

Soil water dynamics, root systems, and plant responses in a semiarid grassland of Southern Patagonia



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ABSTRACT

Distribution of water enables different ecological niches and the coexistence of species. This separation may be in space: vertically in the soil profile or horizontally by lateral root exploration; and in time, as plants may use water at different periods. This study focused on the soil-plant water relation in semiarid Patagonia. Water potential at three depths: 10, 25 and 60 cm, and water content beneath vegetated and bare patches were measured. Access to water in the soil profile was studied in two grasses and a dwarf shrub based on the root biomass. Soil was usually dry at 10 cm ($-1.22 \text{ MPa} \pm 0.25$) and 25 cm ($-1.00 \text{ MPa} \pm 0.14$) during summer. In dry years, it was also dry during autumn ($-1.17 \text{ MPa} \pm 0.32$) at 10 cm depth). At 60-cm depth, soil was moist year-round ($-0.38 \text{ MPa} \pm 0.05$). Soil conditions were not spatially homogeneous, as bare soil patches showed higher water content than vegetated patches. Dwarf shrubs presented both shallow and long roots, that extended laterally instead of exploring deep soil. It is hypothesized that this lateral expansion may give access to water under the bare soil patches, a resource that is not available to the other life forms.

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1. Introduction

In arid and semiarid ecosystems, soil water determines important functional aspects of the ecosystems including the dominance of plant functional types, phenology, and primary production. It exerts the main control over biological processes (Noy-Meir, 1973), and induces different physiological and anatomical adaptations and “trade-offs” in plants that enable them to use different soil water sources (Abbott and Roundy, 2003; Schwinning and Ehleringer, 2001). These differences may lead to niche differentiation and coexistence of species (Chesson et al., 2004).

Soil water availability for plants is associated with the seasonality, frequency and size of rainfall (Loik et al., 2004). In the topsoil water is available for short periods, generated by small rainfalls, the predominant type of rainfall in deserts and semiarid systems (Loik et al., 2004; Reynolds et al., 2004; Sala and Lauenroth, 1982). These small events do not infiltrate deeply in the soil, and the water stored shallow in the soil is lost quickly in the warm season, when

potential evapotranspiration is intense. The plants with shallow root systems can make use of these water pulses (Jobbágy and Sala, 2000; Schwinning et al., 2005) adopting an “opportunistic” strategy (Soriano and Sala, 1983). Leaves of these plants have to tolerate a wide range of water potentials (Schwinning et al., 2005), and maintain partially developed leaf meristems or buds that can be rapidly activated to replace senescent foliage and take advantage of the pulses (Soriano and Sala, 1983).

Water that reaches the deep layers of the soil is a more stable resource. It is not subject to evaporation (Paruelo and Sala, 1995), and therefore has a longer residence time. The recharge of these layers usually coincides with the rainy season, but it may also take place at any time of the year by the occurrence of large rainfall events. Mediterranean (winter) type rain distributions and permeable soils facilitate infiltration and deep soil recharge (Sala et al., 1997). Water in deep layers is utilized mostly by plants that can develop long, thick roots with secondary growth that are capable to explore the entire soil profile. These plants usually bear long-lived and slow-growing foliage (Bucci et al., 2009), and their leaf water potentials are less variable in the year (Schwinning et al., 2005).

A third type of resource that is often overlooked in arid and semiarid system studies are the water pockets under bare soil patches. They are generated in systems that show incomplete

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vegetative cover (Soriano, 1990), because direct evaporation from the soil surface can only draw superficial water as capillary forces loose strength in coarse-textured soils (Noy-Meir, 1973). Low or nil vegetative cover means that they are not subject to transpiration. Annuals that complete development in the interspaces of perennial vegetation may use this resource.

In Patagonia, the dominance of summer or winter rains determines the seasonal pattern of soil water and explains the dominance of different functional types (Sala et al., 1997). Soil-plant water relations studies have so far mostly focused on shrub–grass steppes with winter rain of North and Central Patagonia (Bucci et al., 2009; Paruelo and Sala, 1995; Schulze et al., 1996; Soriano et al., 1987). In these areas grasses use water available in the 0–30 cm layer, while shrubs obtain water mostly from deeper layers. Some woody plants, nevertheless, show dimorphic root systems and can make use of both resources (Bucci et al., 2009; Kowaljow and Fernández, 2011; Rodríguez et al., 2007). Plants with an annual strategy that could use the water available under bare soil patches are missing (Soriano, 1990).

Southern Patagonia has a uniform seasonal distribution of rainfall (Burgos, 1985), and is dominated by grass steppes (Roig, 1998; Soriano, 1956). Soil water dynamics in these areas has received little attention, but the increased dominance of grasses, both in cover (Humano et al., 2005) and productivity (Cibils et al., 2005) points to a different water balance. The present study focuses on the spatial soil water distribution and its relation with root system structure in two grasses and a dwarf shrub in the Magellanic Steppe. The main hypothesis was that the pattern of rainfall distribution reduces the availability of deep soil water. Grasses and shrubs consequently will develop shallow root systems, with high competition potential for the shallow water and similar leaf water potential patterns.

2. Methods

2.1. Study area

Study area was Potrok Aike station, an experimental field of National Institute of Agricultural Technology (INTA) Santa Cruz, at 51° 36' S and 69° 14' W. It is located at 150 m a.s.l., 100 km west from the city of Río Gallegos and 30 km away from the Magellanic Strait shores. Climate is Temperate-cold and semiarid, with a mean rainfall of 200 mm, distributed evenly throughout the year (De Fina et al., 1968). Predominant winds from the SW, show a mean annual intensity of 27 km/h.

Soils are entisols, with Typic Torriorthents and Typic Torripsaments, that show a A-C and A-AC-C sequence. They are relatively deep, sandy loam in texture (85% total sands 0–20 cm depth), with reduced stone content in the surface and abundant fine, medium and thick gravels and stones in the deep horizons. Soil pH is slightly acidic (6.2), and reaches 6.8 deeper in the soil profile. They show higher values of organic matter (2.64%) and nitrogen (0.16%) close to the surface, but these values fall to 0.98% and 0.06% respectively in the A2 horizon (Lamoreaux et al., 2005). Soil water content in the A horizon at field capacity (–0.03 MPa) is 12% weight/weight (Ferrante, 2011). Vegetation is a 60%-cover perennial grass steppe with three strata: tussock grasses, mainly *Festuca gracillima*, with 25% relative cover. Prostrate, dwarf shrubs including *Nardophyllum bryoides* and other species cover 23%. Short grasses and herbaceous forbs constitute the remaining 52% of the vegetative cover, with *Poa spiciformis* as dominant. Ephemeral and annual plant cover is negligible (Humano et al., 2005).

Soil and vegetation variables were analyzed in three experimental plots within one-ha enclosures established in 1999. The sites reflect the environmental variability of the study area in terms

of topography, two of them in 5–10% slopes with N and S aspect and the remaining one in a flat area. Differential insolation patterns between slopes resulted in small differences in the temperature of the soil surface of ca. 1 °C (Ferrante, 2011), but soils and vegetation are otherwise similar.

2.2. Climate

Rainfall and temperature were recorded with an automated meteorological station (Davis Weatherlink 4.04 s, California) between 2001 and 2007. The size of rainfall events was classified using the intervals: 0–5, 5.1–10, 10.1–15, 15.1–20, >20 mm. Dry spells (time between two successive rainfalls) were recorded. Potential daily evapotranspiration (E_{t0}) was estimated from daily temperature and relative humidity values using the Penman–Monteith algorithm (Monteith, 1973).

2.3. Soil water

Three sites in vegetated patches within each experimental plot ($n = 9$) were selected for soil water potential measurements. At each site, a 1-m deep excavation was made to expose the soil profile. One soil psychrometer was placed laterally in the undisturbed soil profile there at three depths: 10, 25 and 60 cm. The excavations were filled up with the extracted soil. The experimental plot had in total 9 sensors ($n = 27$ total sensors in the three experimental plots). Readings were taken with intervals between 15 and 30 days during the period September–May 2001–2004 using a microvoltmeter (Wescor HR 33, USA). At each sampling date (56 in total), 27 psychrometers were read sequentially between 11:00 and 14:00 hs. During the June 2002–June 2003 period, soil temperature at 5 cm depth was recorded hourly using a single TC1047 sensor in each experimental plot ($n = 3$), (Microchip, EEUU) and data loggers.

Spatial distribution of soil water content in different patches was explored in January 2007. A total of 363 patches 10 cm or wider were identified in Canfield lines in experimental plots and adjacent areas. They were classified into: tussock grasses ($n = 108$), short grasses ($n = 109$), dwarf shrubs ($n = 61$) and bare soil ($n = 85$). Soil water content was estimated once at the center of each patch using a 15-cm deep TDR probe (model FM-3 Trime, Eijkelkamp, Giesbeek, The Netherlands).

2.4. Root systems

In order to study root structure and root biomass distribution, nine 60-cm deep excavations were performed adjacent to medium-sized individuals of: *P. spiciformis* ($n = 3$, crown diameter 9 ± 0.7 cm), *F. gracillima* ($n = 3$, crown diameter 28 ± 5.4 cm) and *N. bryoides* ($n = 3$, crown diameter 78 ± 25.8 cm). Low root density was observed deeper than 40 cm in the soil profile in all cases. In order to analyze vertical and horizontal root distribution, samples were taken from the 0–40 cm layer, where most of the roots were observed. A pit was dug directly beneath each plant in order to expose the soil block containing the root biomass. The nail board method (Böhm, 1979) was used to assess root biomass. A board with 5-cm long nails placed systematically in a 5×5 cm pattern was introduced in the visible face of the soil profile of the pits. A second pit was excavated on the opposite side in order to obtain a 5-cm thick monolith of soil. These blocks were $40 \times 40 \times 5$ cm size for *F. gracillima* and *N. bryoides*. Smaller plants of *P. spiciformis* were sampled in $25 \times 40 \times 5$ cm monoliths. Nail boards were washed in horizontal position in the laboratory to remove soil particles. Exposed roots in each 5×5 cm quadrat were cut, oven-dried and weighed. In the case of the shrub, the pit was combined with a

trench that followed the main lateral root. Root systems were photographed, including a ruler to indicate scale. A scheme was drawn over the photographs using digital photo editing software (Adobe Photoshop CS3, version 10).

2.5. Plant water measurements

Leaf water potential of the grasses *F. gracillima* and *P. spiciformis*, and the dwarf shrub *N. bryoides*, was recorded in 13 dates in summer, 5 in autumn and 8 in spring. At each of these dates, five plants of each species were sampled per experimental plot ($n = 15$ per plot). One completely developed leaf or young stem was introduced in the Scholander pressure chamber (Biocontrol, 10 MPa) to record leaf water potential (Turner, 1987). Readings were done at midday, between 11:00 and 14:00 h, when atmospheric demand is highest. In this period transpiration rates are maximum (Lambers et al., 1998) and water potential differences between life forms may be better evaluated. Leaf water potential was evaluated simultaneously with the soil psychrometer readings.

2.6. Data analysis

Soil water content data was analyzed using a randomized complete-block design, with the experimental plots considered as blocks. Leaf water potential was analyzed according to a randomized complete-block design with subsampling. The five readings of a given species, plot and date were considered as subsamples. Differences were tested using one-way ANOVA of GLM process using LSMEANS sentence for unbalanced models (SAS 8.0). All the analysis were performed with a significance level of $p < 0.05$ and Tukey contrasts.

3. Results

3.1. Climate

Mean annual rainfall (\pm SE) was 213 ± 20.6 mm in the 2001–2007 period. Rain was distributed throughout the year with a slightly higher concentration in summer and the beginning of autumn, with drier periods in winter and early spring (Fig. 1). Two above-mean rainfall years occurred in 2002 and 2003, with 268 and 262 mm respectively, and a dry year was recorded in 2001, with 123 mm. The mean annual temperature was 5.9 ± 0.17 °C. January

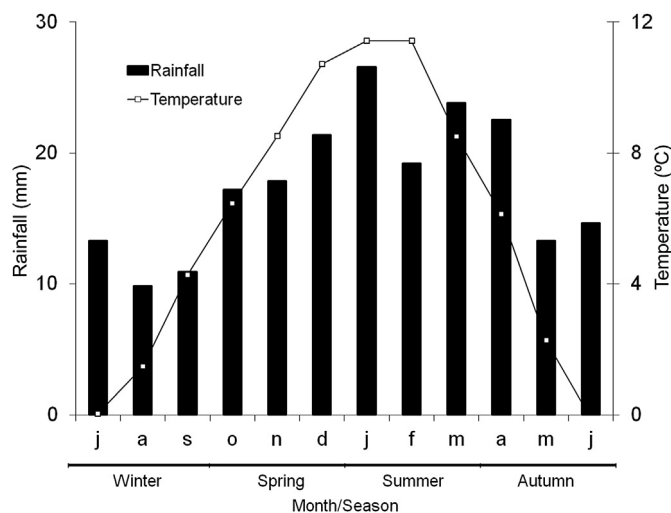


Fig. 1. Mean temperature and monthly rainfall. Period 2001–2007.

and February were the warmer months, with mean temperatures of about 11.5 °C, and June was the coldest, with a mean of -0.3 °C (Fig. 1).

Rain was distributed in a high number of small events, with 90% less than 5 mm, which accounted for 50% of total annual rainfall accumulation (Fig. 2). Events exceeding 15 mm represented 9% of the rain volume. Only seven rainfalls over 10 mm per year were recorded, and the most copious rain recorded was 27.4 mm (Fig. 2). In the wetter years (2002 and 2003) 24 and 38% of rainfall fell in events larger than 10 mm. Dry spells (periods without rainfall) were short, lasting 3.7 days as a mean. Dry intervals of ten days or more were very rare with a frequency of three dry spells per year. The longest period without rainfall in the seven years of the trial was 28 days and was recorded in March of the driest year (2001) (Fig. 2).

3.2. Soil water

Soil profiles (0–60 cm) were close to field capacity (≈ 0 MPa) during winter and early spring (Fig. 3). Shallow layers started to dry in late spring or early summer, and soil water potential at 10 and 25 cm reached the -1 MPa boundaries usually in December–January and remained dry until autumn. In rainy years such as 2002 and 2003 the soil profile recharged early and reached wet conditions in March. Soils showed longer dry spells during 2001 and 2004, and moist conditions were only restored in April or May (Fig. 3). At 60 cm depth, soils remained moist year round and only reached dry conditions in short periods in 2002 and 2004.

The entire soil profile was replenished between April and May even in the drier years (Fig. 3). Soil thermometers indicated that shallow soil layers remain frozen up to 82 days in winter, starting in June (Ferrante, 2011; not shown here). Dry periods in the soil during January–February coincide with those of maximum atmospheric demand (4.1 mm day $^{-1}$) and maximum mean monthly soil surface temperatures (15.3 °C). Soil recharge took place in April–May, when potential evapotranspiration was low (1.3 mm day $^{-1}$) and before the surface froze.

Volumetric soil water content was higher in bare soil areas. A moisture gradient was evident in the different types of vegetated patches, with tussocks < short grasses = dwarf shrubs (Table 1).

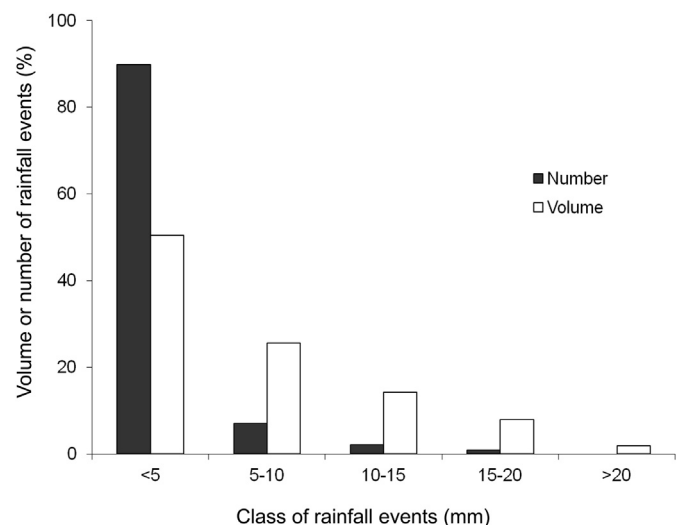


Fig. 2. Distribution of rainfall events grouped by size (mm). Black bars show the percentage of events in each class in relation to the total number of events. White bars show the percentage of the volume that each class of rainfall contributes to the total rainfall in volume. Period 2001–2007.

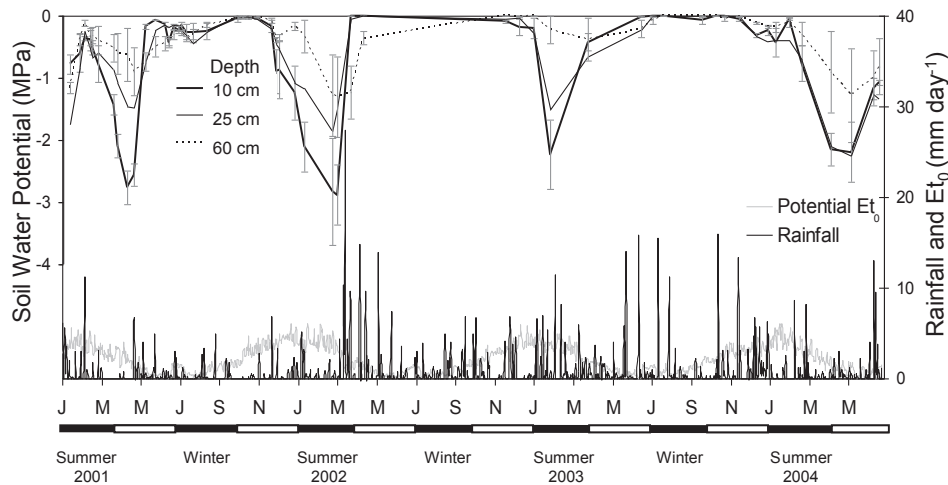


Fig. 3. Soil water potentials (left axis) at 10 cm (bold line), 25 cm (thin line) and 60 cm (dotted line) depths, together with daily rainfall and Pennan–Monteith estimations of daily evapotranspiration (right axis) in mm. Period 2001–2004. $n = 3$ in each depth and date. Vertical bars indicate SE for means of 10 and 60 cm depths.

3.3. Root systems

P. spiciformis, a short grass, had the shallowest root system with 85% of root mass from 0 to 10 cm. At this depth, tussock grass *F. gracillima* and dwarf shrub *N. bryoides* accumulated 63 and 67% of their total root biomass respectively. Root biomass of the grasses decreased sharply from the center to the outside edge of the plant, but this was not evident in the dwarf shrub root system (Fig. 4).

The dwarf shrub developed dense adventitious roots from prostrate stems, while the main tap roots, that reached over 1.5 m long, showed an unusual pattern: instead of exploring deep in the soil profile they curved at a depth of 30–40 cm and extended laterally, deepening slowly as they moved away from the center of the plant (Fig. 5). No physical barrier that could explain this diversion was evident in the soil profile.

Total root biomass of the dwarf shrub *N. bryoides* accumulated over the 40 cm depth was $8.64 \text{ g dm}^{-3} \pm 0.84$ S.E. (dry root matter per dm^3 of soil). Half of biomass were fine roots (<2 mm): $4.50 \text{ g dm}^{-3} \pm 1.02$. This is 2.3 times as much as the root mass accumulated by *F. gracillima* with $1.94 \text{ g dm}^{-3} \pm 0.12$ and 6.6 times more than the root mass of *P. spiciformis* with $0.68 \text{ g dm}^{-3} \pm 0.27$.

3.4. Leaf water potential

Summer leaf water potentials were lower than those recorded in autumn and Spring. Species displayed significantly different leaf water potentials in summer as the dwarf shrub showed higher (less negative) mean leaf water potentials than grasses. Grasses reached values close to -4 MPa, while shrubs reached about -3 MPa (Table 2). Leaf water potentials were also more variable in grasses (SE between 1.3 and 1.5 MPa) than those of shrubs (SE 0.8 MPa). No

differences in leaf water potential were found between the two grass species.

4. Discussion

Climate in the Magellanic steppe differs from other arid and semiarid regions. Rainfall here is distributed year-round with a maximum in summer (Fig. 1), while most of Patagonia has winter-dominated pattern (Paruelo et al., 1998). Rainfalls are small, with over 90% of the events in the <5 mm class (Fig. 2), a distribution that is a characteristic of low mean annual temperature sites (Loik et al., 2004). In areas with similar total rainfall, Reynolds et al. (2004) and Sala and Lauenroth (1982) report only between 35 and 75% of events of this type. Large storms, that explain the difference between wetter and drier years in other arid-lands (Golluscio et al., 1998; Sala and Lauenroth, 1982), are very rare in the study site.

Water that doesn't go through the transpiration pathway may be considered lost from the point of view of the primary productivity (Noy-Meir, 1973), and it includes evaporation, drainage and surface runoff. Evaporation represents between 20 and 70% of the rain in semiarid lands (Le Houérou, 1984). In the Magellanic Steppe, evaporation losses are probably important, as small rainfalls only infiltrate a few cm in the soil and they are subject to direct evaporation from the soil surface, specially during periods of high atmospheric demand. Drainage, defined as the downward movement of water across the bottom of the root zone, may occur in our study site when water reaches deeper than 60 cm, as this soil layer is still subject to transpiration losses (Fig. 3). The lack of a clear rainy season and the low frequency of big rainstorms that characterize the climate at the site probably limit this process. In winter rainfall systems, Paruelo and Sala (1995) estimated that only 20% of total precipitation is lost to drainage and Sala et al. (1992) predicted no losses at all in summer-rainfall semiarid lands. A particular aspect of these soils is that they freeze for a period of up to 2 months, and drainage may only take place in a small temporal window in late autumn and early winter, when the soil profile reaches field capacity, and before sub zero temperatures reduce hydraulic conductance. Surface runoff also appears to be limited as the soils are coarse textured and the water input flow is usually of less than 5 mm/day.

Even with a low annual rainfall, the soil profile remained close to field capacity most of the year. The shallow soil layers only dried

Table 1

Mean values of patch size and soil water content (%) \pm SE under different types of patches Short grasses, Tussock grasses, Dwarf shrubs and Bare soil. Measurements made with TDR, depth 0–15 cm, in summer. Different letters indicate significant differences in soil water content among types of patches ($p < 0.05$).

Type of patch	Short grasses	Tussock grasses	Dwarf shrubs	Bare soil
<i>n</i>	109	108	61	85
Patch Size (cm)	21.35 ± 1.07	24.28 ± 1.32	45.63 ± 3.58	19.04 ± 1.60
Soil water content (%)	$6.41 \pm 0.12\text{b}$	$5.49 \pm 0.13\text{a}$	$6.00 \pm 0.19\text{b}$	$6.96 \pm 0.15\text{c}$

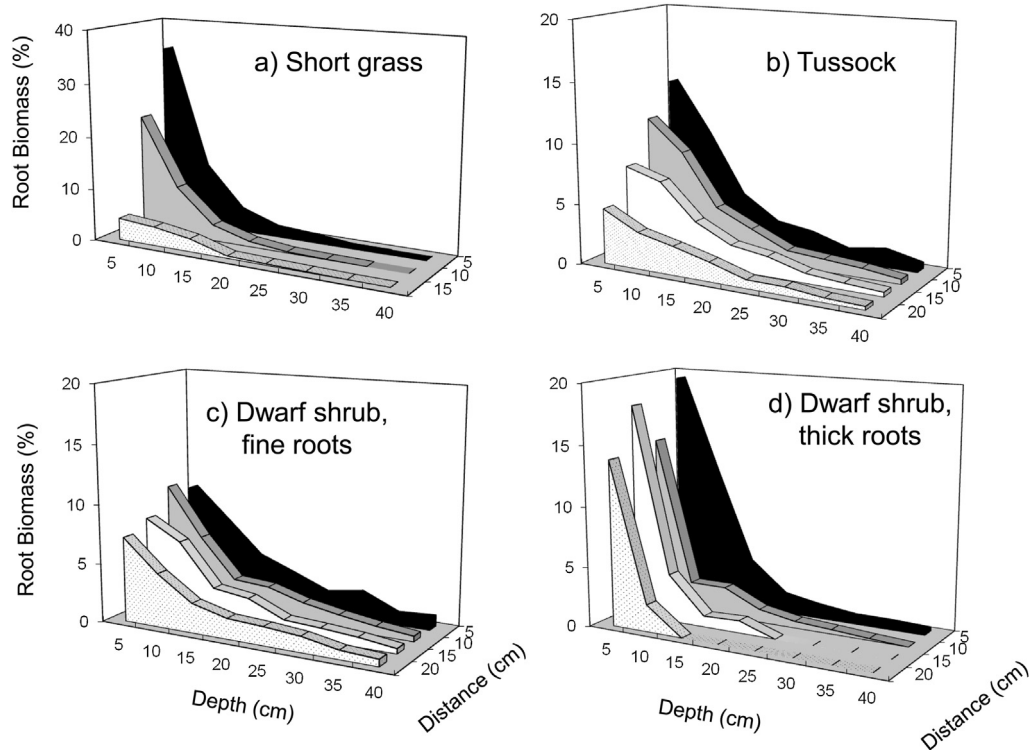


Fig. 4. Root biomass distribution (%). X axis is depth in the soil profile (cm). Z axis is horizontal distance from center of the plant (cm). Values are accumulated percentages in the 0–10 cm depth for each distance. Absolute values of root biomass \pm (SE) are shown in brackets: (a) *Poa spiciformis* ($0.68 \pm 0.27 \text{ g dm}^{-3}$); (b) *Festuca gracillima* ($1.94 \pm 0.12 \text{ g dm}^{-3}$); (c) fine roots $<0.2 \text{ mm}$ diameter ($4.5 \pm 1.02 \text{ g dm}^{-3}$) and thick roots $>0.2 \text{ mm}$ diameter ($4.1 \pm 1.58 \text{ g dm}^{-3}$), of *Nardophyllum bryoides*.

out in summer and remained so until autumn, except in 2001, when rainfall events in February that exceeded 10 mm replenished them in mid-summer. The soil recharged due to a succession of small rains in cold days in autumn that gradually deepened the wetting front (Fig. 3), and the soil profile remained moist throughout spring. The pattern of soil water with high availability in October–November and March–April lead to bimodal vegetation growth curves that are evident in biomass production curves (Ferrante, 2011) and satellite imagery studies (Paredes, 2011).

Shallower soils remain dry over the summer but showed different water contents in vegetated and bare soil areas. These contrasts are important in water-limited systems and have been extensively studied: In the Kalahari savanna, woody vegetated patches showed higher water availability, due to a reduced soil evaporation rate under canopies that facilitates in turn shrub establishment and productivity (D'Odorico et al., 2007). In Mojave and Chihuahuan deserts, on the contrary, vegetated patches

showed lower water availability, due to a higher hydraulic conductivity in coarse-textured interpatches (Caldwell et al., 2008) and to evaporative losses due to canopy interception in vegetated patches (Duniway et al., 2010). In our study, water content was lower in the vegetated patches. Soils directly under these patches lose water by transpiration due to higher root density, and by evaporation from the moist foliage following canopy interception. Tussock patches, that showed lower water content than shrub and short grass-dominated ones have denser canopies and may intercept small rainfall events more effectively. Vegetated patches also retain fine soil particles (Caldwell et al., 2008), and bare soil areas lose them. Coarser textures and higher infiltration rates in interpatches may explain our results as evaporation is not efficient in removing water that reaches deeper than 10 cm in bare soil areas (Noy-Meir, 1973).

Table 2

Leaf water potential (MPa) (mean \pm SE) measured between 11:00 and 14:00 h of three species: *Poa spiciformis* (short grass), *Festuca gracillima* (tussock grass) and *Nardophyllum bryoides* (dwarf shrub) in spring, summer and autumn. Number of dates within each season when measurements were performed (Dates) and total number of plants measured in each season (n). Different letters indicate statistical differences between species in each season ($p < 0.05$).

	<i>Poa spiciformis</i> (short grass)	<i>Festuca gracillima</i> (tussock grass)	<i>Nardophyllum bryoides</i> (dwarf shrub)
Spring	-2.76 ± 0.26 a	-2.61 ± 0.29 a	-2.43 ± 0.21 a
Dates	8	8	8
n	111	110	114
Summer	-3.81 ± 0.41 a	-3.7 ± 0.35 a	-2.71 ± 0.23 b
Dates	13	13	13
n	168	178	174
Autumn	-2.8 ± 0.42 a	-3.13 ± 0.53 a	-2.5 ± 0.26 a
Dates	5	6	6
n	73	80	80

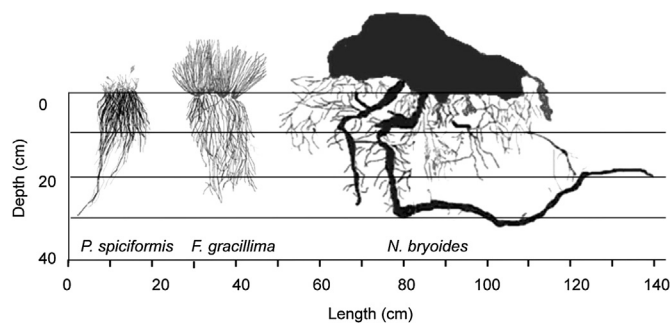


Fig. 5. Diagrams of the root systems of *Poa spiciformis*, *Festuca gracillima* and *Nardophyllum bryoides* drawn from photographs of the soil profiles.

Roots are mostly found in the soil surface, where water and nutrients are available (Fig. 4) (Austin et al., 2004; Jobbágy and Jackson, 2001). Our detailed root sampling 40 cm deep indicates that both grasses and shrubs concentrate over 60% of the root biomass in the 0–10 cm depth. The density below 40 cm is low but some plants reach this depth, as water in the 60-cm deep soil is slowly depleted during summer (Fig. 3). The classical two-layer model of water utilization by grasses and shrubs (Walter, 1971) is not appropriate in this case, as plants “drink from the same cup” (Reynolds et al., 2000). Hunter (1989) indicates that, under these conditions, soil water will disappear at a rate proportional to the number of “drinkers” and to their drinking rates. Few “drinkers” may explain that deep layers in the soil remain moist year-round, as most of the long tap roots of the shrubs deviate and laterally explore shallow soil volumes. In this conditions it may not be adaptive to maintain costly root structures deep in the soil that access water that is only replenished yearly. Shallow soil water, on the other hand, is subject to competition between life forms, but is replenished constantly by the frequent, small rains. Shrub roots may be extending laterally in order to access water in the bare soil areas, and this additional resource may explain higher leaf water potentials and buffer its variations (Table 2). Grasses have only access to a small volume of soil that does not extend beyond the crown area (Fig. 4) and this could explain their lower and highly variable leaf water potentials.

This study showed that the distribution of water in the soil profile is related to structure and function of Magellanic steppe vegetation. Water resource is provided here almost exclusively by small rain events, and both grasses and shrubs develop extremely shallow root systems to utilize a resource that has a short residence time. Deep-root life forms common in Patagonia and other arid and semiarid regions are missing. Woody plants develop root systems that explore shallow soil layers in inter-canopy spaces, instead of deeper into the soil profile under the plant canopy. This horizontal water use may enable niche separation in this water-limited steppe ecosystem. Steppes in good condition show a clear dominance of grasses both in cover (Humano et al., 2005) and in productivity (Cibils et al., 2005), but the similar root distribution pattern between grasses and shrubs implies that the woody plants may outcompete grasses under continuous grazing schemes. Sheep prefer the short palatable grasses instead of shrub leaves, and this may explain the general tendency of replacement of grasses by shrubs in the State and Transition models for the area (Oliva et al., 1998).

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2014.01.009>.

References

- Abbott, L., Roundy, B.A., 2003. Available water influences field germination and recruitment of seeded grasses. *J. Range Manag.* 56, 56–64.
- Austin, A., Yahdjian, L., Stark, J., Belnap, J., Porporato, A., Burke, I.C., Norton, U., Ravetta, D., Schaeffer, S., 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* 141, 221–235.
- Böhm, W., 1979. *Methods of Studying Root Systems*. Springer Verlag, Berlin.
- Bucci, S., Scholz, F., Goldstein, G., Meinzer, F., Arce, M., 2009. Soil water availability and rooting depth as determinants of hydraulic architecture of Patagonian woody species. *Oecologia* 160 (4), 631–641.
- Burgos, J., 1985. Clima en el extremo sur de Sudamérica. In: Boelcke, O., Moore, D., Roig, F. (Eds.), *Transecta botánica de la Patagonia Austral*. CONICET, Instituto de la Patagonia y Royal Society, Buenos Aires, pp. 10–40.
- Caldwell, T.G., Young, M.H., Zhu, J., McDonald, E.V., 2008. Spatial structure of hydraulic properties from canopy to interspace in the Mojave Desert. *Geophys. Res. Lett.* 35 (19).
- Cibils, A., Humano, G., Escalada, J., Torra, P., 2005. Productividad primaria de un pastizal de la Estepa Magallánica seca. In: González, L., Iglesias, R., Cibils, A. (Eds.), *Campo experimental Potrok Aike. Resultado de 15 años de labor técnica*. INTA, Buenos Aires, pp. 59–60.
- Chesson, P., Gebauer, R.L., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S., Sher, A., Novoplansky, A., Walters, J.F., 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* 141, 236–253.
- De Fina, A., Garbosky, A., Gianetto, F., Sabella, L., 1968. *Difusión geográfica de cultivos índices en la Provincia de Santa Cruz*. INTA, Buenos Aires.
- D’Odorico, P., Caylor, K., Okin, G.S., Scanlon, T.M., 2007. On soil moisture–vegetation feedbacks and their possible effects on the dynamics of dryland ecosystems. *J. Geophys. Res. Biogeosci.* 112 (G4), 2005–2012.
- Duniway, M.C., Snyder, K.A., Herrick, J.E., 2010. Spatial and temporal patterns of water availability in a grass–shrub ecotone and implications for grassland recovery in arid environments. *Ecohydrology* 3 (1), 55–67.
- Ferrante, D., 2011. *Distribución del agua en el suelo y su relación con la estructura radicular y producción de biomasa de tres tipos funcionales, en un pastizal de la Estepa Magallánica seca*. Santa Cruz (Master Degree Thesis). University Buenos Aires, Buenos Aires.
- Golluscio, R.A., Sala, O.E., Lauenroth, W.K., 1998. Differential use of large summer rainfall events by shrubs and grasses: a manipulative experiment in the Patagonian steppe. *Oecologia* 115 (1–2), 17–25.
- Humano, G., Oliva, G., Battini, A., Mascó, M., Kofalt, R., Barría, D., 2005. La vegetación del campo Experimental Potrok Aike. In: González, L., Iglesias, R., Cibils, A. (Eds.), *Campo Experimental Potrok Aike. Resultado de 15 años de labor técnica*. INTA, Buenos Aires, pp. 43–46.
- Hunter, R., 1989. Competition between adult and seedling shrubs of *Ambrosia dumosa* in the Mojave Desert, Nevada. *Gt. Basin Nat.* 49 (1), 79–84.
- Jobbágy, E., Jackson, R.B., 2001. The distribution of soil nutrients with depth: global patterns and the imprint of plants. *Biogeochemistry* 53, 51–77.
- Jobbágy, E., Sala, O., 2000. Controls of grass and shrub aboveground production in the Patagonian steppe. *Ecol. Appl.* 10 (2), 541–549.
- Kowalijow, E., Fernández, R.J., 2011. Differential utilization of a shallow-water pulse by six shrub species in the Patagonian steppe. *J. Arid Environ.* 75, 211–214.
- Lambers, H., Chapin III, F.S., Pons, T.L., 1998. Plant water relations. In: *Plant Physiological Ecology*. Springer, New York, pp. 155–209.
- Lamoreaux, M., Migliora, H., Marcolín, A., 2005. Los suelos del Campo Experimental Potrok Aike. In: González, L., Iglesias, R., Cibils, A. (Eds.), *Campo Experimental Potrok Aike. Resultado de 15 años de labor técnica*. INTA, Buenos Aires, pp. 27–30.
- Le Houérou, H.N., 1984. Rain use efficiency: a unifying concept in arid-land ecology. *J. Arid Environ.* 7, 213–247.
- Loik, M.E., Breshers, D.D., Lauenroth, W.K., Belnap, J., 2004. A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. *Oecologia* 141, 269–281.
- Monteith, J.L., 1973. *Principles of Environmental Physics*. Academic Press, London.
- Noy-Meir, I., 1973. Desert ecosystems: environment and producers. *Annu. Rev. Ecol. Syst.* 4, 25–51.
- Oliva, G., Cibils, A., Borrelli, P., Humano, G., 1998. Stable states in relation to grazing in Patagonia: a 10-year experimental trial. *J. Arid Environ.* 40 (1), 113–131.
- Paredes, P., 2011. *Caracterización funcional de la Estepa Magallánica y su transición a Matorral de Mata Negra (Patagonia Austral) a partir de imágenes de resolución espacial intermedia* (Master Degree Thesis UBA). Facultad de Agronomía, Buenos Aires.
- Paruelo, J., Sala, O., 1995. Water losses in the Patagonian steppe: a modelling approach. *Ecology* 76, 510–520.
- Paruelo, J.M., Beltrán, A., Jobbágy, E.G., Sala, O.E., Golluscio, R.A., 1998. El clima de la región Patagónica: Patrones generales y controles sobre los procesos bióticos. In: Swedforest, C.D. (Ed.), *Diagnóstico, estrategias y acciones propuestas para el uso sostenible de los recursos naturales en la Patagonia*. Secretaría de Agricultura, Ganadería, Pesca y Alimentación, República Argentina, Buenos Aires.
- Reynolds, J., Kemp, P., Tenhunen, J., 2000. Effects of long-term rainfall variability on evapotranspiration and soil water distribution in the Chihuahuan Desert: a modeling analysis. *Plant Ecol.* 150, 145–159.
- Reynolds, J.F., Kemp, P.R., Ogle, K., Fernández, R.J., 2004. Modifying the “pulse-reserve” paradigm for deserts of North America: precipitation pulses, soil water; and plant responses. *Oecologia* 141, 194–210.
- Rodríguez, M.V., Bertiller, M.B., Bisigato, A., 2007. Are fine roots of both shrubs and perennial grasses able to occupy the upper soil layer? A case study in the arid Patagonian Monte with non-seasonal precipitation. *Plant and Soil* 300, 281–288.
- Roig, F., 1998. La Vegetación de la Patagonia. In: Correa, M. (Ed.), *Flora Patagónica*. INTA, Buenos Aires, pp. 48–166.
- Sala, O.E., Lauenroth, W.K., 1982. Small rainfall events: an ecological role in semiarid regions. *Oecologia* 53, 301–304.
- Sala, O.E., Lauenroth, W.K., Golluscio, R.A., 1997. Plant functional types in temperate semi-arid regions. In: Smith, T.M., Shugart, H.H., Woodward, F.I. (Eds.), *Plant Functional Types – Their Relevance to Ecosystem and Global Change*. Cambridge University Press, Cambridge, pp. 217–233.
- Sala, O.E., Lauenroth, W.K., Parton, W.J., 1992. Long term soil water dynamics in the shortgrass steppe. *Ecology* 73, 1175–1181.
- Schulze, E.D., Mooney, H.A., Sala, O.E., Jobbágy, E.G., Buchman, N., Bauer, G., Canadell, J., Jackson, R.B., Loreti, J., Oesterheld, M., Ehleringer, J.R., 1996. Rooting depth, water availability, and vegetative cover along an aridity gradient in Patagonia. *Oecologia* 108, 503–511.

- Schwinning, S., Starr, B.I., Ehleringer, J., 2005. Summer and winter drought in a cold desert ecosystem (Colorado Plateau) part I: effects on soil water and plant water uptake. *J. Arid Environ.* 60, 547–566.
- Schwinning, S., Ehleringer, R., 2001. Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *J. Ecol.* 89, 464–480.
- Soriano, A., 1956. Los distritos florísticos de la Provincia Patagónica. *Rev. Investig. Agríc.* 10, 323–347.
- Soriano, A., 1990. Missing Strategies for Water Capture in the Patagonian Semi-desert, vol. 5. Academia Nacional de Ciencias Exactas Físicas y Naturales, pp. 135–139.
- Soriano, A., Golluscio, R., Satorre, E., 1987. Spatial heterogeneity of the root system of grasses in the Patagonian arid steppe. *Bull. Torrey Bot. Club* 114, 103–108.
- Soriano, A., Sala, A., 1983. Ecological strategies in a patagonian arid steppe. *Vegetatio* 56, 9–15.
- Turner, N., 1987. The use of the pressure chamber in studies of plant water status. In: *International Conference on Measurement of Soil and Plant Water Status. Centennial of Utah State University, Utah*, pp. 13–24.
- Walter, H., 1971. *Natural Savannas. Ecology of Tropical and Subtropical Vegetation.* Oliver and Boyd, Edinburgh.