

Relationship between spatial strategies and morphological attributes in a Uruguayan grassland: a functional approach

Altesor, A.^{1*}, Pezzani, F.¹, Grun, S.² & Rodríguez, C.¹

¹Unidad Ecología Funcional, Facultad de Ciencias, Universidad de la República; Iguá 4225, CP 11400, Montevideo, Uruguay; ²Cátedra de Botánica, Facultad de Agronomía, Universidad de la República, Garzón 780, CP 12900, Montevideo, Uruguay;

*Corresponding author; Fax +59825258617; E-mail aaltesor@fcien.edu.uy

Abstract. In a native grassland in Uruguay subjected to continuous grazing by cattle, four permanent plots of 40 × 40 cm were established. Plots were divided into 16 × 16 cells and the presence of species was recorded seasonally during two years. The spatial dynamic of the dominant species was defined through three parameters: persistence, short-distance spread and long-distance spread. The association between the spatial strategies and certain morphological attributes that were presumed to be important to the spatial behaviour of the species, was examined using Correspondence Analysis.

Four types of spatial strategies were observed: (1) persisting over the year in the same cell without showing any type of mobility; (2) continuously growing due to the solid advancing front of ramets, persisting or not persisting (3) in the same cells; and (4) multi-strategy with high persistence and both high short- and long-distance spread. Among the selected attributes, the erect/prostrate habit, the capacity of vegetative propagation by means of bulbs, rhizomes or stolons, the ratio length/width of leaves and the season of active growth were the characteristics most closely associated with the spatial strategies.

Keywords: Functional group; Permanent plot; Small scale; Spatial dynamics.

Nomenclature: Lombardo (1982, 1983, 1984).

Introduction

Recently, the definition of functional types has been given great importance in the study of communities and ecosystems, due to the need to address problems of climate change and declining biodiversity. In this way it becomes easier to predict the rate and the direction of vegetation changes (Thompson et al. 1996).

In several studies, mainly of grasslands, different functional groups have been defined in which, depending on the scope of the study, various attributes of the life history of the species composing the community are used. No single set of functional types will be ideal for all purposes and different criteria may be necessary

according to the scale and purpose of inquiry (Thompson et al. 1996). Díaz et al. (1992) defined functional groups in a mountain grassland under different grazing intensities. They took into account morphological characteristics of the species related to plant defences such as the presence of spines, pubescence of leaves and a prostrate or erect habit. In order to classify the native grassland flora of northeast Kansas, Kindscher & Wells (1995) measured 32 ecomorphological traits including habit, leaves, stem, root and reproductive characteristics of the species. Thompson et al. (1996) used resource capture, storage and release, growth, reproduction, defence, dispersal and seed persistence to define the functional groups of a limestone grassland community. Tilman et al. (1997), on a field experiment, classified the functional groups on the basis of intrinsic physiological and morphological traits, which influence differences in resource requirements and seasonality of growth. Nevertheless, studies that include the spatial behaviour of the species as an important component of their life history are scarce. In grassland communities vegetative growth seems to be more important than reproductive recruitment (Abrahamson 1980). Furthermore, the existence of active spatial dynamics in those plants constitute a mechanism of foraging for space or nutrients (Herben et al. 1993). As a consequence, for this type of community, the definition of the spatial strategy of the species may shed new light on the definition of functional groups.

Such studies are very laborious because they require the study of species at spatial scales fine enough to allow detailed mapping of ramet spread. Nevertheless, this is the only way that allows to correlate the occupation of a given patch from the neighbouring patches. In a grazed grassland in Sweden, van der Maarel & Sykes (1993, 1997) found a high mobility of species at the small scale studied and suggested that most species would reach virtually all microsites within the plot in the course of time. This behaviour was expressed through the idea of the carousel model. The different mobility characteristics may facilitate the coexistence of species and maintain community diversity (Bell 1984). Furthermore, the

random occupation of gaps, that take into account the production, dispersal and death rates of propagules (lottery model), has been also proposed to explain the small-scale coexistence of spatial structured organisms (van Hulst 1992).

Originally, two types of spatial colonization strategies of clonal species were defined by Lovett Doust (1981), extension from mother plants through an advancing front of ramets ('phalanx') and widely-spaced appearance of ramets from mother plants ('guerrilla'). Subsequent papers, including Herben et al. (1993) found other types of strategy which did not fit the original ones, such as the 'sitting' species, which show a high persistence over time.

The aim of this paper is (1) to determine the different spatial strategies of the dominant species of a grassland community in San José, Uruguay, under constant grazing pressure and (2) to relate these strategies to some morphological and ecological traits of the species involved, which are supposed to be related to their capacity of spatial spreading over the time.

Methods

Study site

The study area is located in Mal Abrigo, Departamento de San José, in south-central Uruguay (34° 21' S, 56° 43' W). Mean annual precipitation (period 1941 to 1970) was 1374 mm; no significant seasonality pattern was detected (see Ezcurra & Rodrigues 1986). Mean annual temperature for the same period was 18.9 °C, ranging from a winter monthly mean of 12.6 °C in July to a summer mean temperature of 26.3 °C in January (Anon. 1985).

The site is located on smooth slopes of the crystalline basement, that outcrop in many areas. The soils are generally shallow, developed on loam-clay sediments.

In Uruguay, the area occupied by natural grasslands extends over 140 000 km² (ca. 80 % of the country), of which ca. 90 % are devoted to extensive grazing by cattle and sheep. The introduction of domestic herbivores following the settlement of Europeans, changed the original structure of these grasslands significantly (Gallinal et al. 1938). While the ungrazed vegetation grows 40 - 50 cm tall and is dominated by tussock grasses and some small woody shrubs (Rosengurt 1943), under the current grazing regime the vegetation turns into a short turf less than 5 cm tall, dominated by stoloniferous and caespitose grasses and perennial herbs (Sala et al. 1986; Millot et al. 1987; Altesor et al. 1998).

The study site has been managed under traditional continuous grazing, with Holland cows at a density of

Table 1. List of dominant species (with frequency values > 10), families (FAM) and species code used in Fig. 1.

Species	FAM	Code
<i>Andropogon ternatus</i>	POA	At
<i>Aristida uruguayensis</i>	POA	Au
<i>Bulbostylis juncooides</i>	CYP	Bj
<i>Carex phalaroides</i>	CYP	Cp
<i>Chaptalia exscapa</i>	AST	Che
<i>Chaptalia piloselloides</i>	AST	Chp
<i>Chevreulia sarmentosa</i>	AST	Chs
<i>Galactia marginalis</i>	FAB	Gm
<i>Oxalis macachin</i>	OXA	Om
<i>Paspalum notatum</i>	POA	Pn
<i>Paspalum plicatulum</i>	POA	Pp
<i>Richardia humistrata</i>	RUB	Rh
<i>Schizachyrium tenerum</i>	POA	St

AST = Asteraceae; CYP = Cyperaceae; FAB = Fabaceae; OXA = Oxalidaceae; POA = Poaceae; RUB = Rubiaceae.

about one animal unit (i.e. one cow-equivalent) per 2 ha, and has not been cultivated during the last 25 yr.

In 1995, a rectangular plot of 12 × 15 m was established in a homogeneous area. Within this area, four permanent quadrats of 40 cm × 40 cm were randomly marked. At each sampling date, an aluminium frame divided into 256 subquadrats of 2.5 cm × 2.5 cm was placed on each quadrat. To obtain floristic data, the presence of species that were rooted in the cell or, if not rooted, covered more than 50 % of the cell was recorded once every season (February, May, August and November) during 1996 and 1997. One month before each analysis, the rectangular plot was fenced to prevent disturbance by cattle.

Data analysis

A species-by-plot matrix was prepared that included the species frequencies in the four plots in each season sample from summer 1996 to spring 1997. We eliminated all species that were present in less than three plots and those that were present in three or four plots but showed low frequencies (technically, the exact criterion we used was to eliminate all species that had expected values below 10 in the frequency table, calculating the expected value in the standard way for contingency tables, i.e. row total × column total / table total; see Everitt 1977). The resulting matrix included 13 species (Table 1).

For each species, the pattern recorded was that evident in the season in which the species occurred with the highest frequency. This criterion was used to avoid difficulties due to the life cycle of the species.

The small-scale spatial dynamic of individual species was defined through three parameters.

Table 2. List of morphological traits and their attributes used to construct the attributes × spatial-strategies matrix.

Traits	Attributes	Code
Season of active growth	Cool/warm	Cs/Ws
Vegetative propagation	Yes/no	Vp+/Vp-
Position of dormant buds	Above-ground / below-ground	Ag/Bg
Habit	Erect	E
	Prostrate	P
	Tussock	T
	Rosette	R
	Stoloniferous	St
	Bulbous	B
	Rhizomatous	Rh
Leaf width (Width/length ratio)	Broad (> 1)	Cat. 1
	Medium (0.1 < x < 1)	Cat. 2
	Narrow (< 0.1)	Cat. 3

1. *Persistence*: this is a measure of the tendency of a species to remain within the same cell. Persistence was expressed as the number of cells where the species remained over a 1-yr interval, related to the total appearance at the beginning of the analysis.

2. *Short-distance spread*: continuous growth through an advancing front of ramets. This parameter was expressed as the number of cells where the species newly appeared in the eight adjacent cells surrounding the cell where the species was present in the first sample; this number was related to the number of adjacent cells.

3. *Long-distance spread*: production of widely spaced ramets. This parameter was expressed by the number of cells where the species newly appeared without having been observed in the surrounding eight adjacent cells in the previous year. Edge cells were excluded from this analysis. This measure was expressed relative to the number of cells which did not have the species in question in their neighbourhood.

Differences in the parameters among species were compared by a one-way ANOVA, and a species × spatial-strategy matrix was created. Data for six traits and their attributes, which were presumed to be important to plant ecology, morphology and habit growth (Table 2) were compiled for each species. These attributes were recorded by observations in the field and from literature references (Cabrera 1963; Rosengurt 1979; Lombardo 1982, 1983, 1984). A binary attributes × species matrix was constructed using 16 attributes. This matrix, multiplied by the species × spatial-strategies one, produced an attributes × spatial-strategies matrix, which was submitted to the multivariate ordination technique Correspondence Analysis. We used ORDEN version 2.0 (Ezcurra 1992) for this analysis.

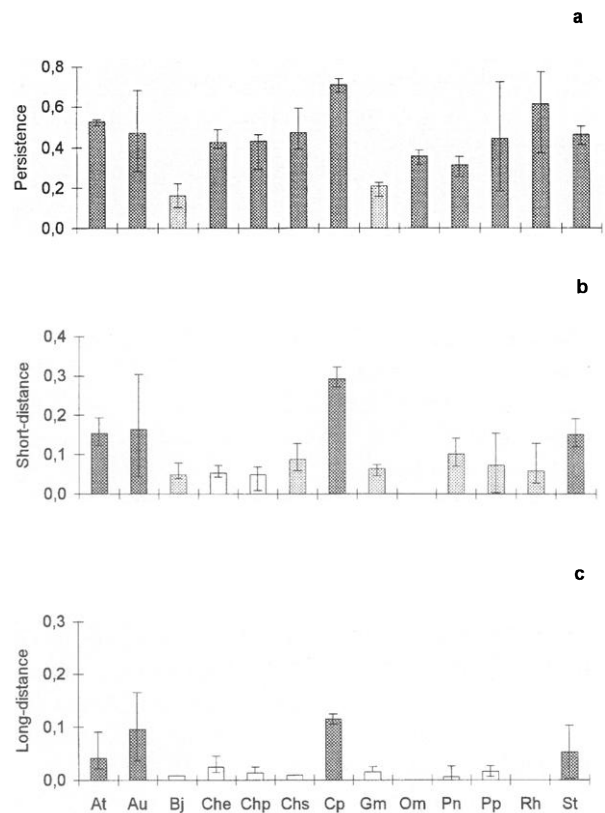


Fig. 1. Median persistence (a), short-distance spread (b) and long-distance spread (c) of the species (for codes see Table 1). Bars indicate 25% and 75% quartiles. High values ■; medium values ▨; low values □.

Results

During the two years of sampling we found a cumulative species richness of 89 species, with a strong hierarchical abundance-distribution of species. Among them, only 13 have medium frequency values higher than 10. These species were used to study their spatial dynamics. The other, mainly rare, species with a fast turnover, were discarded.

As found in the one-way ANOVA all parameters evaluated varied significantly between species. According to the median values (Fig. 1) the short-distance spread ($F = 2.89, p = 0.006$), allowed us to separate the species into three categories: high, medium and low. The differences between the median values of persistence ($F = 1.95, p = 0.05$), were used to discriminate the species into two groups: high and medium persistence. The last parameter used was the median value of long-distance; this was significantly higher ($F = 2.40, p = 0.02$) only for four species. In this way we defined the spatial strategies of the selected plants (Table 3).

One group of species (A), with *Andropogon ternatus*,

Table 3. Spatial strategies of the dominant species. The plants have been classified according to their persistence, short-distance and long-distance spreading capacity.

High persistence		
Short-distance spreading		
High	Medium	Low
A	B	D
<i>Andropogon ternatus*</i>	<i>Chevreulia sarmentosa</i>	<i>Chaptalia exscapa</i>
<i>Aristida uruguayensis*</i>	<i>Richardia humistrata</i>	<i>Chaptalia piloselloides</i>
<i>Schizachyrium tenerum*</i>	<i>Paspalum notatum</i>	<i>Oxalis macachin</i>
<i>Carex phalaroides*</i>	<i>Paspalum plicatulum</i>	
	Medium persistence	
	C	
	<i>Galactia marginalis</i>	
	<i>Bulbostylis juncooides</i>	

* Long-distance spreading high

Aristida uruguayensis, *Carex phalaroides* and *Schizachyrium tenerum* showed all types of spatial behaviour: high persistence and both high short- and long-distance spread. The other two groups of species, showed medium short-distance spread and little or no long-distance spread, but they differed in their persistence values. Group B, with high persistence, is exemplified by *Chevreulia sarmentosa*, *Paspalum notatum*, *P. plicatulum* and *Richardia humistrata*. Group C, with medium persistence values, includes *Bulbostylis juncooides* and *Galactia marginalis*. Group D, with *Chaptalia exscapa*, *C. piloselloides* and *Oxalis macachin*, showed high

persistence and very low short- and long-distance spread.

In the diagram of the Correspondence Analysis of the attribute × spatial strategy matrix of the species (Fig. 2) the first axis accounts for the major part of the variance (76 %). Axis 1 separates groups A and C from group D. Some vegetative characteristics are strongly associated with these spatial behaviour types. The bulbous, rosette and prostrate habits, the absence of vegetative propagation and the broad leaves of the cool-season species are arranged near the group with less spreading capacity (D). On the other hand, the erect and tussock growth forms are closely correlated with the A and C groups. Most of the species have warm season growth and narrow, long leaves.

Axis 2, which explains the 21 % of the variance, separates group B from the other strategy types. This group is composed mainly of stoloniferous species.

Discussion

The results show that the dominant species of the studied grassland community exhibit several strategies of spatial exploration, even in a short period of time. Following the methodology proposed by Herben et al. (1993), we measured the persistence and the long-distance spread of the species. The third parameter we examined, short-distance spread, reflecting the spatial colonization of species through a front of ramets, appeared to be a useful addition.

It was easy to distinguish four different spatial strategy types on the basis of differences regarding these three parameters. Maybe the most striking strategy (type A) was that of the matrix-forming species. These species, mainly grasses, have not only the ability to persist over one year in the same original cell, but also to colonize both close and distant cells. The ability to persist in the same place, and at the same time to be highly mobile, appears to be uncommon. This variety of colonization modes probably allows them to cover a large proportion of the ground throughout the year.

The species with medium spreading capacity (B and C) are taxonomically and morphologically heterogeneous; they include forbs, grasses, graminoids and the only legume of the community (*Galactia marginalis*). At the scale of observation (6.25 cm²), the B-species grow radially from local patches into the interstitial spaces of the matrix. On the other hand, the C-species, show a more scattered pattern during the year, due to their lower persistence.

The D-species, persisting in the same cell over the year and not moving around, are weedy dicots that are present only in the cool season, when the matrix-forming species diminish in size. Because of their

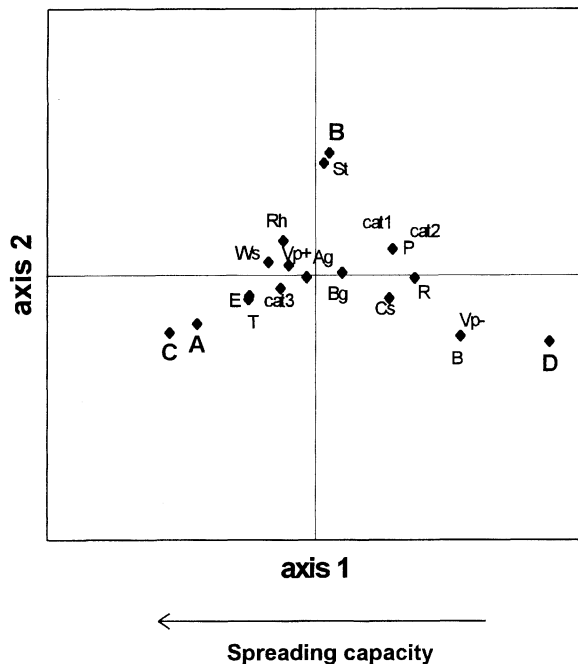


Fig. 2. Correspondence Analysis of the attributes × spatial-strategy matrix. For codes of morphological attributes, see Table 2; for composition of species groups A -D, see Table 3.

weedy behaviour, they opportunistically occupy the spaces left by the rest of species, showing a high frequency during the period of active growth.

The production of widely spaced ramets was found by Herben et al. (1993) in more than 50 % of the selected species studied in a Czech mountain grassland. Undoubtedly, the number of species assigned to this category depends on the scale of observation. Although we used the same method to calculate the long-distance spread, and the size of the subquadrats was very similar to that in the Czech study, we did not find this strategy. Probably this reflects the uncertainty of colonizing distant cells in a dense canopy of matrix-forming species which cover most of the ground, and which could prevent the successful establishment of long-distance ramets or seed recruitment.

In the ordination of the attributes \times strategies matrix, axis 1 reflects the variation in spreading capacity of the species. The spreading species (A and C groups) include erect and tussock growth forms with narrow and long leaves which are both accessible to the cattle and available throughout the whole year. Most of them are warm-season species and all of them have mechanisms of vegetative propagation.

On the other hand, the B- and D-species are prostrate, less mobile and broad-leaved. The first group includes stoloniferous dicots such as *Chevreulia sarmentosa* and *Richardia humistrata*. The grasses *Paspalum notatum* and *P. plicatulum* also represent this type of spatial strategy. The former species has a rhizome that spreads horizontally, and the latter is the only erect species of the group. The D-species include a bulbous dicot (*Oxalis macachin*), and rosette species with a thick root (*Chaptalia exscapa* and *C. piloselloides*) which allow them to survive under the climatic conditions of the warm season. In this period they disappear above-ground and their active vegetative growth, through root offshoots, proceeds only during the cold season. They are all native species with most of their biomass close to the ground, able to colonize gaps arising from disturbance. McIntyre et al. (1995) found that heavily grazed sites had larger proportions of flat rosettes than sites with light grazing. This attribute makes them less accessible to grazers and was considered by Faccelli et al. (1988) and Díaz et al. (1992) to be an adaptation to high grazing pressure.

Since vegetative propagation is the principal form of growth in this community type (Abrahamson 1980; Schmid 1985), it seems important to identify the type of spatial behaviour of these clonal species. Furthermore, the variation in spatial colonizing modes allows different mechanisms of foraging for nutrients or space (Humphrey & Pyke 1997). The strategies described may constitute one of the causes underlying the models

of small-scale coexistence of spatially structured organisms, such as the lottery and carousel models.

In this sense certain attributes, which are easy to record in the field, could be good indicators of the types of colonizing modes. Among the 16 selected attributes, the erect/prostrate habit, the capacity of vegetative propagation by means of bulbs, rhizomes or stolons, the ratio leaf length/width and the season of active growth were the characteristics most closely associated with the spatial strategies. Plant height was not considered in our work. This trait may be relevant in studies of ungrazed sites or to compare different grazing intensities, but this is not the case in our study area, with a long history of continuous grazing regime that maintains plant height less than 5 cm tall.

Analysis of the grassland community from a functional perspective including spatial strategies, can allow a better understanding of the high species richness in the subhumid grasslands with a long history of grazing.

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