Journal of Arid Environments 82 (2012) 130–135

Contents lists available at SciVerse ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Contrasting nutrient-capture strategies in shrubs and grasses of a Patagonian arid ecosystem

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ARTICLE INFO

Article history:
Received 23 October 2010
Received in revised form
17 February 2012
Accepted 21 February 2012
Available online 28 March 2012

Keywords:
Arid ecosystems
Grass-shrub competition
Nitrogen cycling
Water–nitrogen interactions
Water relations

ABSTRACT

Shallow-rooted grasses and deep-rooted shrubs dominate arid ecosystems where nitrogen is concentrated in the upper layers of the soil and water is distributed throughout. Analysis of mineral nitrogen and absorption patterns using a tracer indicated that shrubs in Patagonia absorbed nutrients from the lower, relatively nutrient-poor layers of the soil. Are they, consequently, at a competitive disadvantage with grasses that have the opposite pattern? Studies of nitrogen economy indicated that shrub and grass species have similar N-use efficiency but that they achieve it through opposite mechanisms. Shrubs have a conservative N economy absorbing annually only small fraction of their N content, whereas grasses have a more open N economy. This study about N-capture strategies in conjunction with previous studies about water-use by shrubs and grasses in the Patagonian Steppe suggest a coupling of N and water-capture strategies. Our findings have implications for the response of arid and semiarid ecosystems to global warming, nitrogen deposition, and biodiversity change. For example, climate change scenarios predict, for most arid regions, decreases in moisture availability that will result in a reduction in deep water, which in turn will reduce shrub density and result in a less conservative nitrogen economy.

1. Introduction

Arid and semiarid ecosystems account for one third of the area of world terrestrial ecosystems (Verstraete and Schwartz, 1991) and they are made up of varying proportions of two dominant types of plants; grasses and woody plants (shrubs and small trees). These two types of plants have contrasting rooting patterns (Jackson et al., 1996), with shallow roots for grasses and predominantly deep roots for shrubs. Most of the soil nitrogen in arid and semiarid ecosystems is concentrated in the upper layers of the soil (Jobbágy and Jackson, 2000; West and Klemmedson, 1978) whereas other nutrients such as Ca, Mg and Na have a deeper distribution (McCulley et al., 2004). In contrast to the N distribution, soil water is distributed throughout the entire soil profile. The exact distribution of moisture in the soil profile depends on seasonality of inputs and soil texture (Sala et al., 1997). If both plant types absorb nutrients from the same layer where they absorb water, deep-rooted shrubs would be at a competitive disadvantage with grasses because the former would be absorbing from nutrient-poor layers and the latter from nutrient-rich layers. However, the coexistence of these two types of plants challenges the idea that one has a competitive advantage over the other.

Where are these plant types absorbing the bulk of their nutrients? How does the water absorption pattern constrain the nutrient economy of each plant type? Or vice versa, how does the nutrient economy determine the water-absorption pattern? Are strategies to acquire resources that have contrasting soil availability patterns, such as water and nitrogen, coupled or mutually constrained? In order to address these questions, we carried out a tracer experiment and estimated the components of the nitrogen economy of dominant grasses and shrubs in the Patagonian steppe, which is a good model for the study of arid ecosystems because of its mixture of shrubs and grasses and because there is good understanding of their water absorption patterns. An experiment, where grasses and shrubs were alternatively removed and the soil water monitored, clearly showed that grasses absorb water mostly from upper soil layers and shrubs mostly from deep soil layers (Sala et al., 1989).

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doi:10.1016/j.jaridenv.2012.02.015

2. Materials and methods

2.1. Site description

The Patagonian steppe is a cold and arid ecosystem with an annual precipitation of 170 mm concentrated during fall and winter, and monthly temperatures that range between 2 and 14 °C (Sala et al., 1989). Vegetation is dominated by two types of plants, shrubs and grasses, that account for 96% of the aboveground productivity and each of them contributes approximately half of total production (Jobbágy and Sala, 2000). Three species of grasses (*Poa ligularis* Nees apud Steudel, *Stipa speciosa* Trin. et Rupr., and *Stipa humilis* Vahl.) and three species of shrubs (*Mulinum spinosum* Cav (Pers), *Adesmia volckmanni* (Philippi) and *Senecio filaginoides* (De Cand)) (Ulibarri, 1986) account for more than 90% of plant cover interspersed in a matrix of bare soil, which occupies 62% of the area (Soriano et al., 1994). Soils are coarse textured and have a well-developed caliche layer at 60 cm depth (Sala et al., 1989). The studies reported in this paper were located at the Río Mayo Experimental Station in Chubut Argentina (45° 11′ S, 70° 16′ W).

2.2. Soil nitrogen content

Shrubs and grasses in the Patagonian steppe are distributed in two patch types; (i) shrubs surrounded by a dense ring of grasses and (ii) scattered grass tussocks in a bare soil matrix (Soriano et al., 1994). To account for the spatial heterogeneity of the steppe, we dug 10 soil pits of 1.2 m depth by 1.5 m width, and in each one, we collected soil samples underneath a shrub, under a grass in the ring around the shrub, under a bare soil patch, and underneath a scattered grass tussock. Soil samples were collected in each location at 5, 15, 30, 60 and 100 cm depths in the month of January (mid-summer). Instead of calculating the linear average of N content in different microsites, we reported average values for the steppe that resulted from weighting each location according to its cover in the steppe (shrub 12%, grass in the shrub ring 5%, bare soil 62%, and scattered tussocks 21% (Soriano et al., 1994)). Soil samples were collected in the field, brought rapidly to the laboratory where they were sieved through a 2-mm mesh and 10-g subsamples were extracted in 50 ml 2 N KCl. Soil extracts were analyzed with an Alpkem autoanalyzer (O-I Corporation, College Station, TX) that performs a colorimetric analysis. Soil nitrogen concentrations were corrected by soil water content, which was calculated after drying subsamples at 105 °C for 48 h (Robertson et al., 1999). We performed analysis of variance to assess differences among depths, independently for NO_3^- and NH_4^+ ($N = 10$).

2.3. Nutrient absorption patterns of shrubs and grasses

In order to address the question from where in the soil profile shrubs and grasses absorb nutrients, we performed an experiment using lithium (Li) as a non-radioactive tracer (Martin et al., 1982). Lithium has several advantages making it an ideal element for this type of study; it is present in low concentration in the soil, is absorbed freely by roots, and is non-toxic at low concentration. Our experiment consisted in locating a LiCl solution in the soil adjacent to grass and shrub individuals at different depths and measuring Li concentration in the leaves a few days later. Our experimental design had 5 treatments, resulting from a water only control and 4 depths of LiCl injection (10, 30, 60 and 100 cm), and 4 replicates. We randomly selected 20 pairs of individuals of *P. ligularis* and *M. spinosum*, which were chosen as representatives of the grass and shrub plant-functional types based on previous research results (Sala et al., 1989). Selected grasses were not associated with shrub individuals. We located 10 ml of 10% LiCl solution at a different depth for each treatment and we harvested leaves 16 days later. Each pair of individuals received LiCl solution at one of the 4 depths and there were four replicates. To deliver the LiCl solution at the desired depth, we used a plastic tube attached to a steel rod, and after delivering the tracer, we added another 10 ml of distilled water to flush the tube. We applied the LiCl solution on December 3, when all shrub and grass species are physiologically active and before the onset of mid-summer drought (Golluscio et al., 2005). Prior to the tracer application, we measured soil water potential with PC 55 Wescor thermocouple hygrometers (Spanner, 1951), calculated water content in the entire profile using a soil water potential data and site-specific retention curve and added the amount of water to bring the upper 120 cm of the profile to field capacity. We watered the soil profile to field capacity because we wanted to evaluate potential root absorption that would not have been limited by soil water availability. We oven dried the harvested leaves at 70 °C for 48 h, ground them, and placed them in a muffle furnace at 500 °C for 6 h. Li was extracted from the ash with HCl and measured by atomic absorption spectrometry. Results were expressed in g m^{-2} by multiplying the leaf Li concentration (mg kg^{-1} of oven-dried leaves) by the green biomass of each plant type (kg m^{-2}). We performed analysis of variance for Li concentration to assess differences between shrubs and grasses for each depth ($N = 4$).

Martin et al. (1982) tested the value of Li as a tracer in barley (*Hordeum sativum*) and beans (*Vicia faba*). To confirm the value of Li as a tracer, we conducted a growth-chamber experiment where we double-labeled with LiCl and $(^{15}NH_4)\ 2SO_4$. We were interested in evaluating whether Li behaves as an analog of NH_4^+, which is also a cation and the dominant species of mineral N in soils of the Patagonian steppe (Austin and Sala, 2002). The experiment used plants of *Lolium multiflorum* Lamarck growing in pots of 80 cm height and 5.6 cm diameter. We used *L. multiflorum* because it is a standard material with abundant information available in the literature. Growth chamber provided day–night alternate temperature of 25–20 °C, and 10 h of 219 μmol PAR $m^{-2}\ s^{-1}$ light (PAR = Photosynthetically Active Radiation). We simultaneously applied 10% LiCl solution and 1.16 N $(^{15}NH_4)\ 2SO_4$ solution at 5, 15, 30, and 60 cm depth using 4 replicates per depth. We applied the label solutions from the side of the pots using disposable syringes. Eight days after the double labeling, we harvested the aboveground portion of the plants and measured Li and ^{15}N concentrations. Li concentration was measured using the same technique described above, and ^{15}N using a mass spectrometry technique at the Department of Crop and Soil Sciences, Michigan State University. Regression analyses indicated that absorption of Li was significantly and linearly related to the absorption of NH_4^+.

$$\mathrm{Li}\left(\mathrm{mg\ g^{-1}}\right) = 0.04 + 0.31\ ^{15}\mathrm{N{-}NH_4}\left(\mathrm{mg\ g^{-1}}\right); \quad \left(r^2 = 0.48,\ p < 0.01,\ N = 16\right)$$

Our results suggest that LiCl is a good tracer to estimate the potential for NH_4^+ absorption from the soil. The main advantages of Li over ^{15}N are the low cost and the simple manipulation that allows for large number of replicates, which are needed in most field experiments.

2.4. Nitrogen economy of shrubs and grasses

To assess the consequences of absorption patterns on the N economy of the dominant groups of plants, we estimated N-use efficiency (NUE, g of biomass produced per g of N absorbed) and its components, nitrogen productivity (NP) and residence time (RT)