THE SEED BANK OF AN OLD PAMPEAN PRAIRIE AND ITS RELATION WITH THE STANDING VEGETATION[1]

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ABSTRACT - The seed bank of a prairie which has not been ploughed for at least 40 years was analysed and compared with standing vegetation. There were 28 species in the seed bank: 18 monocotyledoneae and 10 dicotyledoneae, plus five unknown species. In the standing vegetation there were 39 species: 19 monocotyledoneae and 20 dicotyledoneae. Seed bank and standing vegetation share 18 out of 49 known species and their similarity is 54% (Sorensen index). The seeds have an aggregate distribution, therefore the bank is very heterogeneous.

Index terms: Argentina; grasslands; old fields; "pampa"; prairie; seed bank; spatial pattern.

BANCO DE SEMENTES DUMA ANTIGA PASTAGEM PAMPEANA, E SUA RELAÇÃO COM A VEGETAÇÃO EM SUPERFÍCIE

RESUMO - Analisou-se o banco de sementes de uma pastagem que não foi arada pelo menos durante 40 anos. Comparou-se com a vegetação do lugar. Acharam-se 28 espécies no banco de sementes: 18 monocotiledôneas e 10 dicotiledôneas, mais cinco espécies desconhecidas. Na vegetação foram arroladas 39 espécies: 19 monocotiledôneas e 20 dicotiledôneas. O banco de sementes comparte 18 espécies, das 49 conhecidas, com a vegetação, e a similitude entre elas é de 54% (Índice de Sorensen). As sementes têm distribuição agregada, constituindo um banco muito heterogêneo.

Termos para indexacão: Argentina; pastagem; pampa; banco de sementes; padrão espacial.

INTRODUCTION

Vegetation regeneration is largely dependent on the seed bank and when propagules are removed from the soil, plant colonization and soil cover take longer to develop (Marks & Mohler, 1985). Weed invasions depend on the seed rain, but also on the seed bank.

The amount of buried seeds reported to be in the arable layer of soils from the pampean region in Argentina is 11,730 seeds/m^2 in old pastures, 8,556 seeds/m^2 in wheat-soybean rotation soils (Leguizamón et al., 1981) and 6,675 seeds /m^2 immediately after sowing wheat in a continuously cropped field (Lewis & Leguizamón, 1991). However, seed bank densities reported elsewhere are very variable, 4,120 seeds/m^2 in vegetable cropped soils of Britain (Roberts & Neilson, 1982), 2,019 seeds/m^2 in the seed bank of Illinois tallgrass prairie (Johnson & Anderson, 1986), an average of 3,749 seeds/m^2 in a semiarid grassland of Texas (Kinucan & Smeins,1992) and 6,470 seeds/m^2 in a Missouri tall grass prairie (Rabinowitz, 1981). Far higher densities were found in a freshwater tidal marsh (Leck & Graveline, 1979) and as much as 42,612 seeds/m^2 in a prairie glacial marsh (Valk & Davies, 1978). Even higher densities were quoted from different sources, up to 70 thousand seeds/m^2 (Symonides, 1986).

Roberts (1981, 1986) emphasizes that there is a very low correlation between species representation in the seed bank and that in the standing vegetation in any plant community, other than those subject to frequent disturbance. Johnson & Anderson (1986) found a weak linear relationship between species abundance in the seed bank and species importance value in above-ground vegeta-

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tion; however, in Mediterranean pastures seed bank and vegetation were floristically similar, although there was low correspondence between vegetation and seed bank in recently ploughed and intensely disturbed plots (Lavassor et al., 1990).

Long term experiments on plant regeneration and weed invations were set up on a *Stipa* and *Bothriochloa laguroides* grassland. *Stipa* (*S. neesiana, S. papposa* and *S. hyalina*) grasslands, the "flechillares", were the most important communities of the SE of Santa Fe Province, Argentina, within the Pampa region (Lewis et al., 1984, 1985).They are used for cattle grazing, though nowadays their area has been reduced and most stands have been put to agriculture. Before analysing the regeneration of plants it is necessary to know the sources of propagules; therefore, in this paper we analyse the seed bank of this prairie, and compare it with the standing vegetation.

MATERIALS AND METHODS

The seed bank and vegetation of a *Stipa* grassland near Máximo Paz in Southern Santa Fe Province, Argentina, was analysed. The stand was used for cattle raising and was not ploughed for at least 40 years. Intense grazing was alternated with fallow periods, allowing grassland recovery.

Plant regeneration experiments were set up on a 20 x 10 m rectangle. Seed bank was determined by the wet sieving technique (Leguizamón, 1983) in 10 soil cores, 8 cm in diameter by 10 cm deep, taken 4 m apart from each other, five on the northern and five on the southern side of the experimental rectangle. Samples were classified with Minimal Variance Cluster technique using MULVA programs (Wildi & Orloci, 1990). The seeds spatial distribution pattern was determined by Morisita's Index of Aggregation (Johnson & Anderson, 1986), as calculated with the following equation:

$$I_\delta = \frac{\sum_{i=1}^{N} n_i(n_i - 1)}{n(n-1)} N$$

where N is the number of samples, n_i is the number of individuals (seeds) in sample i and n is the total number of individuals in all samples. When the individuals are randomly dispersed, $I_\delta = 1.0$; if they are uniformly dispersed, I_δ is smaller than 1.0, or greater than 1 if they are aggregated.

Vegetation was analysed on late Spring 1987, Autumn 1988 and again in late Spring 1988 on five fixed 1 m^2 quadrats, 2 along the northern, 2 on the southern and 1 on the eastern side of the same 20 x 10 m rectangle. On the three analysed seasons the general plant cover, stratification (height of different layers) and the floristic lists of all quadrats were recorded. The importance of each species was determined as cover and abundance using Braun-Blanquet's (1979) combined scale. With these data an association table was made. Similarity between seed bank and vegetation was determined with Sorensen (1948) index.

Nomenclature follows Cabrera & Zardini (1978).

RESULTS AND DISCUSSION

Quadrats were very similar to each other in any of the three analysed seasons (Table 1).The dominant species are *Stipa neesiana* and *Bothriochloa laguroides* although overgrazing reduced their cover on the second Spring. Species in group I appear in all seasons, those in group II form a Spring guild, *Cirsium vulgare* is the only important *Autumn species* and *Chaptalia excapa* the only preferential of the Spring 1988. Species in group V disappeared on the spring 1988 and the ones in group VI are rarities.

A total of 39 species were recorded in the vegetation out of which 7 were annuals and 32 perennials, 19 monocotyledoneae (including 13 gramineae and 3 cyperaceae) and 20 dicots.

The density of the seed bank was 28,523 seeds/m^2. The buried seed density of this grassland was higher than those reported by Rabinowitz (1981), Johnson & Anderson (1986) and Kinucan & Smeins (1992) for the same type of communities from North America, even if allowances are made for the different methods used in estimating it. The wide range of buried seeds densities reported throughout the world for different ecosystems suggests that these data are only of regional or very localized importance, and comparisons of communities very far apart from each other are meaningless.

Within the region and using the same estimation method the density of this seed bank was also higher than those reported by Leguizamón et al. (1981) and Lewis & Leguizamón (1991). However, our results are consistent with these ones, as

TABLE 1. Association table of above ground vegetation. Scores of species in quadrats are cover abundance values.

Season	Spring 1987					Autumn 1988					Spring 1988					
Number of releves	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	
General cover %	100	85	85	80	85	100	100	100	100	100	90	85	80	70	85	
Height Upper Layer	80	75	75	75	75	50	40	40	45	50	30	30	40	30	8	
Lower Layer											8	8	8	8		
Stipa neesiana	4	3	3	4	3	4	2	3	2	2	1	+	1	+		
Bothriochloa laguroides	3	3	3	3	4	2	3	2	3	4	2	2	3	2	+	
Cynodon dactylon	1	2	3	1	1	2	4	3	3	3	+	3	1	2	3	
Eragrostis lugens	+	+	1	+	+	1	1	1	1	2		+	+	+	+	I
Cyperus reflexus			+	+	+		+		+	+		+			+	
Verbena litoralis				+	+				+	+				+		
Pterocaulon subvirgatum		+					+					+			+	
Spergularia villosa		1			+		+					1			+	
Briza subaristata	2	+	3	1	+	1					3	+	2	2		
Bromus unioloides	+	+									+		+	+	+	
Carex bonariensis	+	1	1	+	2		+				1	3	+	+	2	
Lolium multiflorum	+	1		1	+						3		2	1	2	
Juncus sp.	1				1	1				+	1			1	1	II
Hordeum euclaston	1	1	+	+	+						1	+			1	
Juncus balticus	+		+	+												
Hordeum stenostachys		+		1							1	1		1	+	
Paronychia sp.		+	+	+								+				
Modiolastrum gilliesii				+								+				
Chaptalia exscapa									+	+	+	+	+		+	III
Cirsium vulgare						1	+	+		+				+		IV
Relbunium richardianum	+	+	1	1			+	+	1							
Paspalum dilatatum	+	+	+			3	1	2	+		+					
Panicum milioides	+	+			+		+	+	1	+						V
Dichondra microcalyx	+	+	+		+	+	+	+		+						
Gamochaeta sp.					+		1		+							
Cyperus cayennensis		+		+			1									
Oxypetalum solaenoides		+					1									
Medicago lupulina	1															
Sisyrinchium minutiflorum	+															
Conyza bonariensis		+	+													
Graphalium gaudichaudianum		1														VI
Conyza chilensis			+		+											
Baccharis coridifolia				+	+											
Plantago myosurus				+												
Stipa hyalina											+					
Sporobolus indicus												+				
Ambrosia tenuifolia												+				
Chevreulia sp.														+	+	
Marrubium sp.															+	

it seems that density increases with community age and the community analysed here was by far the oldest. Disturbance may deplete seed banks (Hopkins & Graham, 1984), so the younger the community the lower the density of the seed bank, though it is not always the case (Beatty, 1991).

Seed bank composition is shown in Table 2. A total of 28 known species were recorded in the seed bank out of which 6 were annuals and 22 perennials, 12 were gramineae, 4 cyperaceae, 2

TABLE 2. Seed bank composition.

	Seed average/sample	Seeds/m^2	% Seeds/sample
Cyperus cayennensis	7,4 ± 9,55	1472,92	5,16
Eragrostis lugens	8,1 ± 5,15	1612,26	5,65
Briza subaristata	16,7 ± 26,87	3324,04	11,65
Cyperus reflexus	18,8 ± 14,36	3742,03	13,11
Carex bonariensis	11,5 ± 8,91	2289,01	8,02
Spergularia media	9,6 ± 16,34	1910,82	6,69
Stipa neesiana	3,8 ± 2,66	756,36	2,65
Bothriochloa laguroides	3,4 ± 3,63	676,75	2,37
Hordeum euclaston	2,4 ± 2,46	477,70	1,67
Centunculus minimus	30,2 ± 81,64	6011,14	21,07
Sisyrinchium minutiflorum	5,6 ± 10	1094,74	3,86
Portulaca oleracea	4,4 ± 3,66	875,79	3,07
Spergularia villosa	0,4 ± 0,7	79,61	0,28
Lolium multiflorum	5 ± 5,41	995,22	3,49
Chenopodium album	0,6 ± 0,7	119,42	0,42
Panicum milioides	0,7 ± 0,67	139,33	0,49
Nicotiana longiflora	0,8 ± 1,4	159,23	0,55
Juncus balticus	0,4 ± 0,7	79,61	0,28
Cyperus sp.	6,3 ± 7,3	1253,98	4,40
Dichondra microcalyx	0,9 ± 1,45	179,14	0,62
Malva parviflora	0,1 ± 0,32	19,90	0,07
Cynodon dactylon	0,2 ± 0,63	39,80	0,14
Bromus unioloides	0,3 ± 0,95	59,71	0,21
Paronychia sp.	0,6 ± 1,9	119,42	0,41
Verbena litoralis	1,5 ± 4,74	298,56	1,04
Setaria geniculata	0,2 ± 0,42	39,80	0,14
Panicum bergii	0,2 ± 0,63	39,80	0,14
Stipa trichotoma	0,1 ± 0,32	19,90	0,07
Undetermined 1	1,2 ± 3,8	238,85	0,83
Undetermined.2	0,6 ± 0,7	119,42	0,41
Undet.3 (Cyperaceae)	0,6 ± 0,97	119,42	0,41
Undet.4 (Gramineae)	0,6 ± 0,97	119,42	0,41
Undetermined 5	0,2 ± 0,63	39,8	0,14

other monocots and 10 dicots. Also there were seeds of five unknown species, a gramineae, a cyperaceae and three dicots.

Qualitative similarity between vegetation and seed bank was 54% (Sorensen index) and they share 18 out of 49 known species. Similarity between standing vegetation and seed bank in this case was lower than that found by Lavassor et al. (1990). Again, in this aspect literature is very contradictory, and in most cases, similarity between reported vegetation and seed bank is very low, but if it is considered that seed rain is the most important factor affecting seed bank composition (Hester et al., 1991; Bertiller, 1992), steady state communities will be very similar to their seed banks.

Quantitative differences were even greater; the most abundant species in the bank (*Centunculus minimus*) was not recorded in vegetation at all and *Stipa neesiana* and *Bothriochloa laguroides* were not the most important species of the bank altough they were the dominant species in vegetation. Dominant grasses often are underrepresented in seed banks (Rice, 1989); also annuals may have

transient seed banks (Andrew & Mott, 1983; Feldman & Lewis, 1990), and there may be differential seed predation of different species. Among the species of the analysed community which were not represented in the seed bank there were 9 (41%) pappus bearing compositae, and one asclepiadaceae (*Oxypetalum solanoides*) which also has seeds with pappi; pappus bearing seeds are easily dispersed, therefore, it is possible that these species regeneration rely more on the seed rain than on the seed bank. In any case, most of vegetation species which are not represented in the seed bank are rarities.

The seed bank samples were very different from each other, therefore the seed bank is very heterogeneous. Samples could be grouped in four distinct clusters (Fig. 1 and Table 3). Sample 8 was a marginal or anomalous one and most of *Centunculus minimus* seeds were recorded in it; apart from this sample this species was almost irrelevant in the bank. This anomalous sample accounted for the most outstanding quantitative differences between seed bank and vegetation.

The heterogeneity of the seed bank may arise from the fact that seeds are clumped so their distribution is uneven in the soil and among samples (Johnson & Anderson, 1986; Bigwood & Inouye,

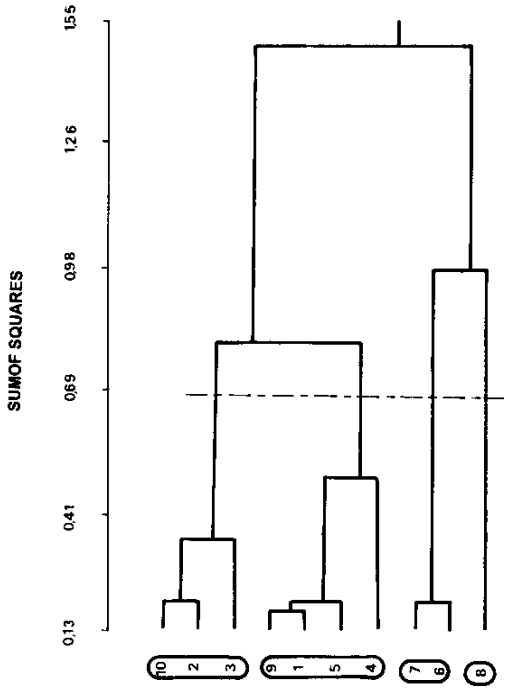

FIG. 1. Dendrogram of the seed sample groups obtained by the Minimal Variance Cluster technique.

TABLE 3. Seed bank of soil samples.

Soil samples	Seed sample groups											Morisita's Index
	10	2	3	9	1	5	4	7	6	8	Σ	
Cyperus reflexus	30	29	16	4	32	7	9	2	14	45	188	1.48
Briza subaristata	10	11		1	1	2	3	87	34	18	167	3.28
Eragrostis lugens	10	14	5	6	16	4	3	4	4	15	81	1.25
Carex bonariensis	4	4	4	7	30	7	21	6	15	17	115	1.46
Stipa neesiana	2	2	10	1	4	2	3	3	5	6	38	1.20
Portulaca oleracea	7	1	1	3	1	9	9	3	1	9	44	1.42
Centunculus minimus	6	9		3	2		2	18		262	302	7.56
Cyperus sp.	21		4	2		3	6	9	1	17	63	2.08
Lolium multiflorum	3	1	2			3	4	9	15	13	50	1.89
Sisyrinchium minutiflorum		8		1	1			30		16	56	3.78
Hordeum euclaston	2	2	2	1	3	8			5	1	24	1.59
Spergularia media	14	1		7	54	11	5			4	96	3.53
Bothriochloa laguroides	2	5	3	2	13	3	2	1	3		34	1.78
Cyperus cayennensis	11	10	5	5	8	3	32				74	2.39
Panicum milioides	1	1	1	2		1	1				7	0.47
Chenopodium album	1	2				1	1	1			6	0.66
Spergularia villosa		2	1						1		4	1.66

Continue...

TABLE 3. Continue.

Soil samples	Seed sample groups											Morisita's Index
	10	2	3	9	1	5	4	7	6	8	Σ	
Nicotiana longiflora	2	2								4	8	2.85
Juncus balticus			1					1	2		4	1.66
Setaria geniculata	1							1			2	0.00
Dichondra microcalyx				4		1			1	3	9	2.50
Malva parviflora						1					1	0.00
Cynodon dactylon									2		2	10.00
Bromus unioloides								3			3	10.00
Paronychia sp.								6			6	10.00
Verbena litoralis								15			15	10.00
Panicum bergii				2							2	10.00
Stipa trichotoma	1										1	0.00
Undetermined 1			12								12	10.00
Undetermined 2	3			1		1			1		6	2.00
Undetermined 3	1					1		1		3	6	2.00
Undetermined 4										2	2	10.00
Undetermined 5	1			1		2				1	6	1.00

1988; Manders, 1990; Dessaint et al., 1991). Morisita's index shows that most species were very unevenly distributed in the seed bank; only two (*Panicum milioides* and *Chenopodium album*), had a uniform distribution and very few, such as *Eragrostis lugens* and *Stipa neesiana*, had an approximately random distribution (Table 3).

CONCLUSIONS

1. The seed bank density was higher than that reported for the same type of communities from other parts of the world and also higher than those reported for other communities within this region

2. Qualitatively, standing vegetation and the seed bank had a 54% similarity; but on a quantitative base, similarity was lower, in part due to the fact that the dominants, *Stipa neesiana* and *Bothriochloa laguroides*, and other grasses were underrepresented in the seed bank.

3. The seed bank was very heterogeneous, due mainly to the fact that most species' seeds have a clumped distribution in the soil.

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