis* were higher or similar in intercanopy locations than in canopy locations. The physical presence of *L. divaricata* canopy frequently reduced soil moisture availability for understory plant growth, in part because of canopy interception of precipitation.

Keywords: *Larrea divaricata*; *Stipa tenuis*; plant–plant interactions; facilitation; competition; Monte region; Argentina; plant–water relations; throughfall

Introduction

Plant–plant interactions are major determinants of plant community structure and function. Positive (facilitation) and negative (competition, allelopathy) interactions occur simultaneously and are dynamic (Callaway & Walker, 1997). For example, plants can improve microclimate, reduce the probabilities of herbivore damage, or improve soil properties for other plants (Callaway, 1995). But they can also limit the growth of other plants by reducing the availability of light and soil water (e.g. Breshears *et al.*, 1997) or by excreting allelopathic substances (Williamson, 1990). It has been hypothesized that negative interactions are more important under more productive conditions, whereas positive interactions are more important under less productive (harsh) conditions (Bertness & Callaway, 1994).

In arid and semi-arid ecosystems, plant–plant interactions mediated by water are important because soil moisture drives primary production and influences nutrient dynamics. In these regions, grasses and shrubs are often presumed to co-exist by

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partitioning soil water vertically, with grasses taking up most of the water from the upper layers of the soil and shrubs taking up most of the water from the lower layers of the soil (Walter, 1971). However, shrubs can have positive and negative effects on the water status of grasses. Examples of positive interactions are hydraulic lift from moist lower soil layers to dry upper soil layers (Caldwell *et al.*, 1998) and reduced evapo-transpiration demands under shrub canopy (Callaway, 1995), whereas an example of negative interaction is the interception of precipitation by shrub canopy (Branson *et al.*, 1981). Raindrops are either intercepted by foliage and subsequently evaporated or transported to the soil at the base of shrub by stemflow, or they proceed through the foliage to the soil surface as throughfall.

Larrea divaricata is a dominant species in the Monte region of Argentina. In the southern part of the region, *Stipa tenuis* grows both under the canopy of *L. divaricata* and in the open intershrub spaces; hereafter, canopy and intercanopy locations, respectively. The primary objective of this study was to assess the effects of *L. divaricata* on soil moisture and on water potential and growth of *S. tenuis*. In addition, throughfall at canopy locations and root distribution of *S. tenuis* in the soil profile were measured to help in the interpretation of the results.

Materials and methods

Study site

The study was conducted on an ungrazed site located in the vicinity of Viedma, province of Río Negro, Argentina (40°48′S; 63°W), in the southern part of the Monte Phytogeographical Region (Cabrera, 1976). The climate is temperate, semiarid. Mean annual air temperature is 14°C. Average annual rainfall is 350 mm, with a homogeneous distribution along the year. Most of the precipitation events take place as rainfalls of 5 mm or less. The average potential evapo-transpiration is 1037 mm. Soils are deep and sandy, with a 5% slope. The physiognomy of the vegetation is a shrubby steppe. The overstory layer is dominated by *L. divaricata*, a multi-stemmed evergreen shrub that can reach up to 3 m height. The understory layer is dominated by *S. tenuis*, a cool-season perennial shortgrass.

Bulk precipitation, throughfall, and soil water content

Bulk precipitation and throughfall were measured from the winter of 1998 to the winter of 2000. Bulk precipitation at the study site was recorded with an automatic rain gauge located in an open area. Throughfall was estimated on five plants of *L. divaricata*, which were selected to encompass the range of sizes of the species within the study area. Twelve metallic jars were placed at ground level underneath the canopy of each selected plant. Four jars were placed close to the trunk, four at the canopy mid-point, and the last close to the border of the canopy. Throughfall was measured immediately after each rainfall event.

Soil water content was periodically measured using time-domain reflectometry (TDR) from the fall of 1999 to the winter of 2000. On each occasion, measurements ($n = 5$) were taken at 0–10 cm and 10–25 cm depth at canopy and intercanopy locations. The gravimetric determination of soil moisture was used to adjust the data from TDR.

Stipa tenuis water potential, growth, and root distribution

Predawn leaf water potential was measured using the pressure chamber technique (Scholander *et al.*, 1965). In order to minimize water loss, leaves were rapidly transported (less than 10 s) from the plants to the pressure chamber a few meters away. The portion of leaves external to the seal of the chamber was small and it was never recut. Measurements were made on completely expanded green leaves from five random selected plants of *S. tenuis* growing at canopy locations and from five plants of *S. tenuis* growing at intercanopy locations. Observations were carried out periodically from the winter of 1999 to the fall of 2000.

The growth of *S. tenuis* at canopy and intercanopy locations was estimated at tiller and plant level. At tiller level, the response variable was the total length of green blades per tiller at different times of the growing cycle. At each location, five tillers were identified on each of ten plants by placing wire loops at their bases. Measurements were carried out periodically on the same originally marked tillers from the spring of 1998 to the fall of 2000. At plant level, the response variables were basal area, current season above-ground biomass, proportion of above-ground green biomass, and proportion of reproductive biomass. At the end of the growing cycle (December), 50 plants of *S. tenuis* growing at canopy locations and another 50 growing at intercanopy locations were randomly selected and clipped at ground level. In the laboratory, after measuring basal area, the biomass of each plant was sorted into reproductive and vegetative structures, and classified into live, senescent, and standing-dead compartments. Finally, the entire material was oven-dried at 70°C for 2 days, and weighed.

The distribution of root biomass of *S. tenuis* in the upper 60 cm of the soil profile was estimated by extracting a soil monolith of 50 cm width, 60 cm length, and 10 cm depth underneath each of the five individuals by means of a needle-board (Böhm, 1979). A trench was dug beneath each plant, so as its crown lay in the middle of the soil monolith, and samples were extracted by using a wooden board (50 cm × 60 cm) provided with 10-cm long nails. Samples were taken to the laboratory, separated into 5 cm layers, and washed with tap water to eliminate soil particles from the roots. All extraneous roots were separated by hand and eliminated. Finally, roots were oven-dried at 70°C for 2 days, and weighed.

Statistical analysis

All the response variables measured at canopy and intercanopy locations were compared through *t*-tests for each date separately.

Results and discussion

Bulk precipitation, throughfall, and soil water content

Bulk precipitation was close (6% below) to long-term average in the period of measurements (winter 1998–2000). Most of the precipitation events (62%) occurred as rainfalls of 5 mm or less, contributing to approximately 20% of total rainfall.

Throughfall in *L. divaricata* averaged $77{\cdot}6 \pm 19{\cdot}2$ % of bulk precipitation. There were points under the shrub canopy where throughfall was over bulk precipitation (about 6% of measures), which can be attributed to dripping from stemflow. Overall, the range of throughfall values in *L. divaricata* were in the range of throughfalls reported for a variety of woody species (Branson *et al.*, 1981). However, in a more specific comparison, average throughfall in *L. divaricata* was above the 56% average throughfall reported for *L. tridentata* (Martinez-Meza & Whitford, 1996). Plant factors (leaf size, position, surface texture, branch arrangement, branch inclination) and rainfall conditions (air temperature, rain intensity, rain angle, wind velocity) interact to determine different partitioning of bulk precipitation (Branson *et al.*, 1981), and may help explain the differences between the two *Larrea* species.

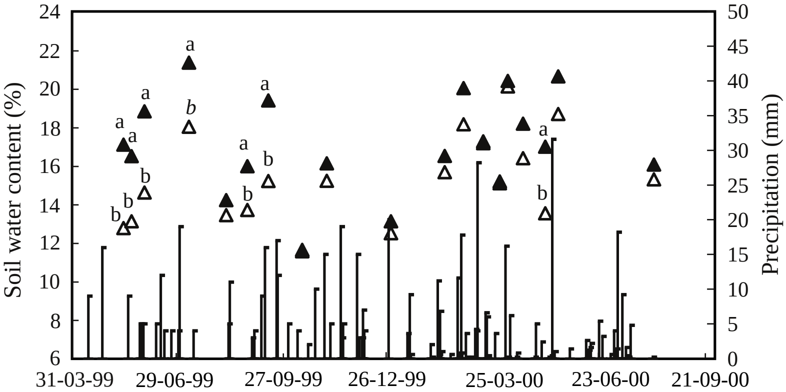

Figure 1. Precipitation and soil water content at 0–10 cm depth for canopy and intercanopy locations. Different letters on each date indicate significant ($p<0{\cdot}05$) difference between locations. (△), canopy location; (▲), intercanopy location; (—) rainfall.

In the first 10 cm of the soil profile, the effect of *L. divaricata* on soil moisture was negative ($p<0{\cdot}05$) or neutral ($p>0{\cdot}05$) (Fig. 1). Negative effects were more frequent in the cool season (late fall, winter, and early spring), whereas neutral effects prevailed in the warm season. The largest negative effects occurred in the cool season of 1999, in coincidence with scarcity of precipitation and small rainfall events. These results are in agreement with a recent report on the effects of desert shrubs on annual plants (Tielbörger & Kadmon, 2000), contradicting the hypothesis that negative interactions prevail under benign conditions (Bertness & Callaway, 1994). Negative effects in the cool season were consistent with the redistribution of bulk precipitation caused by *L. divaricata*. The interception of precipitation by woody species has been shown to reduce soil moisture underneath the canopy of woody plants in semi-arid regions (e.g. Belsky *et al.*, 1989; Breshears *et al.*, 1997; Smit & Rethman, 2000). Also, litter accumulation was probably higher at canopy locations than at intercanopy locations and may have intercepted a higher proportion of precipitation, particularly from small rainfall events (Naeth, 1991). Very little water penetration of the soil took place beneath a dense cover of grass foliage and litter after 5 mm of rain had fallen (Glover *et al.*, 1962). For large rainfall events, litter interception of throughfall water may be overcompensated by greater potential for infiltration under canopy (Dunkerley, 2000). The neutral effects in the warm season may have been caused by amelioration of solar radiation at canopy locations. Shading, by reducing water loss, may have balanced interception losses of precipitation associated with the presence of *L. divaricata*. Many studies have shown that the effect of one plant on another plant can easily shift when conditions change (reviewed by Holmgren *et al.*, 1997). On the other hand, the effect of *L. divaricata* on soil moisture at 10–25 cm depth was neutral ($p>0{\cdot}05$) (data not shown), which can be attributed to the prevalence of rainfall events that wet the top of the soil profile only.

Water potential, growth, and root distribution of Stipa tenuis

Predawn leaf water potential of *S. tenuis* was higher ($p<0{\cdot}05$) (seven out of 13 observations) or similar ($p>0{\cdot}05$) at intercanopy locations than at canopy locations (Fig. 2). This pattern was in agreement with soil water content trends in the upper 10 cm of the soil profile at the two locations. Plant water potential responses suggest that *S. tenuis* is able to make use of small increases of soil water content in the first 10 cm of the soil profile after small rainfall events. Consistently, the larger proportion

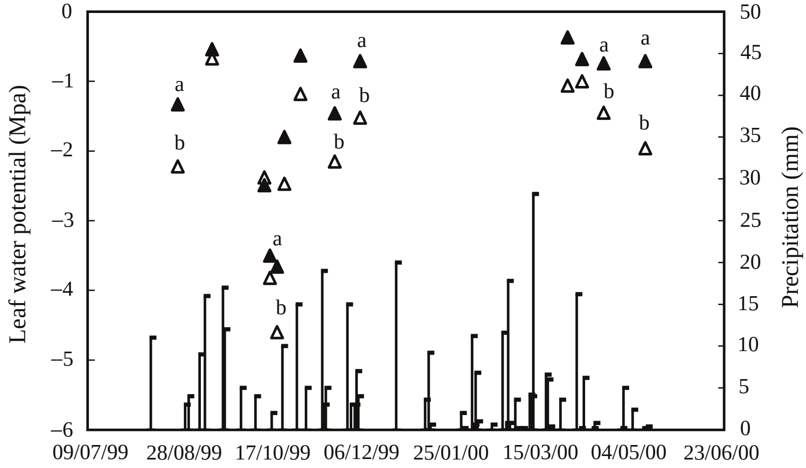

Figure 2. Precipitation and predawn leaf water potential of *Stipa tenuis* for canopy and intecanopy locations. Different letters on each date indicate significant ($p<0{\cdot}05$) difference between locations. (△), canopy location; (▲), intercanopy location; (—) rainfall.

of *S. tenuis* roots was found in the upper 5 cm of the soil profile. Root biomass distribution in the soil profile was as follows: 42%, 14%, 11%, 4%, 6%, and 23%, at 0–5, 5–10, 10–15, 15–20, 20–25, and 25–60 cm depth, respectively. The upper 25 cm of the soil profile accumulated 78% of total root biomass (0–60 cm depth). Small rainfall events have been shown to be ecologically significant for species with short response time to a rainfall stimulus and shallow rooting depth (Sala & Lauenroth, 1982, 1985).

The total length of green blades per tiller was higher ($p<0{\cdot}05$) or similar ($p>0{\cdot}05$) at intercanopy than at canopy locations (Fig. 3), except for the measurement on January 12, 1999. Also, basal area, current season above-ground biomass, and proportion of above-ground green biomass were higher ($p<0{\cdot}05$), whereas the proportion of reproductive biomass lower ($p<0{\cdot}05$), at intercanopy than at canopy locations, respectively (Table 1). Therefore, the spatial heterogeneity in soil moisture induced by the physical presence of *L. divaricata* is of sufficient magnitude to affect biotic processes, such as plant growth. A similar effect of *L. tridentata* on perennial grasses and forbs on a Chihuahuan Desert watershed has been recently reported (Whitford *et al.*, 2001). Perennial grass cover and annual plant cover were significantly lower under the shrub canopy than in adjacent grassland areas, which the authors argued may have been due to the interception and redistribution of precipitation by the shrub canopy.

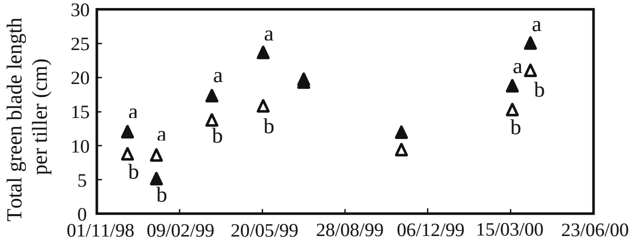

Figure 3. Total green blade length per tiller of *Stipa tenuis* for canopy and intercanopy locations. Different letters on each date indicate significant ($p<0{\cdot}05$) difference between locations. (△), canopy location; (▲), intercanopy location.

Table 1. *Tiller and plant level responses of* Stipa tenuis *for canopy and intercanopy locations*

Variable	Location	
	Canopy	Intercanopy
Basal area ($cm^2 plant^{-1}$)	65·9a	139·6b
Current season above-ground biomass ($g plant^{-1}$)	2·6a	3·9b
Proportion of above-ground green biomass	0·18a	0·25b
Proportion of reproductive biomass	0·72a	0·65b

Note: Different letters in each row indicate significant ($p<0{\cdot}05$) difference between locations.

Conclusions

Our results showed that *L. divaricata* creates spatial heterogeneity in soil moisture. During the cool season more water is available in the top soil at intercanopy locations, which is relevant for two reasons. First, *S. tenuis* is a C_3 grass that vegetates during the cool season of the year. Second, *S. tenuis* has more than half of its roots in the upper 10 cm of the soil profile. Therefore, the practical implication of our results is that brush control would favor forage production in degraded communities of *L. divaricata* and *S. tenuis* characterized by increases in shrub density and biomass.

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