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Plant functional types and ecological strategies in Patagonian forbs

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Abstract. We identified four major functional types of forbs in the Patagonian steppe, taking into account phenological and morphological traits: (1) shallow-rooted mesophytic species (annuals), (2) shallow-rooted non-mesophytic species, (3) deep-rooted evergreen species, and (4) deep-rooted deciduous species. The major attributes differentiating these groups were the date at which seasonal growth ended, rooting depth, sprouting depth, distance between shoots of the same plant, and degree of 'mesophytism'. We used Cluster and Principal Components Analyses to identify the groups, and the attributes determining them. Late-growth-cycle types had deep roots and/or high 'xerophytism'. Late-cycle-xerophytic types had a great sprouting depth, and late-cycle-deep-rooted types had a great distance between shoots of the same plant.

On the basis of current knowledge of the structure and functioning of the Patagonian steppe, we suggested three explanations to account for these correlations. 1. Late-cycle forbs survive summer water deficit if they have xerophytic characteristics that reduce transpiration water losses, and/or they have deep roots that increase water uptake. 2. Sprouting depth results from the shift of active buds to dormant buds at the end of the cycle. Summer forbs have a great sprouting depth because only buds which are located deep in the soil survive hot and dry summers. 3. Distant shoots of summer forbs allow them simultaneously to use the high protection against desiccating winds provided by shrubs, and the ample water availability of bare soil patches. All the functional types of forbs depend on winter water recharge to begin their cycles, but each one completes its cycle by using a different portion of the water resources available in spring and summer.

Keywords: Arid ecosystem; Competition; Mesophyte; Microsite; Morphological trait; Multivariate analysis; Phenology; Steppe; Xerophyte.

Nomenclature: Correa (1971-1984).

Introduction

The contrast between small numbers of abundant species and large numbers of rare species is a common feature of most plant communities (Whittaker 1965). In the Patagonian steppe in southern South America, grasses and shrubs are the dominant groups of plants. They account for 96 % of the above-ground net primary production and 97 % of the canopy cover, but only 59 % of the total number of species (Golluscio, León & Perelman 1982; Fernández A., Sala & Golluscio 1991). The same pattern occurs across different ecosystems from deserts to forests, where grasses, shrubs or trees account for most of the biomass. Forbs, defined as non-gramineous plants without woody aerial structures (Whicker & Detling 1988), make a small contribution in terms of cover or biomass, usually < 15 % but never > 40 %, but an important contribution to the total number of species, ranging from 40 to 80 % (Lauenroth & Dodd 1978; Golluscio, León & Perelman 1982; Franklin 1988; Komárková & Mc Kendrick 1988; Mac Mahon 1988; Sala 1988).

Does this combination of a large contribution to the diversity and a small contribution to the biomass result from some special forb strategy? To investigate the main traits that contribute to determine the strategies of forbs, where strategies are sets of characteristics determining a similar ecology (Grime 1979), we posed four specific questions about forbs of one grass-shrub community in the Patagonian steppe in South America:

1. Can functional types be distinguished among forb species? Functional types are groups of species which share morphological and physiological attributes, use similar resources and play a similar role in the ecosystem (Hawkins & MacMahon 1989).
2. What are the ecological attributes that serve to distinguish the forb functional types?
3. What are the associations among attributes?
4. What is the ecological significance of such associations?

To answer these questions, we recorded phenological and morphological traits of the main forb species and classified them using multivariate techniques (cf. Lausi & Nimis 1986; Lausi, Nimis & Tretiach 1989; Montalvo et al. 1991; Leishman & Westoby 1992; Díaz, Acosta & Cabido 1992). Selected traits were rooting depth, 'mesophytism' (see below for a definition), phenology, and the horizontal structure of plants. We chose rooting depth because soil water dynamics are very different at different soil depths (Sala et al. 1989; Sala, Lauenroth & Parton 1992). Mesophytism is important because it is related to a high growth rate at the expense of a high transpiration rate, and thus high water requirements (Orians & Solbrig 1977). Phenology is a key feature in arid environments or where rainfall and temperature have a seasonal pattern (Jackson & Bliss 1984). The horizontal structure of plants determines their ability to use resources that are heterogeneously distributed in space (Pitelka & Ashmun 1986).

Materials and Methods

The study site is situated near Río Mayo, Chubut, Argentina (45 °41' S, 70 °16' W) in the *Stipa speciosa-Stipa humilis-Adesmia campestris-Berberis heterophylla -Poa lanuginosa* community (Golluscio, León & Perelman 1982). The 5-yr average above-ground net primary production (ANPP) is 60 $g m^{-2} yr^{-1}$, and the total canopy cover is 49 % (Golluscio, León & Perelman 1982; Fernández A., Sala & Golluscio 1991). Forb ANPP, estimated harvesting eight $5 m \times 0.2 m$ plots at peak biomass, was 2.8 $g m^{-2} yr^{-1}$. Grasses, shrubs and forbs account for 64 %, 33 % and 3 % of the canopy cover and 53 %, 43 % and 4 % of ANPP respectively. Shrub root systems are concentrated in lower soil layers and grass roots in the upper layers (Soriano, Golluscio & Satorre 1987; Fernández A. & Paruelo 1988). The dominant species are the shrubs *Mulinum spinosum*, *Senecio filaginoides* and *Adesmia campestris* and the grasses *Stipa speciosa*, *Stipa humilis* and *Poa ligularis*. Mean monthly temperatures range from 1 °C in July to 15 °C in January. Mean annual rainfall, recorded over 37 yr, was 136 mm (Fernández A., Sala & Golluscio 1991). The soil profile is recharged during fall and winter, when 70 % of the annual rainfall occurs (Sala et al. 1989).

We excavated (Böhm 1979), observed, sketched, and kept in a herbarium ten individuals of each of 24 main forb species. We recorded maximum rooting depth, maximum depth at which stems originated, and maximum distance between two stems from the same belowground system. We determined phenological stages (French & Sauer 1974) for two years with a frequency ranging from 0.3 (winter) to 2 (spring-summer) observations/month. We also recorded morphological features associated with xeromorphism (Evenari et al. 1975; Solbrig et al. 1977). We classified plant species as mesophytic when their leaves were simultaneously green, complete, unfolded, not sclerophyllous, and not covered by hair or wax. We classified them as xerophytic species when they possessed two or more of the following traits: sclerophyllous, microphyllous, folded, pubescent leaves, with grey or purple pigmentation, foliar waxes, and thick cuticle. Intermediate species were those with only one xerophytic trait.

To answer question 1, regarding the existence of functional types among forb species, we performed a classification by cluster analysis, with the Minimum Variance Clustering algorithm and relative Euclidean distance as a measure of similarity (Orlóci 1978), using the PCORD package (McCune 1987). We arranged data in a 24 species × 6 attributes matrix and adjusted the values of the attributes to standard deviation to make results independent of the scale of the attributes. The attributes were maximum rooting depth (ROOT), sprouting depth (SPRO), distance between shoots of the same plant (DIST), month of beginning of the growing cycle (BEGI), month of end of growing cycle (ENDO), and degree of mesophytism (MESO). Plant species were categorized as mesophytic (1), intermediate (0), or xerophytic (– 1). The level of classification that we selected was the relative Euclidean distance at which no more single species were added to any group. Modal values of all the attributes were used for each species because 50 % of them had no variance (BEGI, ENDO, and MESO), and because we aimed at understanding the variability between, and not within species.

To analyze the internal consistency of the classification we submitted untransformed data to the multi-response permutation procedure (MRPP, Biondini, Mielke & Berry 1988) using the PCORD package (McCune 1987). This non-parametric technique calculates the Euclidean distance in the hyperspace of the measured attributes between all pairs of species of each group. Then, it calculates the average Euclidean distance within each group as a measure of its internal homogeneity. It then calculates δ, as the average of the mean Euclidean distances within the different groups weighted by the size of each group. Finally, it computes the probability of obtaining a lower δ, calculating δ for all the permutations possible with the same data set, number and size of groups. The lower this probability, the more acceptable is the clustering obtained. In order to evaluate the significance of the differences between the groups, we used the same technique but taking the groups by pairs (Biondini, Mielke & Berry 1988).

We assessed the relative importance of each attribute in determining the forb functional types (question 2) by Principal Components Analysis, PCA. We performed the PCA on untransformed attribute values and used correlation coefficients as a measure of similarity between species (Orlóci 1978). Location of any species on the different PCA axes results from different linear combinations of the values of the attributes. The importance of an attribute on one axis is proportional to

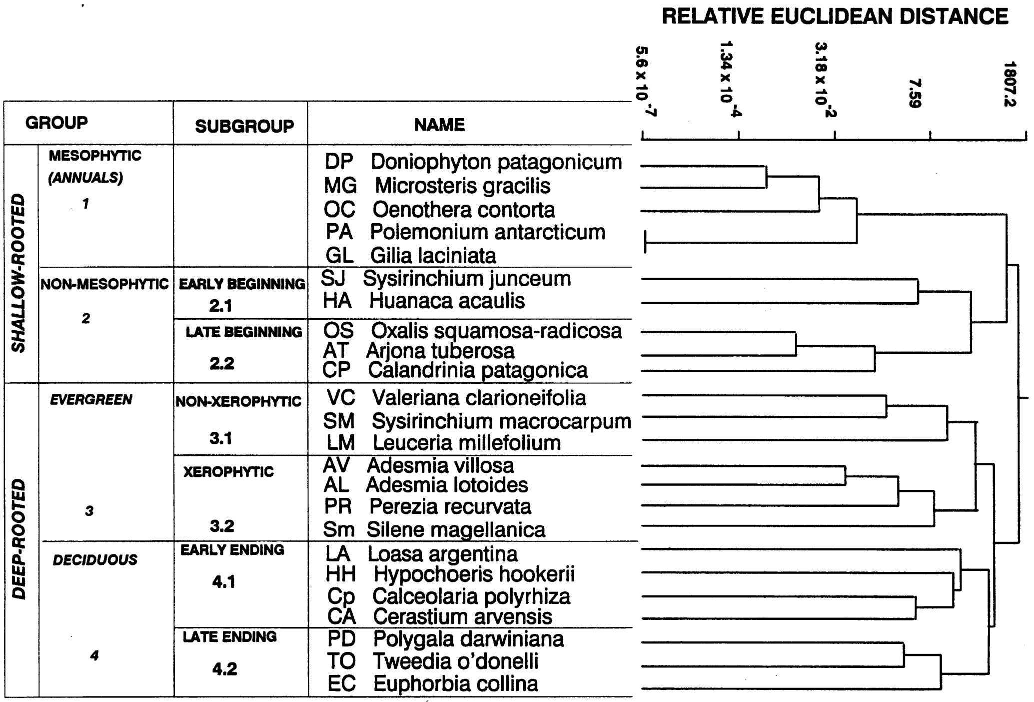


Fig. 1. Classification of 24 forb species of the Patagonian steppe by cluster analysis using the Minimum Variance algorithm with relative Euclidean distance as measure of similarity. Attributes were adjusted to standard deviation.

its coefficient in the linear combination defining the axis. To evaluate the statistical significance of such relative importance we used Kendall correlation (Sokal & Rohlf 1969) between the position on the axis and the value of the attribute for each species. We evaluated the association among attributes (question 3) also using Kendall correlations.

Results

Four major functional types of forbs were identified: (1) shallow-rooted mesophytic species (annuals), (2) shallow-rooted non-mesophytic species, (3) deep-rooted evergreen species, and (4) deep-rooted deciduous species (Fig. 1). Group 2, shallow-rooted non-mesophytic, was subdivided into those with early (2.1), and late (2.2) start of the growth cycle. Group 3, deep-rooted evergreen, was subdivided in xerophytic (3.2), and non-xerophytic (3.1). Group 4, deep-rooted deciduous, was subdivided into early end of growth cycle (4.1) and late end of growth cycle (4.2). Characteristics of the 24 species are summarized in Table 1.

The probability of finding a better classification was very low as indicated by the MRPP analysis ($\delta = 19.55$; the probability of finding a δ lower than the calculated value was 0.00019). Significant differences were found between all pairs of groups ($p < 0.05$), except between the two deep-rooted ones (Groups 3 and 4; $p = 0.42$). In addition, percent chaining of the obtained cluster was satisfactorily low (1.07 %).

The major attributes differentiating forb functional types were the date of the end of cycle (ENDO), the rooting depth (ROOT), the sprouting depth (SPRO), the degree of mesophytism (MESO), and the distance between shoots of the same plant (DIST). The first PCA axis, which accounted for 46 % of the variance, had four terms with significant positive loadings: ENDO, ROOT, SPRO and DIST; and one with significant negative loading: MESO (Fig. 2). Annuals (Group 1) were at one extreme because they have a simultaneously early end of the cycle, short rooting and sprouting depths, short distance between shoots, and high mesophytism (Fig. 2). At the other extreme were the deep-rooted evergreen-xerophytic species (Subgroup 3.2) and deep-rooted deciduous late-ending species (Subgroup 4.2), which have simultaneously high and low values, respectively for the attributes with significant positive and negative loadings on axis one.

The second axis had only two terms with significant positive loadings (MESO and DIST) and accounted for 21 % of the variance. Shallow-rooted species with a late start of the cycle (Group 2.2) were clearly different from the rest on this second axis because it was the only group

Table 1. Morphological and phenological traits of 24 Patagonian forbs. ROOT = maximum rooting depth, SPRO = maximum sprouting depth; DIST = maximum distance between shoots of the same plant; MESO = mesophytic degree; TYPE = type of xerophytic adaptations (f: folded leaves; GP: grey pigmentation; s: sclerophyllous leaves; m: microphyllous leaves; W: foliar waxes; P: pubescence; DL: dissected leaves; TC: thick cuticles; BEGI = month of pre-emergence growth, phenophase number 1 (French & Sauer 1974); ENDO = month of dormancy post-flowering, phenophase number 14 (French & Sauer 1974). All the attributes ranged between more than 80 % and less than 120 % of the modal values for all the species.

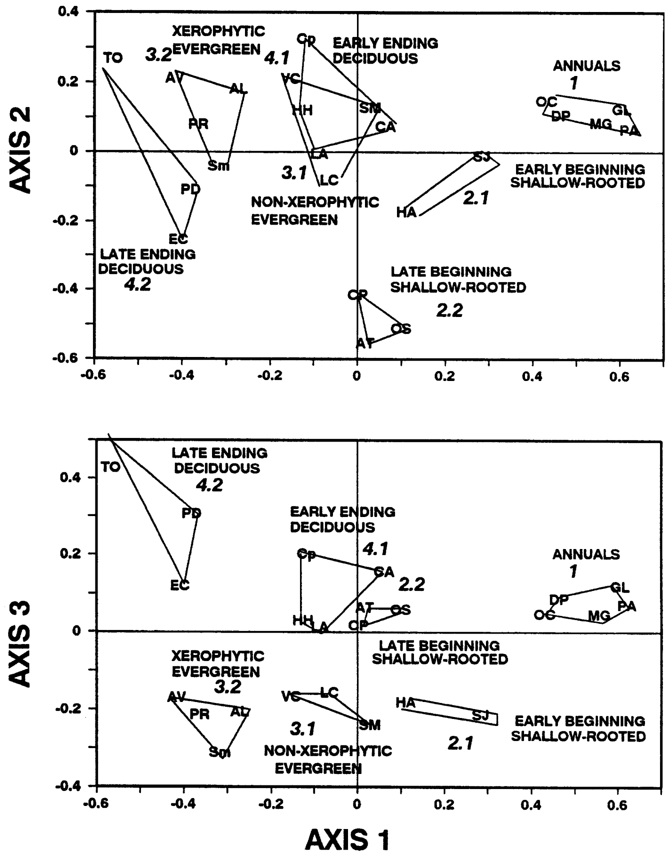
	Group		Species	Traits						
	No.	Name		ROOT (cm)	SPRO (cm)	DIST (cm)	MESO	TYPE	BEGI (month)	ENDO (month)
SHALLOW-ROOTED	1	Mesophytic (Annuals)	*Doniophyton patagonicum*	30	0-3	15	M	-	5	12
			Microsteris gracilis	30	-	5	M	-	5	12
			Oenothera contorta	30	-	15	M	-	5	1
			Polemonium antarcticum	30	-	10	M	-	5	11
			Gilia laciniata	30	-	15	M	-	5	11
	2.1	No-Mesophytic Early beginning	*Sysirinchium junceum*	25	5	10	I	f	3	1
			Huanaca acaulis	30	5	15	X	DL-m	5	1
	2.2	No-Mesophytic Late beginning	*Oxalis squamosa-radicosa*	25	5-10	5	X	m-f	10	1
			Arjona tuberosa	25	10	5	X	GP-s-m	10	1
			Calandrinia patagonica	30	5	10	X	m-P	10	2
DEEP-ROOTED	3.1	No-Xerophytic Evergreens	*Valeriana clarioneifolia*	50	5	20	I	W	3	3
			Sysirinchium macrocarpum	40	0-5	10	I	f	3	3
			Leuceria millefolium	45	2-5	10	X	DL-W	5	2
	3.2	Xerophyte Evergreens	*Adesmia lotoides*	40	5	50	X	GP-P	3	3
			Adesmia villosa	50	5-10	50	X	GP-P	3	3
			Perezia recurvata	35	5-15	50	X	s-m-TC	3	3
			Silene magellanica	45	5-15	15	X	s-m	3	3
	4.1	Early ending Deciduous	*Loasa argentina*	45	10	20	I	DL	5	1
			Hypochoeris hookeri	40	5-10	40	I	W	5	2
			Calceolaria polyrhiza	45	5-10	50	M	-	5	2
			Cerastium arvense	30	5-15	40	M	-	5	1
	4.2	Late ending Deciduous	*Euphorbia collina*	60	5-10	10	X	W-TC	10	3
			Tweedia o'donelli	60	5-10	80	I	m	10	3
			Polygala darwiniana	45	5-15	40	I	m	10	3

with low values for both attributes. Axis 3 had only one term with a significant positive loading (BEGI: date of start of the growth cycle) and accounted for 15 % of the variance. On this axis, evergreens (groups 3.1 and 3.2), and shallow-rooted with an early start (2.1), were very different from the rest because they had the earliest start of the growth-cycle (Fig. 2).

The degree of mesophytism showed a high negative correlation with the sprouting depth and the date of the end of the cycle (see legend of Fig. 2). This attribute, in turn, had high positive correlations with sprouting depth, distance between shoots of the same plant, and rooting depth (Fig. 2). Species with a late end of the cycle had either low mesophytism and/or deep roots. Those with a late end of the cycle and low mesophytism had a great sprouting depth. Species with a late end of the cycle, and deep roots had a great distance between shoots of the same plant.

Discussion

Forb species that have a late growth-cycle showed a high degree of xeromorphism and/or have deep roots (legend Fig. 2); this may be related to the seasonal and spatial pattern of water availability characteristic of the Patagonian steppe. Precipitation in the area occurs mainly during the cold season. During winter the entire soil profile is wet while at the beginning of summer available water is located only in deep soil layers, and at the end of the summer the entire soil is dry (Sala et al. 1989). We suggest that late-cycle forbs survive summer water



Attribute	BEGI	SPRO	DIST	ROOT	ENDO	MESO
(a)						
Axis 1	− 0.11	− 0.45 **	0.38 **	− 0.45 **	− 0.55 **	0.37 **
Axis 2	− 0.59 *	− 0.24	0.49 **	0.30	0.07	0.50 **
Axis 3	0.75 **	0.03	0.36	0.16	− 0.22	0.48 *
(b)						
BEGI	1	0.10	− 0.24	− 0.13	− 0.19	0.01
SPRO	-	1	0.27	0.22	0.37	− 0.36
DIST	-	-	1	0.46	0.39	0.06
ROOT	-	-	-	1	0.59	− 0.15
ENDO	-	-	-	-	1	− 0.46
MESO	-	-	-	-	-	1

Fig. 2. Location of the forb species of the Patagonian steppe along the first three axes of the Principal Components Analysis. Letters correspond to the species names and numbers to groups (functional types) and subgroups as in Fig. 1. Kendall correlation coefficient (τ):
(a) between the score on each axis and the value of each attribute for each species (** $= p < 0.01$; * $= p < 0.05$);
(b) between attributes.

deficits because they have xerophytic characteristics that reduce transpiration water losses, and/or they have deep roots that extend the period of summer water uptake. At the other extreme of the length-of-growing-cycle gradient, the annuals have the highest mesophytism and restrict their cycle to the period when water availability in the upper soil layers is high. As a consequence of this pattern, the four groups are located in different positions on the plane defined by rooting depth and date of end of cycle (Fig. 3).

Rooting depth has also been shown to be essential to explain resource partitioning among life forms in other systems (Wieland & Bazzaz 1975; Knoop & Walker 1985; Cody 1986; Davis & Mooney 1986; Sala et al. 1989). Negative correlations between length of cycle and mesophytism have been reported for several semi-arid mediterranean ecosystems (Mooney & Dunn 1970; Montenegro, Aljaro & Kummerow 1979; Hoffmann & Walker 1980). It suggests that the relationship between cycle length and mesophytism may be a general characteristic of plant species of arid and semi-arid ecosystems.

The positive correlation between the length of the growing cycle and the sprouting depth may be related to the water and temperature regimes of the soil profile. In the Patagonian steppe, as in other arid and semi-arid ecosystems, not only water deficit but also temperature amplitude are maxima in upper layers during the summer (Sala et al. 1989; Nobel 1989). While subterranean buds remain active they are vulnerable to water and temperature stress. Buds of late-cycle plants enter into dormancy at the end of summer. Depth of active buds at the end of the cycle is what determines sprouting depth the next growing season. Therefore, we suggest that in late-cycle species, which have active buds during the summer, deep buds and consequently deep sprouting depth may increase survival. There should be, however, a limit in sprouting depth, imposed by the emergence cost that also increases with depth. Sprouting from deep layers imposes high costs onto the plants; it reduces the amount of resources allocated to growth of above-ground parts and then decreases their maximum growth rate (Tilman 1988).

We suggest that the positive correlation between the end of the cycle and distance among shoots of the same plant is related to the horizontal heterogeneity of resources characteristic of the Patagonian steppe. The community has two interspersed types of structural patches: scattered grasses and shrubs surrounded by a dense ring of grasses (Aguiar, Soriano & Sala 1992).

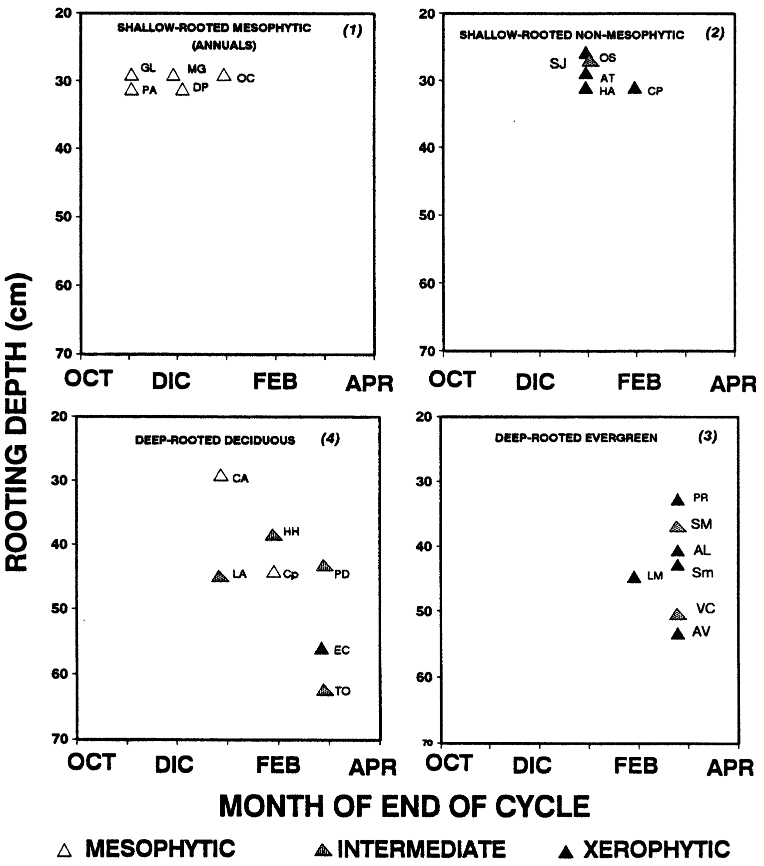


Fig. 3. Location of the 24 Patagonian steppe species belonging to the four functional types in the plane defined by rooting depth (ROOT) and date of the end of the cycle (ENDO). Species abbreviations as in Figs. 1 and 2.

This pattern determines spatial heterogeneity of resources, both above and below-ground. Soil water availability is higher but protection from desiccating winds is lower in bare soil patches than in shrub/grass ring patches (Soriano & Sala 1986). This contrast is more evident in summer than in any other season. If shoots of spreading plants were functionally connected, late cycle species with long distance among shoots would be better suited to take advantage simultaneously of the protection of the shrubs and of the ample water availability of the bare soil patches. Evidence from other systems suggests that functional connections between ramets of spreading plants is common (Pitelka & Ashmun 1986; Tissue & Nobel 1990).

Strategies represent adaptive plant responses selected under ecological pressures (Schulze 1982). The wide variety of ecological pressures acting on the Patagonian forbs could be arranged hierarchically in an ecological space (Kolasa 1989). Winter recharge is the main environmental constraint for all functional types. It determines a prolonged water availability event from mid-fall to beginning of spring, which affects every soil layer and every horizontal microsite. Differences in water dynamics among layers and microsites only become apparent from mid spring to late summer (Sala et al. 1989; Aguiar, Soriano & Sala 1992).

We propose that forb strategies reflect the hierarchical structure of the temporal pattern of soil water dynamics. All the functional types depend on winter recharge to begin their growth cycles. At a detailed scale, each group has a particular strategy to complete its cycle by using a portion of the water resource available during spring and summer. At the beginning of spring there is a great deal of water available in the entire soil. The more mesophytic forbs (Groups 1 and 4.1), with a high relative growth rate, could use this resource with an advantage over the more xerophytic shrubs and grasses (Orians & Solbrig 1977). In late spring and summer, high water availability is constrained to the bare soil patches and the deepest layers, while the upper soil layers are occasionally wet by the rare spring-summer rainfalls. Spreading perennial types (Groups 3.2 and 4) are able to use water available in bare soil patches, deep-rooted perennial types (groups 2 and 4) are able to use deep water, and late cycle forbs (groups 3 and 4.2) may use infrequent summer rainfalls.

The high number of forb species can be explained as follows. First, the dominant grasses and shrubs of the

Patagonian steppe are adapted to using not only the most abundant resources but also the less variable and most reliable forms of them (Sala, Lauenroth & Parton 1992). What is left by the dominants are small amounts of the resources which are highly variable in space and time. Then, the forbs, as a group, are adapted to using such resources. We suggest that different forb species use different portions of the water resource which are not fully used by the dominant. This is an explanation for the small size of individuals and for the large heterogeneity in morphology, phenology, and physiology as well as for the large number of species that form this group.

The major result of this work, from our point of view, is the large heterogeneity in morphology, phenology, and physiology which we found among forb species. In contrast, the variability in ecological characteristics within dominant shrubs and grasses is very small. The grass and shrub functional types are relatively homogeneous in above- and below-ground architecture, phenology, and water relations (Soriano & Sala 1983; Soriano, Golluscio & Satorre 1987; Fernández A. & Paruelo 1988; Sala et al. 1989; Fernández A., Sala & Golluscio 1991). Two ecological roles have been described for shrubs and grasses (Soriano & Sala 1983). However, it was impossible to identify a similar unique ecological role for forbs. Similarities among forbs occur at the subgroup level. The only characteristic they share is the use of resources (highly variable in space and time) which were left unused by the dominant species.

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