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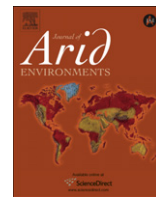
Contrasting nutrient-capture strategies in shrubs and grasses of a Patagonian arid ecosystem

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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.

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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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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^+.

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

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)

(Aerts and Chapin, 2000; Berendse and Aerts, 1987) in the 3 dominant-grass species and 3 dominant-shrub species.

$$\mathrm{NUE}\left(\mathrm{g\ gN}^{-1}\right) = \mathrm{NP}\left(\mathrm{g\ gN}^{-1}\ \mathrm{yr}^{-1}\right){*}\mathrm{RT(yr)}$$

Nitrogen productivity is the aboveground production per unit N in aboveground biomass and it was estimated as the ratio between aboveground net primary production (ANPP, g m^{-2} yr^{-1}) and the amount of N in the aboveground biomass (gN m^{-2}). The residence time is the average time that an absorbed atom of N is tied up inside the plant and it was calculated as the ratio between the aboveground N content (gN m^{-2}) and the annual N uptake (gN m^{-2} yr^{-1}). The inverse of RT indicates the fraction of the N content met with newly absorbed N, in contrast with retranslocated N, which was absorbed in previous years. Finally, NUE represents the units of biomass produced per unit of N absorbed and was calculated as the product of RT and NP.

In order to estimate nitrogen use efficiency (NUE), and its two components RT, and NP (Aerts and Chapin, 2000; Berendse and Aerts, 1987), we needed to estimate aboveground net primary production (ANPP), aboveground N content, and annual N uptake for each of the 3-dominant grass and 3-dominant shrub species. We estimated ANPP using a harvest technique equating ANPP with peak biomass (Sala and Austin, 2000), but used different sampling schemes to assess grass and shrub peak biomass. We harvested grasses at peak biomass using 20 randomly located 0.2 × 5 m plots, separated harvest material of each species in green biomass and current-year standing dead and oven-dried at 70 °C for 48 h. We estimated shrub ANPP using the method developed by Fernandez et al. (1991) for the Patagonian steppe and harvested 20 plots 0.1 × 0.25 m located on top of randomly selected individuals of each shrub species. Production per unit shrub was translated into production per unit steppe area by measuring diameter of each individual where samples were collected and the density of each shrub species in the steppe. Fernandez et al. (1991) provided the allometric relationship to calculate production of each shrub species per unit area of steppe based on estimates of production per unit shrub area and its height, diameter, and density.

We estimated aboveground N content as the sum of the products of standing dead and green biomass times their N concentrations. We estimated grass N concentration in green and standing dead material at peak biomass in the 20 plots harvested to estimate ANPP. Similarly, we estimated N concentration in shrub-green leaves, which were collected in the plots used to estimate ANPP. Estimates of N concentration in shrub-standing dead (gold color) required two different approaches for *M. spinosum*, which maintains senesced leaves attached to the stems, and *S. filaginoides* and *A. volckmanni*, which drop most of their leaves at the end of the growing season. *M. spinosum* senesced leaves were collected from 0.05 × 0.15 m plots located on top of 20 randomly selected individuals. In the second case, we collected the litter produced during the current year, in January and April, using 20 cylindrical containers 20 cm in diameter and 15 cm in height, which were located underneath randomly selected individuals. Containers were located on the soil and had a bottom; therefore current-year litter was isolated from older already existing on the soil. Total N content in green leaves and standing dead material was estimated using a Kjeldahl technique (Nelson and Sommers, 1980).

In order to estimate annual N uptake, we assumed that the ecosystem was in a steady state, and consequently that the annual N loss equaled the annual N uptake (Berendse and Aerts, 1987) and that ANPP equaled annual senescence (Shaver et al., 1992). As a consequence, we calculated annual N uptake as the product of aboveground net primary production and N concentration of gold-color standing dead (Berendse and Aerts, 1987). N in this compartment represents the total N lost per year from the aboveground plant parts into the soil because this is the N that was not retranslocated to perennial organs and had not been leached out of the litter yet (Austin and Vitousek, 2000; Cornelissen et al., 1999). We used Wilcoxon non-parametric statistical analysis on NP, RT, and NUE because of variance heterogeneity. We performed statistical analysis using Statistica software package (Statistica, 1995) and $\alpha = 0.05$. Statistical analysis of RT in shrubs posed an additional problem because the denominator of RT was annual N uptake, which was calculated as the product of ANPP and standing-dead N concentration. These two variables required destructive sampling; and consequently we were not able to measure them in the same individuals or estimate their covariance. We developed 3 scenarios of maximum, minimum and no covariance by ranking both terms of the product in the same or opposite order, or assuming null covariance. In the latter case, we used mean standing-dead N concentration for all replicates of each species. The interpretation of the statistical analysis was identical under the 3 scenarios. Here, we only report results of the statistical analysis with null covariance.

3. Results

Soil mineral nitrogen in the Patagonian steppe was concentrated in the upper layers of the soil (Fig. 1). NH$_4^+$ was the dominant species of mineral N in the Patagonian steppe with a minimal contribution of NO$_3^-$, although the relative contribution of NO$_3^-$ to total N was larger in this ecosystem than in other more mesic Patagonian ecosystems (Austin and Sala, 2002). NO$_3^-$ had an even shallower distribution than NH$_4^+$ with extremely low values beyond 5 cm of depth whereas NH$_4^+$ concentrations stayed above 1 μg g^{-1} for all layers above 60 cm.

Our experiment using Li as an analog of NH$_4^+$ indicated that grasses absorb Li and most likely NH$_4^+$ from the upper layers of the soil and shrubs absorb from deep layers (Fig. 2). Grasses showed a disproportionately large absorption from the uppermost layer, a smaller value at 30 cm, and practically no absorption at 60 and 100 cm of depth. On the contrary, shrubs showed no absorption in the shallow layers and most of the absorption occurring at 30 and 60 cm of depth. No plant type absorbed at 100 cm depth, which was the maximum depth that we explored with our experiment. A growth-chamber experiment where we double-labeled with LiCl and ^{15}NH$_4$ 2SO$_4$ (see Methods) indicated that Li absorption was significantly related with the absorption of NH$_4^+$, which is also a cation.

Our results suggest that shrub species could be at a competitive disadvantage with grasses because the former absorbed nutrients from a relatively nutrient poor layer whereas grasses absorb from a relatively richer layer. To assess the consequences of the

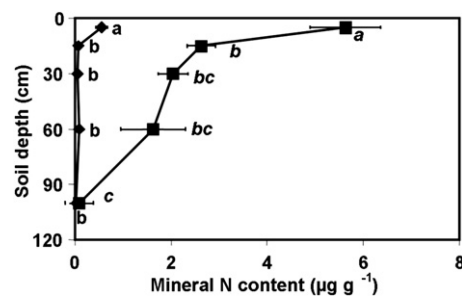**Fig. 1.** Distribution of mineral nitrogen in the soil profile of the Patagonian steppe. Each data point is the mean of 10 independent samples and bars represent standard errors (see methods section for experimental details). Diamonds represent NO$_3^-$ distribution and squares NH$_4^+$. Different letters indicate significant ($p < 0.05$) differences among depths, independently for NO$_3^-$ or NH$_4^+$.
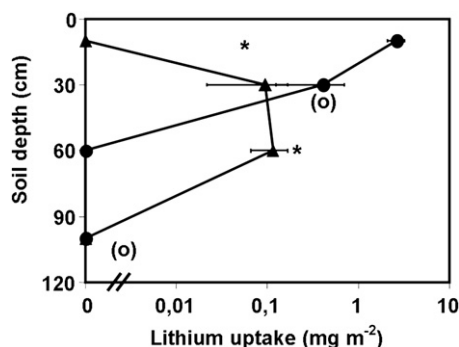
Fig. 2. Nutrient absorption patterns of shrubs and grasses in the Patagonian steppe assessed by patterns of LiCl absorbed from different depths (see methods section for experimental details). Triangles represent average absorption by the dominant shrub species *Mulinum spinosum* and circles by the dominant grass species *Poa ligularis* ($N = 4$). Bars represent standard errors. LiCl was used as a non-radioactive tracer after a growth chamber study showed a high correlation between ($^{15}NH_4)_2SO4$ and LiCl experimentally injected at different depths. (*) Significant differences $p < 0.05$ between shrub and grass species for each depth; (○) non-significant differences $p > 0.05$.

absorption pattern reported in the previous paragraph on the N economy of the dominant group of plants, we estimated N-use efficiency and its components N productivity and residence time in the 3 dominant-grass species and the 3 dominant-shrub species. N productivity (NP) was significantly ($p < 0.05$) higher in grasses than in shrubs (Fig. 3). The three species of grasses performed very similarly with very small differences among grass species. Among the shrub species, *M. spinosum* had higher values of N productivity than the other two shrub species. Although aboveground net primary production of grasses was quite similar to the production of shrubs, the N content in aboveground biomass was much lower in grasses than shrubs resulting in a much higher N productivity for grasses (Table 1).

N residence time showed opposite patterns to those observed for N productivity (Fig. 3B). N residence time was negatively correlated with N productivity ($r = -0.96$, $n = 6$, $p < 0.05$) as found by Eckstein and Karlsson (Eckstein and Karlsson, 1997). The three grass species showed N residence times significantly lower than the three shrub species. Residence times of grass species were approximately 3 years, whereas those of shrub species ranged from 6 to 14 years. Differences in N residence time within groups of plant species (shrubs or grasses) complemented trends observed in N productivity. There were no significant differences among grass species; and the shrub species (*S. filaginoides*) with the lowest N productivity showed the highest N residence time. Contrasting patterns in N productivity and N residence times between grasses and shrubs yielded similar NUE values. The NUE for the group of grasses was 172 g gN^{-1} and for shrubs was 125 g gN^{-1}. The statistical comparison between the group of grasses and shrubs yielded no significant differences ($p > 0.05$). However, there were differences in NUE among species (Fig. 3C). The dominant grass species *S. speciosa* and the dominant shrub species *M. spinosum* had the same NUE but the other two grass species had NUE values significantly higher than the other two shrub species.

4. Discussion

This work shows that dominant grasses and shrubs of the Patagonian Steppe have contrasting nitrogen-capturing strategies. Grasses absorb N predominantly from upper soil layers and shrubs from lower soil layers, as shown by the tracer experiment (Fig. 1). Soil N concentration declined with depth (Fig. 2) but grasses that absorb from a relatively N-rich layer achieve a similar N-use
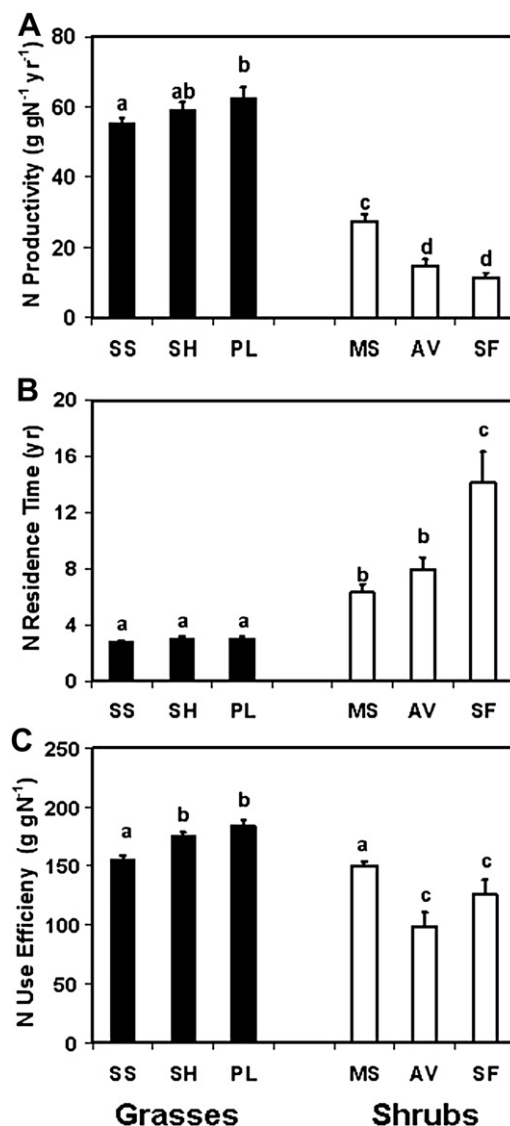
Fig. 3. Nitrogen use efficiency (NUE) and its components, N productivity and N residence time, for the 6-dominant species of the Patagonian steppe, the grasses SS *Stipa speciosa*, SH *Stipa humilis*, PL *Poa ligularis*, and the shrubs MS *Mulinum spinosum*, *Adesmia volckmanni*, and SF, *Senecio filaginoides*. (A) Nitrogen productivity (NP) calculated as the ratio between aboveground net primary production and the amount of N in the aboveground biomass. (B) Nitrogen residence time (RT) calculated as the ratio between the aboveground N content and the annual N uptake. (C) Nitrogen use efficiency represents the aboveground production per unit absorbed nitrogen and was calculated as the product of NP and RT. Different letters indicate significant differences ($p < 0.05$) among species, Wilcoxon test for panels A and B; and Tukey test for panel C (see methods section for details). The statistical comparison between the group of grasses and shrubs for NUE yielded no significant differences ($p > 0.05$).

efficiency than shrubs that absorb N from deeper and poorer soil layers. Both grasses and shrubs achieve similar N-use efficiencies because of contrasting patterns in N productivity and N residence time that offset each other (Fig. 3). Whereas grasses annually absorbed 30% of their N content, shrubs absorbed only between 7 and 17% of their N content. Grasses have a high N productivity and low N residence time indicating that this group has an open N cycle whereas shrubs have the opposite pattern. Grasses drop litter into the top soil layer, near to most of their roots, and absorb each year a large fraction of their N content. In contrast, shrubs have a much more conservative N economy absorbing, each year, from the soil only a small fraction of their N content, and dropping litter far from

Table 1
N content, aboveground net primary production and N concentration in green leaves for the 6-dominant species of the Patagonian steppe. Different letters indicate significant differences among species ($p < 0.05$).

Species	N content in biomass (gN m^{-2})		Aboveground primary production (g m^{-2} yr^{-1})		Green leaves N (%)	
	Mean	SE	Mean	SE	Mean	SE
Grasses						
Stipa speciosa	0.38 a	0.07	20.5 a	3.88	0.85 a	0.07
Stipa humilis	0.12 b	0.04	7.9 bc	2.85	0.73 b	0.05
Poa ligularis	0.12 b	0.02	7.5 bc	1.31	0.78 ab	0.05
Shrubs						
Mulinum spinosum	0.36 a	0.00	10.1 b	0.90	0.90 ad	0.06
Adesmia volckmanii	0.41 a	0.01	6.0 c	0.71	1.92 c	0.15
Senecio filaginoides	0.82 c	0.03	9.2 b	0.93	0.98 d	0.12

most of their roots. This study shows the link between N-absorption patterns and the N economy of individual plant species and functional groups and suggests the co-evolution of rooting patterns and physiological characteristic such as resorption rates.

Previous work for this same ecosystem using plant-functional group removals and detailed monitoring of soil-water-potential has shown that shrubs and grasses also have contrasting water-absorption patterns (Sala et al., 1989). Grasses absorb water from the uppermost layer and shrubs from lower layers. Removal of shrubs had no effect on the water status of grasses and removal of grasses resulted in a small and infrequent enhancement of the leaf water potential of shrubs. Even though, grasses and shrubs absorb water from different parts of the soil profile, grass removal indirectly affected soil water availability by increasing soil water in upper layers that eventually led to recharge of deep-layers, which were exclusively explored by shrubs. Deep percolation events occur in this ecosystem but are rare (Paruelo and Sala, 1995).

The patterns for N and water absorption described above suggest that N- and water-capturing strategies are coupled in the dominant grass and shrub species of the Patagonian steppe. Strategies to acquire N were positively related to strategies to acquire water, and morphological and physiological characteristics (from rooting depth to phenology) that determined water capture at the same time determined patterns of N utilization.

Plants absorbing water from deep layers have some advantages. Water in deep-soil layers is not lost via bare soil evaporation and consequently plants do not compete with bare-soil evaporation. Soil water in the upper layers is a transient resource that rapidly disappears via bare soil evaporation if it is not used by plants. The fraction of water absorbed by plants relative to total available water is larger in lower than upper soil layers (Sala et al., 1992). In addition, in many ecosystems with coarse textured soils and winter-concentrated precipitation, such as the Patagonian steppe, deep layers are refilled every year and show lower inter-annual variability than upper layer soil water availability (Sala et al., 1997). The disadvantage of plants absorbing only from deep layers is the low N concentration of these layers. Use of deep water in the Patagonian steppe has only been feasible when coupled with a conservative N economy. Grasses and shrubs, have opposite strategies for capturing water and N that yield similar NUE. The complementarity of resource use between shrubs and grasses and the similarity of the end results through opposite strategies explain the long-term stability of an ecosystem co-dominated by shrubs and grasses.

We suggest that the new concepts derived from our experiments in the Patagonian steppe could be extrapolated to other regions of the world where shrubs and grasses share the differential rooting pattern observed in the Patagonian steppe. Indeed, a review of 250 published articles (Jackson et al., 1996) showed that

in general shrubs have much deeper roots than grasses. Shrubs have 21% of their roots in the upper 10 cm of the soil profile whereas grasses have 44% in the same soil layer. Differential rooting patterns for shrubs and grasses similar to those found in the Patagonian steppe have been reported from the North American Great Plains (Lee and Lauenroth, 1994) to the steppes of South America to the African savannas (Knoop and Walker, 1985). However, some studies using ^{15}N as a tracer highlighted that some shrub species with shallow roots are not able to absorb water and N from this layer (BassiriRad et al., 1999) cautioning about extrapolating function from structure. We hypothesize that intermediate rooting patterns, such as those of shrubs with both shallow and deep roots, may be associated with N-capture strategies that fall in between the N-absorption and N-residence time patterns reported here for the Patagonian Steppe.

Our results have major implications to our understanding of the response of arid and semiarid ecosystems to climate change, nitrogen deposition, and biodiversity change, which are the major global-change drivers. The tight link between N and water capturing strategies suggest that changes in the availability of one resource may have rapid and direct effects on the other. Anthropogenic changes in the composition of plant types will have effects on N and water economy. If climate change results in drier conditions in arid and semiarid regions (Seager et al., 2007), deep soil water resources will be reduced. Under these conditions, results from this study predict decreased shrub density and a less conservative nitrogen economy for the affected ecosystems. Similar changes would occur in ecosystems where woody plants are harvested for fuel (Hiemstra-van der Horst and Hovorka, 2009). Removal of the woody plants would convert the vegetation to one dominated by grasses with short N residence times in biomass and therefore high N turnover. Therefore, a reduction in the shrub component would have atmospheric consequences because N atoms are most vulnerable to being lost from the ecosystem via gaseous loss or leaching when in inorganic form. The most common nitrogen gas emitted from ecosystems, N_2O, has a warming potential 300 times that of CO_2 thus providing strong feedback to the atmosphere (Melillo et al., 2009). In addition to impacts on the atmosphere, reduction of the shrub component and shift to a more open N economy would increase leaching N losses, which have been widely shown to have negative effects on riparian and riverine ecosystems (Howarth et al., 1996).

This study of N-capturing strategies in conjunction with previous studies of water-use strategies in the Patagonian Steppe (Paruelo and Sala, 1995; Sala et al., 1989) suggest a tight link among three key elements of the functioning of ecosystems; species composition and N and water cycles. Consequently, changes in any of these three elements will have consequences on the other two. Whereas, we have some understanding of the direct effects of each one of these three elements on ecosystem functioning, we have a much poorer understanding of their interactions and feedbacks that govern this complex system.

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