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Ecological strategies in a Patagonian arid steppe*

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Abstract

The vegetation in the Coironal arid steppe consists of grasses and shrubs. The objective of this paper was to test Walter's hypothesis that woody vegetation and grasses compete for water in the upper layers of the soil, but woody vegetation has exclusive access to a source of water at deeper levels.

Analysis of root profiles and patterns of leaf and soil water potential led us to accept the hypothesis for this arid steppe. Additional information on phenology and on the ability of the major grass species to respond to watering permitted to identify two ecological strategies corresponding to grasses and shrubs. Grasses behave as opportunists having always leaves ready to grow as soon as water becomes available. They have a shallow root system and are able to respond very rapidly to increases in soil water availability. In contrast, woody species have a clear-cut periodic pattern of growth and dormancy. They possess thick horizontal roots running below 35–40 cm and utilized water stored in lower layers of the soil.

A diagrammatic model summarizes the role of periodic and opportunistic species upon water circulation in the ecosystem. The effect of changes in the proportion of the two groups upon water dynamics is also discussed.

Introduction

The vegetation of the Coironal arid steppe in SW Chubut, Argentina, consists of grasses, shrubs and herbs. Dominant grasses are *Stipa speciosa, Stipa humilis* and *Poa ligularis*. Shrubs as *Mulinum spinosum* and *Adesmia campestris* as well as some herbs and cushion plants complete the sparse vegetation of this region (Soriano, 1956a, b). The three mentioned grasses account for 98% of the aboveground biomass of grasses and herbs (Soriano *et al.*, 1976). Total cover seldom exceeds 40% of the soil surface.

The mean annual precipitation is 168 mm, recorded at the closest meteorological station in Gobernador Costa over 10 years. Most of the precipitation occurs during the period March to August which corresponds to the coldest time for the southern hemisphere (Fig. 1). Mean monthly temperatures range from 2 °C in July to almost 14 °C in January. The climatic diagram (Walter, 1968) for this site shows the occurrence of a humid period from April to August and a very dry warm season. Soils are mainly derived from glacial and volcanic materials. The texture is mainly coarse, and different sizes of gravel and stones (Patagonian pebbles) are commonly found throughout the solum (Soriano, 1983).

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* Nomenclature follows Nicora (1978) and Cabrera (1971).

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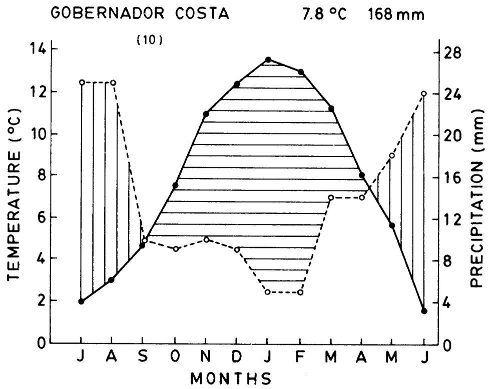

Fig. 1. Climatic diagram for Gobernador Costa, Chubut, Argentina. Mean annual temperature (° C) and mean annual precipitation (mm). Number in parentheses below the station location indicates the number of observation years. Mean monthly temperature (—) and mean monthly precipitation (---) are drawn at a ratio of 1 ° C:2 mm. Vertically shaded areas represent a humid period defined by precipitation > temperature at the 2:1 scale. Horizontally shaded area represents a drought period defined by temperature > precipitation at the 2:1 scale.

Sheep grazing has been practiced since the beginning of this century all over the region. It is difficult to assess its impact on the vegetation during the whole period since no examples are known of areas which were not grazed by sheep (Soriano, 1952). Approximately 6 500 000 sheep graze the 225 000 km^2 of Chubut grazing lands, according to unpublished data from 1978, which illustrates the importance of the steppe vegetation as a source of wool and meat.

Walter (1964, 1971) proposed the two-layer hypothesis for savannas. He suggested that woody vegetation and grasses compete for water in the surface layers of the soil, but woody vegetation has exclusive access to a source of water relatively deep underground. The objective of this work was to test Walter's hypothesis for the arid steppe of Patagonia and analyze associations between phenological patterns and the two groups included in the hypothesis. This approach allowed us to distinguish groups of species with similar ecological strategies (Grime, 1979, 1982).

Methods

In an attempt to characterize the phenology of the different components of the steppe, phenophases of all species were periodically recorded following the technique proposed by French & Sauer (1974). Using information on all species, two patterns were identified and species grouped according to their phenology.

For characterizing root distribution of the two previously identified groups two methods were followed. Belowground biomass of herbaceous plants was estimated by taking cylindrical soil cores of 5.5 cm diameter in December and March. Twenty samples were taken each time from 0–15 cm and 15–30 cm deep. Roots and subterranean organs were separated by washing, dried at 70 °C and weighed. This method was not suitable for studying the root systems of dominant shrubs. Instead the method of digging trenches and careful drawing the root system (Böhm, 1979) was utilized for *Adesmia campestris* and *Mulinum spinosum.*

Plant water status of the major grasses and shrubs was assessed by measuring the daily course of leaf water potential. Shrub species selected were *Adesmia campestris* and *Mulinum spinosum* and the grass species *Stipa speciosa* and *Poa ligularis.* Leaf water potential was measured using the pressure chamber technique (Scholander *et al.,* 1965). The daily course was estimated by measuring leaf water potential before dawn at 04.00, and at 08.30, 14.20 and 17.00. Ten replications were used each time which was adequate to maintain the standard error below 10% of the mean. This number of replications was obtained by measuring daily courses on two dates: *Mulinum spinosum* and *Poa ligularis* on 13 January 1983 and the other couple on 19 January 1983.

In an attempt to assess the velocity in the response to watering, ten plants of *Poa ligularis* were thoroughly watered on the afternoon of January 13. Ten other plants were selected as controls. Leaf water potential was measured before dawn of the next day and at midday on January 14 and 15. One leaf of each plant was used in each case. Leaf elongation was the other response variable selected. A thin rod was firmly thrust into the soil next to the tiller selected for measurement. A plastic ring joined the tiller to the rod; another plastic ring was inserted to join an incompletely expanded leaf to the rod. The length of the leaf was marked on the rod using a narrow strip of tape. Length increments were measured on January 14, 15 and 18.

The status of soil water was assessed by measuring soil water potential with thermocouple hygrometers (Spanner, 1951) placed at depths of 10 and 40 cm. Three replications were installed at each level.

Results and discussion

Phenological responses allowed us to group dominant species in two different types (Fig. 2). The three dominant grasses kept at least one non-expanded leaf in each live tiller at all seasons. The reproductive cycle started in October and rapidly finished early summer. On the other hand, dominant shrubs showed a clear-cut periodic pattern of growth and dormancy. They spent winter time inactive and the reproductive cycle extended throughout the entire growing season.

Grasses which were included in the first phenological group distributed their root systems in the upper sandy soil (Table 1). Root biomass decreased rapidly with depth. Biomass in the 15–30 cm horizon was just 30% of what was observed in the upper horizon. This is a characteristic feature of semi-arid and arid systems which not only concentrate material but also activity at or very near the soil surface (Clark, 1977; Woodmansee *et al.*, 1981). Species of the second phenological group possessed thick horizontal roots running below 35–40 cm (Fig. 3). The deep horizons explored by these roots were characterized by large pebbles of 5 cm or more in diameter, often cemented with calcium carbonate (Soriano, 1983).

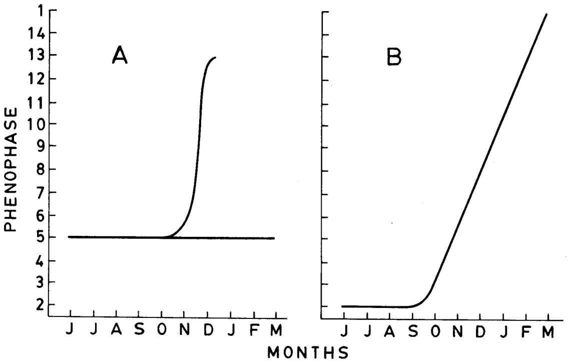

Fig. 2. Phenological response for group A, opportunistic grasses, and B, periodic shrubs. Phenophases are: 1. pre-emergence growth/winter dormancy; 2. first visible growth; 3. first leaves fully expanded; 4. middle leaves fully expanded; 5. first leaves senescent, middle leaves fully expanded; 6. late leaves fully expanded; 7. developing floral buds, middle late vegetative; 8. mature floral buds, late vegetative; 9. floral buds and open flowers; 10. buds, flowers and green fruits; 11. as 10 plus ripe fruit; 12. green fruit and ripe fruit; 13. ripe fruit and dispersing seeds; 14. flowering-induced dormancy.

Table 1. Belowground biomass (g · m^{-2}) (±1 SE; $N = 20$).

Depth (cm)	Harvest	
	December 1977	March 1978
0–15	272 ± 42	165 ± 13
15–30	79 ± 15	65 ± 6

Daily courses of leaf water potential showed big differences between grasses and shrubs (Figs. 4 and 5). *Poa ligularis* and *Stipa speciosa* presented leaf water potentials which consistently were lower than those of *Mulinum spinosum* and *Adesmia campestris.* Differences before dawn were of 1.5 MPa which increased toward midday when atmospheric water demand reached its maximum. No significant differences ($p < 0.05$) were observed within the shrub and grass categories.

Upper and lower layers of the soil showed large differences in their water status (Fig. 6). Upper layers had soil water potentials between -6 and -8 MPa which meant that neither grasses nor shrubs could presumably extract water out of these layers. On the other hand, deeper layers presented soil water potentials which indicated that the soil was very near field capacity.

The large differences in the water status of shrubs and grasses together with the large differences in water availability between upper and lower layers of the soil suggested that both growth forms might utilize water stored in different locations. Root distributions of the two growth forms brought further support to the idea that water in the upper layers was mainly utilized by grasses and water in lower layers by shrubs. All this information led us to accept the two-layer hypothesis for this arid steppe.

Poa ligularis showed a remarkably rapid response to watering. Ten hours after being thoroughly irrigated leaf water potentials were significantly ($p < 0.05$) higher than the control plants (Fig. 7). Differences were of almost 2 MPa before dawn of the first day and reached a maximum of 2.4 MPa in the afternoon of the second day after watering. A rapid response of leaf elongation was also

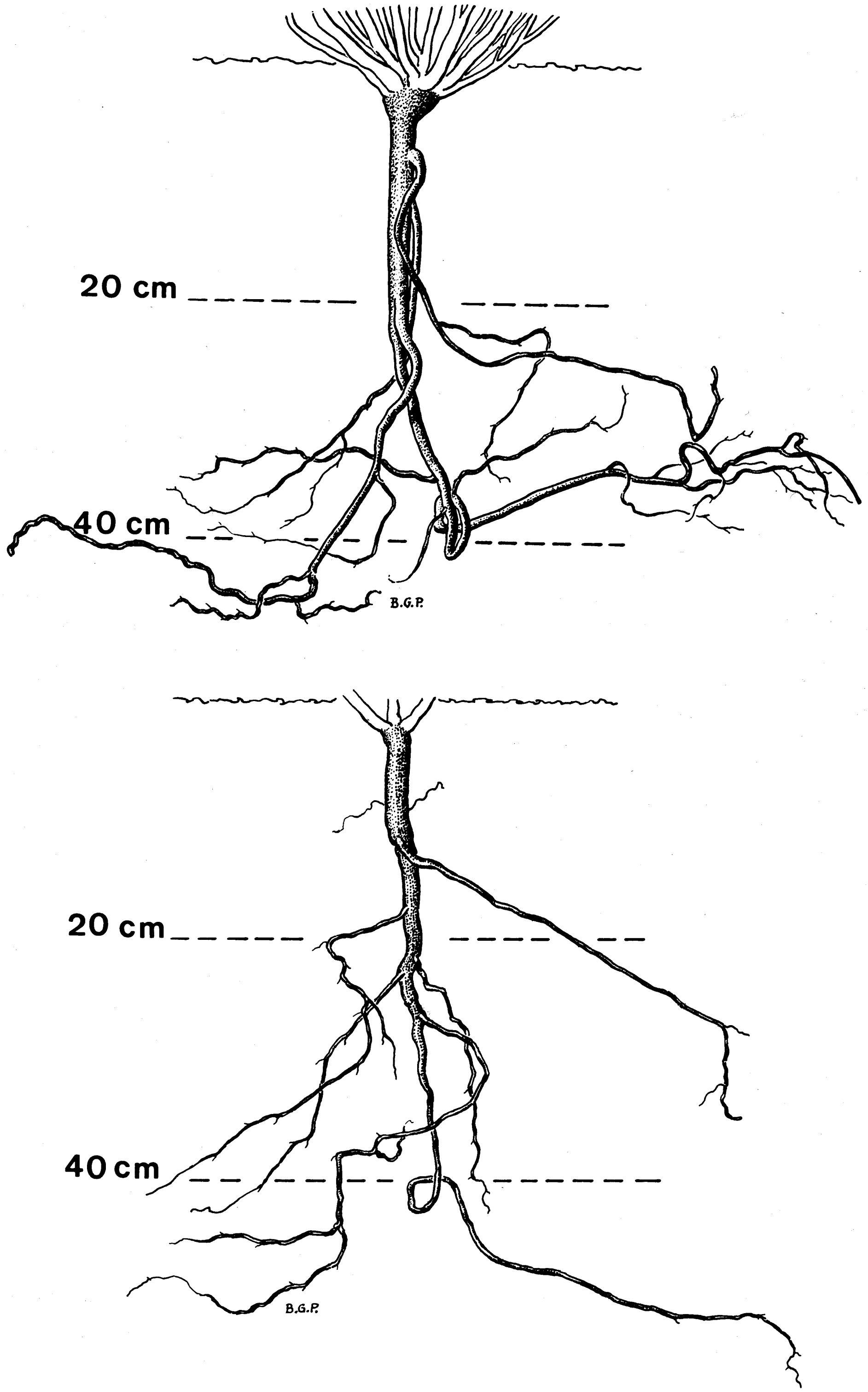

Fig. 3. General aspect of root system of A: *Adesmia campestris,* and B: *Mulinum spinosum.*

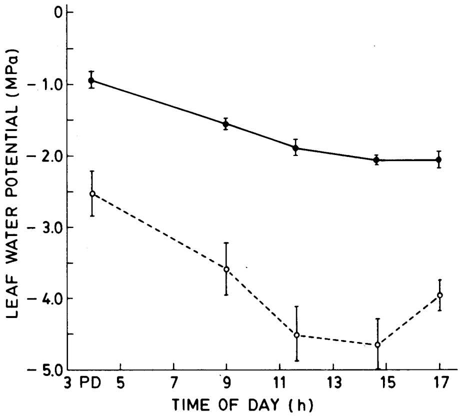

Fig. 4. Daily pattern of leaf water potential (± standard error; *N* = 10) for *Adesmia campestris* (—), and *Stipa speciosa* (---).

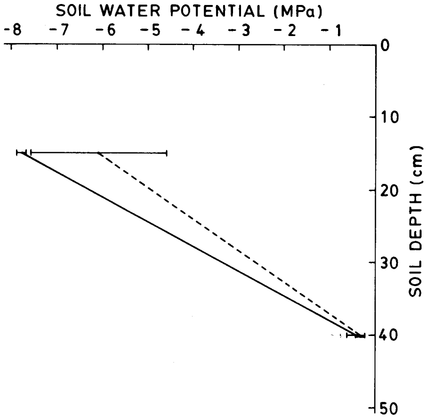

Fig. 6. Soil water potential as a function of depth (± standard error; *N* = 3) on 13 January 1983 (---), and 19 January 1983 (—).

observed. No growth was detected in the control while watered plants had an average leaf elongation of 1.57 mm during the first day after watering.

Two strategies prevail in this ecosystem. Grasses which belong to the first group behave as opportunistic species, always having leaves ready to grow as soon as water becomes available. We hypothesize that the response of species of this group to small precipitation events (a few millimeters which just wet the upper horizon) would be similar to the observed response to large events. The dominant grass species of the North American shortgrass steppe was able to rapidly respond to 5 mm events (Sala & Lauenroth, 1982). The strategy of woody species is of a clear periodic behaviour, which is associated with the utilization of a water source. This source presumably has a periodic pattern as well. A list of opportunistic and periodic species for the region is given in Table 2.

These two types of strategies may be referred to

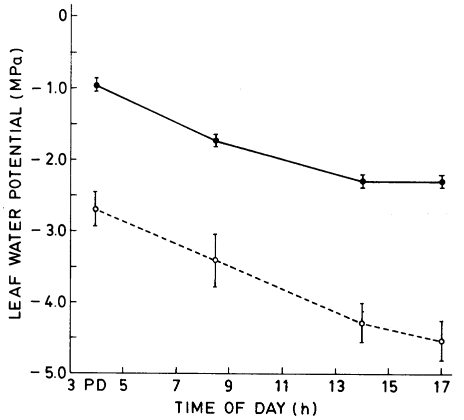

Fig. 5. Daily pattern of leaf water potential (± standard error; *N* = 10) for *Mulinum spinosum* (—), and *Poa ligularis* (---).

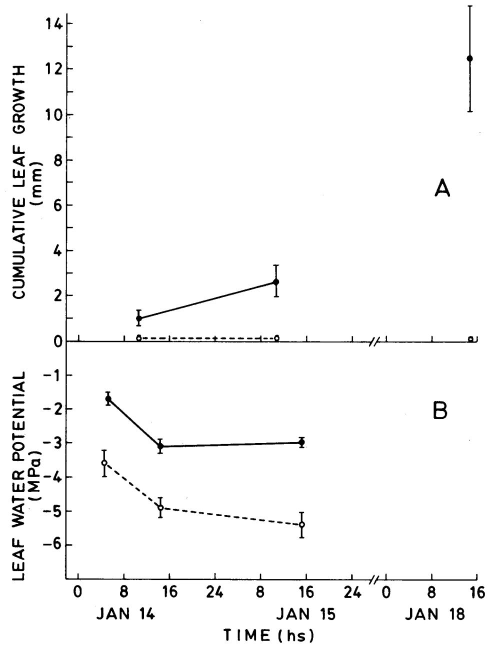

Fig. 7. (A) Cumulative leaf growth (mm), and (B) leaf water potential (MPa) for *Poa ligularis* (± standard error; *N* = 10). Irrigated plants (—) and control (---).

Table 2. List of species included in the two different strategies.

Opportunistic species	Periodic species
Stipa speciosa Trin et. Rupr.	*Mulinum spinosum* (Cav.) Pers.
Stipa humilis Vahl	*Adesmia campestris* (Rendle) Skottsb.
Poa ligularis Nees ap. Steud.	*Acantholippia seriphioides* (A. Gray) Mold.
Stipa ibari Phil.	*Lycium chilense* Miers ex Bert.
Stipa psilantha Speg.	
Carex argentina Barros	
Festuca argentina (Speg.) Parodi	
Bromus setifolius Presl.	

as arido-active and arido-passive types of plants only in a very broad sense (Evenari *et al.,* 1975). Environmental conditions in Patagonia are very different from those prevailing in the Negev. In this case opportunistic chamaephytes can be considered arido-active in the sense that they have green leaves, both incompletely and fully expanded, even during the driest periods. However, growth is at all times modulated by water availability. On the other hand, the periodic strategy exhibited by phanerophytes cannot be considered strictly equivalent to arido-passivity. In these species the main part of the dormant period corresponds with the coldest and least arid time of the year.

A diagrammatic model (Hall & Day, 1977) using symbols according to Forrester (1961) attempts to summarize the role of the two groups identified here upon water dynamics in the Coironal ecosystem (Fig. 8). The model distinguishes, as previously suggested, small and large rainfall events as different resources (Sala & Lauenroth, 1982). Small events wet only the upper layers of the soil and large events wet both upper and lower layers. The group of the opportunistic species would utilize mainly water of the upper zone. On the other hand, periodic species would use the water of the lower layers. A phenological pattern controls water absorption with this second group. We do not know how much water is extracted from deep and upper layers by opportunistic and periodic species respectively. Therefore we do not have enough information to evaluate the degree of competition for water between the two groups. Moreover, we ignore if changes in the demand of water from the upper layer will affect the supply to the lower layers and to the periodic species. Soriano *et al.* (1980) provided some indirect evidence when they analyzed the effect of excluding ungulates for 25 years. Grasses and herbaceous species increased as well as root biomass in the upper horizon while the density of shrubs decreased. We suggest that these observations may be explained by supposing that the opportunistic species interfere with the refill of the deep layers rather than use water from these layers. This interpretation is certainly compatible with the idea of water in upper and lower layers as different resources. Another explanation could be that ungulates alter the competitive ability of grasses and shrubs through their effects on the infiltration rate rather than through the exercise of their preference. Walker *et al.* (1981) chose the latter for explaining the effect of grazing upon the grass–shrub equilibrium. Soil characteristics in Patagonia as well as the scarce precipitation made the infiltration explanation very unlikely.

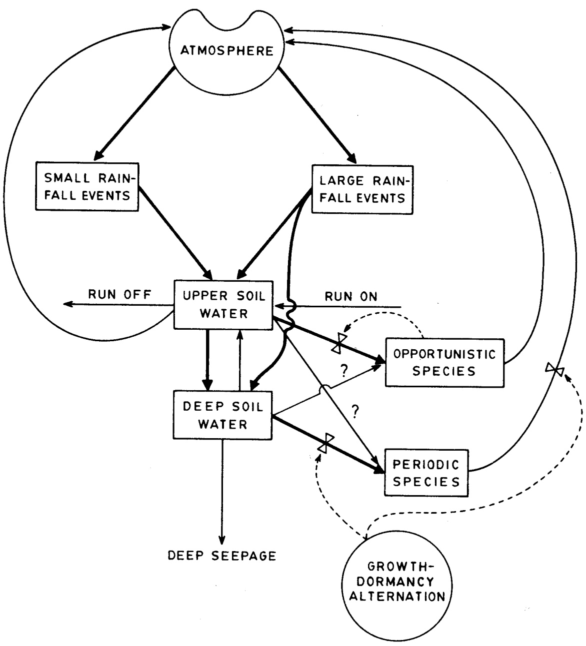

Fig. 8. A diagrammatic model of the water circulation in the Coironal ecosystem.

References

Böhm, W., 1979. Methods of Studying Root Systems. Springer-Verlag, Berlin. 188 pp.

Cabrera, A. L., 1971. Compositae. In: M. N. Correa, (ed.). Flora Patagónica, Vol. VII. Colección INTA. 451 pp.

Clark, R. E., 1977. Internal cycling of ^{15}nitrogen in shortgrass prairie. Ecology 58: 1322–1333.

Evenari, M., Schulze, E. D., Kappen, L., Buschbom, U. & Lange, O. L., 1975. Adaptive mechanisms in desert plants. In: F. J. Vernberg, (ed.). Physiological Adaptations to the Environment, pp. 111–129. Cambridge Univ. Press, Cambridge.

Forrester, J. W., 1961. Industrial Dynamics. MIT Press, Cambridge, Mass. 464 pp.

French, N. & Sauer, R. H., 1974. Phenological modeling in grasslands. In: H. Lieth, (ed.). Phenology and seasonality modeling. Ecological Studies, Vol. 8, pp. 227–236. Springer-Verlag.

Grime, J. P., 1979. Plant Strategies and Vegetation Processes. Wiley, Chichester. 222 pp.

Grime, J. P., 1982. The concept of strategies: use and abuse. J. Ecol. 70: 863–865.

Hall, C. A. S. & Day, J. W., 1977. Systems and models: terms and basic principles. In: C. A. S. Hall & J. W. Day, (eds.). Ecosystem Modeling in Theory and Practice: An Introduction with Case Histories, pp. 6–36. John Wiley, New York.

Nicora, E. G., 1978. Gramineae. In: M. N. Correa, (ed.). Flora Patagónica, Vol. III. Colección INTA. 563 pp.

Sala, O. E. & Lauenroth, W. K., 1982. Small rainfall events: an ecological role in semiarid regions. Oecologia 53: 301–304.

Scholander, P. F., Hammer, H. T., Bradstreet, E. D. & Hemmingsen, E. A., 1965. Sap pressure in vascular plants. Science 148: 339–346.

Soriano, A., 1952. El pastoreo en el territorio del Chubut. Rev. Arg. Agr. 19 (1): 1–20.

Soriano, A., 1956a. Los distritos florísticos de la Provincia Patagónica. Rev. Inv. Agr. 10 (4): 349–347.

Soriano, A., 1956b. Aspectos ecológicos y pasturiles de la vegetación patagónica relacionados con su estado y capacidad de recuperación. Rev. Inv. Agr. 10 (4): 349–372.

Soriano, A., Alippe, H., Sala, O. E., Schlichter, T., Movia, C., León, R., Trabucco, R. & Deregibus, V., 1976. Ecología del pastizal de Coirón Amargo (*Stipa* spp.) del sudoeste de Chubut. Academia Nacional de Agronomía y Veterinaria, Buenos Aires, Argentina 30 (11): 1–28.

Soriano, A., Sala, O. E. & León, R. J. C., 1980. Vegetación actual y vegetación potencial en el pastizal de Coirón Amargo (*Stipa* spp.) del SW de Chubut. Bol. Soc. Arg. Bot. 19: 309–314.

Soriano, A., 1983. Deserts and semi-deserts of Patagonia. In: N. E. West, (ed.). Temperate Deserts and Semi-deserts, pp. 423–459. Elsevier Scientific Publishing Company, Amsterdam.

Spanner, D. C., 1951. The peltier effect and its use in the measurement of suction pressure. J. Exp. Bot. 2: 145–168.

Walker, B. H., Ludwig, D., Holling, C. S. & Peterman, R. M., 1981. Stability of semi-arid savanna grazing systems. J. Ecol. 69: 473–498.

Walter, H., 1964. productivity of vegetation in arid countries. The savannah problem and bush encroachment after overgrazing. In: The Impact of Man in the Tropical Environment. IUCN Publ. NS. 4: 221–229.

Walter, H., 1968. Die Vegetation der Erde in öko-physiologischer Betrachtung. Gustav Fischer Verlag. Stuttgart. 1001 pp.

Walter, H., 1971. Ecology of tropical and subtropical vegetation. Oliver & Boyd, Edinburgh.

Woodmansee, R. G., Vallis, I. & Mott, J. J., 1981. Grassland nitrogen. In: E. W. Clark & T. Rosswall, (eds.). Terrestrial Nitrogen Cycles. Stockholm Ecol. Bull. 33: 443–462.

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