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Resource partitioning between shrubs and grasses in the Patagonian steppe

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Summary. Experiments were conducted in the Patagonian steppe in southern South America to test the following hypotheses: (a) grasses take up most of the water from the upper layers of the soil and utilize frequent and short-duration pulses of water availability; (b) shrubs, on the contrary, take up most of the water from the lower layers of the soil and utilize infrequent and long-duration pulses of water availability. Grasses and shrubs were removed selectively and the performance of plants and the availability of soil resources were monitored. Results supported the overall hypothesis that grasses and shrubs in the Patagonian steppe use mainly different resources. Removal of shrubs did not alter grass production but removal of grasses resulted in a small increase in shrub production which was mediated by an increase in deep soil water and in shrub leaf water potential. The efficiency of utilization of resources freed by grass removal was approximately 25%. Shrubs used water exclusively from lower soil layers. Grasses took up most of the water from upper layers but they were also capable of absorbing water from deep layers. This pattern of water partitioning along with the lack of response in leaf nitrogen to the removal treatments suggested that shrubs may be at a disadvantage to grasses with respect to nutrient capture and led to questions about the role of nutrient recirculation, leaching, and nitrogen fixation in the steppe.

Key words: Resource partitioning – Steppe – Water use – Shrubs – Patagonia

Vegetation of arid and semiarid regions is dominated by one of two plant life forms: grasses or shrubs. They form the grasslands and shrublands of the world. Large areas of grasslands in North America and Africa have slowly changed into shrublands and savannas (Buffington and Herbel 1965; Walker et al. 1981; van Vegten 1983; Neilson 1986). A large human effort is continually devoted to reversing this process under the assumption that resources freed by removal of woody plants will be utilized by grasses. The ultimate goal of this activity is to increase the amount of forage available for domestic animals.

The objective of this work was to develop and test a conceptual model of resource partitioning between grasses and shrubs for the Patagonian steppe in southern South America. The model should be able to answer questions such as: For which resources and to what degree do shrubs and grasses compete? The model was developed deliberately at the level of organization of life forms because they represent functional groups for the steppe. Species in each group share morphological and physiological characteristics that result in a common ecological role. Patterns of resource partitioning found at this level will be more easily generalized for other arid and semiarid regions than patterns found at a finer scale, such as the species scale. Walter (1971) first suggested partitioning of resources between life forms in his two-layer hypothesis for savannas. This hypothesis has been explored for tropical savannas in general (Walker and Noy-Meir 1982) and for a South African savanna in particular (Knoop and Walker 1985).

Our conceptual model of resource partitioning between grasses and shrubs primarily focused on water. It included two axes: (1) the depth from which each life form was able to absorb water and (2) the residence time, the time water remains within the range of water potential available to plants. The hypotheses that form the basis of the model were: (1) that grasses take up most of the water from the upper layers of the soil and utilize frequent and short-duration pulses of water availability, (2) that shrubs, on the contrary, take up most of the water from the lower layers of the soil and utilize infrequent and long-duration pulses of water availability.

A deduction from our hypotheses is that removal of shrubs will not increase the water status or productivity of grasses, and will result in an increase in the availability of deep soil water. A complementary deduction is that removal of grasses will not increase the water status or the productivity of shrubs, and will result in an increase in the availability of water in the upper layers of the soil. To test these deductions, an experiment was carried out in which grasses or shrubs were selectively removed and the performance of plants and the availability of soil water resources were monitored.

Study site

Experiments were conducted in the Patagonian region of Argentina, in the vicinity of Rio Mayo (45°41′S, 70°16′W). The experimental area was located in the Occidental floristic district (Soriano 1983) in a *Stipa speciosa* Trin. et Rupr., *Stipa humilis* Cav., *Adesmia campestris* (Rendle) Skottsb., *Berberis heterophylla* Juss. and *Poa lanuginosa* Poir. community (Golluscio et al. 1982). The vegetation is

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a mix of tussock grasses and shrubs that have a basal cover of 32% and 15% respectively, the rest being bare ground. The dominant grasses are *Poa ligularis* Nees ap. Steud., *Stipa speciosa* and *Stipa humilis*. The dominant shrubs are *Mulinum spinosum* (Cav.) Pers., *Adesmia campestris* and *Senecio filaginoides* DC.

Average annual precipitation is 170 mm and most of it occurs during the winter (March to August). Mean monthly temperatures range from 2° C in July to almost 14° C in January. Soils are derived from glacial and volcanic materials. Their texture is coarse and gravel and stones are commonly found throughout the soil profile. A caliche layer is found at approximately 60 cm depth (Paruelo et al. 1988).

Methods

The experimental design consisted of a control and two treatments in which shrubs or grasses were experimentally removed. There were four replicates of each treatment and control. Treatments were allocated randomly to twelve 20 m × 20 m plots separated by 10-m wide alleys. Grasses and shrubs were manually removed from the plots every year after May 1983. Large animals were excluded from the experiment.

The treatments were evaluated for three growing seasons from late 1983 to mid 1986. The response variables were aboveground primary production, leaf water potential, leaf nitrogen content, and soil water potential. Plant variables were evaluated in individuals of one grass species *Poa ligularis*, and one shrub species *Mulinum spinosum*, except grass primary production which was assessed for the entire life form. These two species are representative of the life form grasses and shrubs (Soriano and Sala 1983). Changes in the availability of water were evaluated by measuring soil water potential at different soil depths. Analysis of variance was performed on response variables and differences were considered significant when $p \leq 0.05$.

Results of removal experiments hinged on both life forms using similar amounts of water. The following data suggest that this is the case of the Patagonian steppe. Peak biomass, as recorded in this experiment, was 39 g m^{-2} (SE = 3.4, $n = 4$) and 20 g m^{-2} (SE = 2.0, $n = 4$) for grasses and shrubs respectively. Maximum leaf area index (LAI), which was estimated using an empirical relationship between leaf area and green biomass ($r^2 = 0.99$, $p \leq 0.01$, $n = 10$ for grasses; $r^2 = 0.88$, $p \leq 0.01$, $n = 10$ for shrubs) was 0.11 for grasses and 0.04 for shrubs. Transpiration, measured in g HO per g (dry matter) of green biomass per day, ranged between 11 (SE = 0.8, $n = 3$) and 3 g g^{-1} d^{-1} (SE = 0.1, $n = 3$) for the grass *Poa ligularis* and between 8 (SE = 1, $n = 3$) and 2 g g^{-1} d^{-1} (SE = 0.1, $n = 3$) for the shrub *Mulinum spinosum* (Paruelo, personal communication). These data suggest that the contribution of shrub transpiration to total transpiration water loss was 26%–29%.

Primary production of grasses was evaluated using the harvest technique. Aboveground biomass was harvested in 20 × 500 cm quadrats. One randomly located quadrat was harvested per replicate of the no-shrub treatment and the control. Harvested material was separated into green and standing dead and oven-dried at 73° C for 48 h. For the 1984–85 growing season, biomass was harvested in May, September, November and January; for the 1985–86, growing season biomass was harvested in May, December and January. Production was calculated from these time series of biomass using the method of summation of positive increments in green biomass (Singh et al. 1975). Standard errors of production were calculated using the technique described by Sala et al. (1988).

Shrubs have a turnover rate and mode of growth different from grasses, and the growth of the year is easily identifiable. Therefore, primary production of shrubs was estimated using a different technique. At the end of the growing season, the growth of the year was harvested in 10 × 25 cm quadrats located on the top of modal-size shrubs (50–60 cm tall). In each of the four treatments and four control plots, five quadrats were harvested and the oven-dried mass was measured. For statistical purposes the number of independent replications in all cases was 4.

Production per unit ground area (g m^{-2} yr^{-1}) was calculated as the product of production per plant (g $plant^{-1}$ yr^{-1}) and shrub density (number of plants per m^2). Production per plant (PP) was calculated from production per quadrat (PQ), the variable measured in the field. The relationship between PP and PQ was assessed by harvesting first one quadrat and then the entire production in 15 individuals of *Mulinum spinosum* (Fernández A. 1986). Regression analysis was performed between measured PP and PP estimated as production per cm^2 of quadrat × shrub surface. Shrub surface was calculated assuming hemispherical shape and measuring the radius. The regression equation was:

$$PP = 0.28 * (PQ/250 * 2\pi R^2) \qquad r^2 = 0.95 \; p \leq 0.01$$

where 0.28 is the slope of the regression, 250 is the size of quadrats (cm^2) and R is the average radius of *Mulinum spinosum*. A slope different from 1 means that shrubs are not perfect hemispheres and that production is not uniform throughout the shrub surface.

Production of each treatment was calculated from measured PQ for each treatment, average radius of *Mulinum spinosum*, and average density. Average radius and density were estimated along four transects that included 394 individuals (Fernández A. 1986). The estimate of production per unit ground area was based on the assumption that production of *Mulinum spinosum* was similar to production of the other shrub species.

Leaf water potential was evaluated using the pressure chamber technique (Scholander et al. 1965). Standard precautions (Turner 1981, 1988) were taken against errors associated to this technique. In order to minimize water loss between sampling and measurement we enclosed grass leaves in a plastic tube, 3 mm in diameter, prior to severing them from the plant. Shrub twigs were transported from the plot to the pressure chamber a few meters away in a plastic container. The sample was not enclosed while in the pressure chamber because condensation was unlikely to occur under dry Patagonian conditions. The portion of leaves and twigs external to the seal of the chamber was always very small and it was never recut. The endpoint, when the sap just reached the cut surface of the xylem, was accurately estimated with the help of a dissecting microscope. One new branch of the shrub *Mulinum spinosum* and one expanding leaf of *Poa ligularis* per replication were used on each occasion. The senescent tip of the leaves of *Poa ligularis* progresses as they mature and by the time they are fully expanded a large portion of their length is already senescent. Therefore we selected expanding leaves which had most of their blades green. Leaf water potential was measured at the time of the day of maximum water vapor demand (14.00 h) on 14 different occasions during three growing seasons.

Leaf nitrogen content was estimated in leaves of shrubs and grasses in both the treated and the control plots during December 1984. We harvested 2 subsamples per plot, each from a different plant. Subsamples were composed of 13 new shrub branches or 30 expanding grass leaves with no more than 1 cm of senescent tip. Analysis was accomplished using a micro-Kjeldahl procedure (Nelson and Sommers 1980).

Soil water potential was measured with Wescor PCT 55 thermocouple hygrometers using the dew point technique and a Wescor HR 33 mirovoltmeter (Spanner 1951). We placed hygrometers horizontally in order to minimize temperature gradients (Wiebe et al. 1977). Hygrometers were located at depths of 5, 15, 30, and 60 cm. One set of hygrometers was located in each plot and measured at mid-morning on the same days as measurements of leaf water potential.

Results

Removal of shrubs did not result in a significant increase in the production of grasses (Fig. 1). On the contrary, shrub production was significantly increased as a result of the removal of grasses. The increase in the production of shrubs was much smaller than the decrease in total production as a result of removing grasses. Total production was higher in the intact system than in any of the removal treatments. Water resources freed by grass removal were inefficiently used by shrubs, and resources freed by shrub removal were apparently not used by grasses. In the intact system, shrubs accounted for 38%–43% of total production suggesting that the amount of resources freed in the different treatments should have been similar.

Midday leaf water potential of the grass species was not significantly different between the control and the shrub removal treatment at any time (Fig. 2a). The lack of response of grass leaf water potential to the removal of shrubs agreed with the lack of response observed in production. Removal of grasses resulted in a significant increase in the shrub leaf water potential twice during the 1983–84 growing season; once during the 1984–85 growing season and never during the 1985–86 growing season (Fig. 2b).

Grasses, and more clearly shrubs, showed a seasonal pattern of leaf water potential. The water status was highest during the winter months when most precipitation occurs and when the atmospheric water demand is lowest. Water status decreased throughout the spring to a minimum in mid-summer or early autumn. As a consequence of this pattern differences due to the experimental removals occurred only during the summer months.

The nitrogen content in the leaves of shrubs and grasses was not significantly different between the removal treatments and the controls (Table 1). On the contrary, there were large significant differences between life forms. Shrubs showed a significantly higher nitrogen content than grasses. This difference between grasses and shrubs has been observed in other systems (Hobbs et al. 1981).

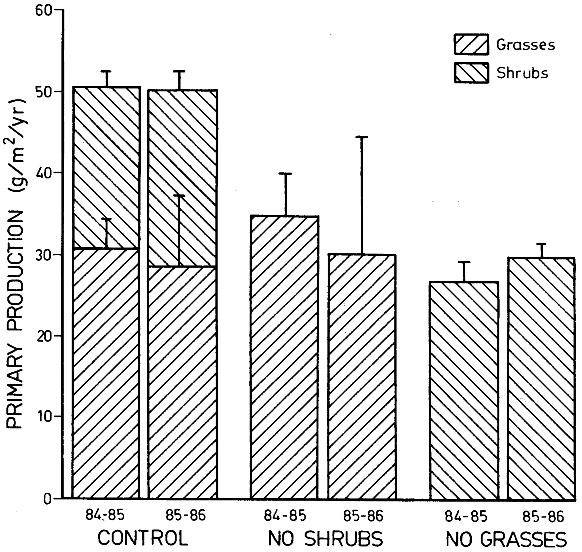

Fig. 1. Aboveground net primary production (+standard error) of grasses and shrubs for the control, in which the vegetation structure has not been altered, and treatments, in which grasses or shrubs have been removed. Data for the growing seasons of 1984–85 and 1985–86

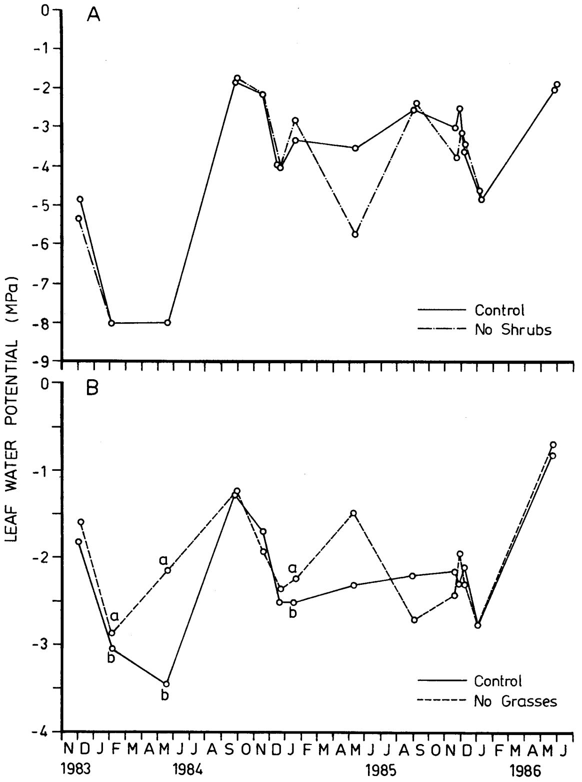

Fig. 2A, B. Leaf water potential at 1400 h of **A** the grass *Poa ligularis* and **B** the shrub *Mulinum spinosum* for the control and the treatments in which all the individuals of the other life form (shrubs or grasses) have been removed. Different *letters* indicate significant differences ($P \leq 0.05$) between treatment and the control. Absence of letter for a date indicates that differences were non-significant

Soil water potential clearly showed the seasonal pattern suggested by leaf water potential data. The entire soil profile became saturated during the winter and spring months when most of the rainfall occurred (Fig. 3). During the summer, the soil dried and attained very low water potential values by mid-summer or early autumn. The seasonal pattern was attenuated from 1983 to 1986 as a result of an increase in precipitation. From May 1983 to April 1984 the area received only 41 mm of precipitation. During this same period for 1984–85, precipitation was 185 mm, and 230 mm for 1985–86. No differences as a result of the experimental removals were observed during the winter months or at the end of the growing season. Differences among treatments were observed during the drying of the soil.

Removal of grasses resulted in significant increases in soil water potential at 15, 30, and 60 cm of depth (Fig. 3b–

Table 1. Nitrogen content (mg/g) of leaves ($n=4$) of the grass *Poa ligularis* and the shrub *Mulinum spinosum* in the control and the removal treatments. Different letters indicate significant differences ($P \leq 0.05$)

	Poa ligularis	*Mulinum spinosum*
Control	6.2^a	9.9^b
Removal treatment	6.9^a	10.3^b

d). The upper layers of the soil dried rapidly and quickly shifted from saturation to a very dry condition. The drying of the soil at 60 cm in the no-shrubs treatment suggests that grasses were able to absorb water from this depth. Removal of shrubs did not result in any significant increase in soil water potential suggesting that shrubs may absorb water from layers deeper than 60 cm, which is the depth at which the caliche layer is located.

During recharge of the soil in the autumn the control tended to have higher soil water potentials at 15 cm than any of the removal treatments (Fig. 3b). This suggests that vegetation might play an important role in capturing moisture in the form of snow during this part of the year, which otherwise would be blown away. These data did not show any significant differences on this trapping effect between tussock grasses and shrubs.

Discussion

This work supports the overall hypothesis that grasses and shrubs in the Patagonian steppe use mainly different resources. Resources upon which shrubs based their growth could not be utilized by grasses. Only a portion of the resources used by grasses were utilized by shrubs. The efficiency with which any life form used resources freed by the removal of the other was calculated as the ratio of the increase in production of the life form which remained undisturbed over the production of the removed life form in the control. Resources freed by the removal of grasses were utilized by shrubs with an efficiency of only 22% in 1984–85 and 28% in 1985–86. The small increases in shrub production as a consequence of grass removal were mediated by an increase in deep soil water and in shrub leaf water potential.

Our results support the hypothesis about water use by shrubs. In the Patagonian steppe, shrubs apparently used water exclusively from the lower layers of the soil. On the contrary, the hypothesis about grasses was not fully supported by the results. Grasses indeed take up most of their water from the upper layers of the soil, but their removal also increased the water potential of lower layers and in treatments with no shrubs the drying of these layers also occurred. This evidence suggested that grasses are able to use this water resource. Additionally, they may influence the input to these layers by their water use patterns (Knoop and Walker 1985). The depth of penetration of a rainfall event depends among other factors upon the water content of the upper layers of the soil (Hanks and Ashcroft 1980). Our results suggest that grasses absorb water from the upper layers and maintain them dryer. Rainfall events, which in the treatments with grasses did not reach deeper soil layers, did so in the absence of grasses.

The pattern of water use by shrubs and grasses matches

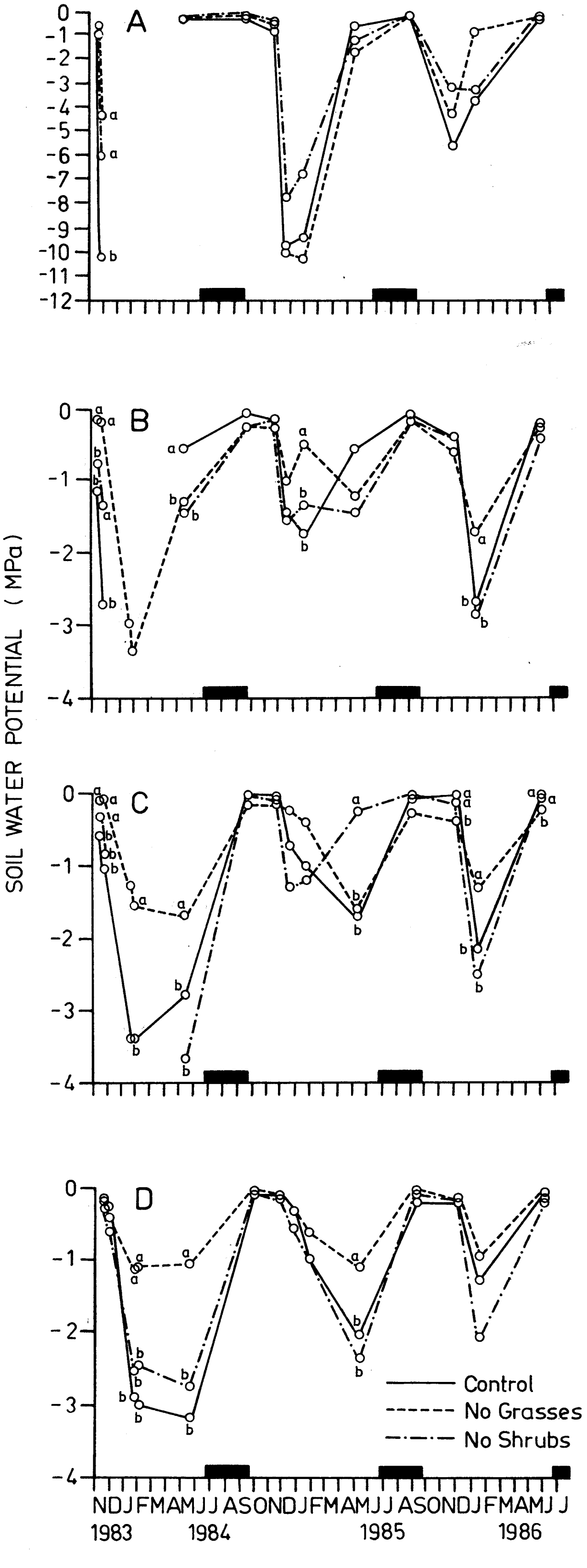

Fig. 3A–D. Soil water potential at **A** 5, **B** 15, **C** 30, and **D** 60 cm, for the control in which the vegetation structure has not been altered, for the grass removal treatment and the shrub removal treatment. Different *letters* indicate significant differences ($P \leq 0.05$) among treatments. Absence of letter for a date indicates that differences were non-significant. *Shaded bar* indicates winter months for southern hemisphere the pattern of root distribution in the soil profile. Grasses posess most of the roots in the upper layer of the soil; 54% of their root biomass is located in the 0–10 cm layer (Soriano et al. 1987). In contrast, roots of the dominant shrub *Mulinum spinosum* reach a depth of 100 cm and maximum root density occurs at 55 cm which is approximately the depth where the caliche layer starts (Fernández A. and Paruelo 1988).

These results for the Patagonian steppe are similar to those obtained for African savannas by Knoop and Walker (1985). Contrary to Walter's (1971) and Walker and Noy-Meir's (1982) models, grasses have access to water in both the upper and lower layers of the soil, not just upper layers of the soil. Shrubs only have access to the lower layers rather than access to both upper and lower layers.

Differences among species in rooting depth and the associated water uptake strategies have been described previously for other plant communities (Wieland and Bazzaz 1975; Poole and Miller 1975; Cody 1986; Davis and Mooney 1986). This, along with data presented here, led to the idea that soil water is not a single resource. Water in the upper layers has different seasonality and shorter residence time than deep water, and plant traits which confer an advantage in shallow-water use are not usually optimal for use of deep water.

The pattern of water partitioning between grasses and shrubs described here for the steppe has implications for the nutrient economy of both life forms. A unique characteristic of carbon and mineral nutrient cycles in arid and semiarid systems is the concentration of material and activity at or near the soil surface (Cole et al. 1977; Woodmansee et al. 1981). Since nutrients and water are mostly absorbed together, it implies that shrubs in the Patagonian steppe may be at a disadvantage to grasses with respect to nutrient capture. Grasses obtain most of their water from the zone supposedly richest in nutrients. This contrasts with the leaf nitrogen content values which were higher in shrubs than grasses. Does this suggest that shrubs have a tighter nutrient recirculation than grasses? Is leaching a major process in this system? Is nitrogen fixation an important component of the nitrogen budget of shrubs?

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